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RESEARCH ARTICLE

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Large-scale phylogenomic insights into the evolution of the Hymenochaetales

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ABSTRACT

The Hymenochaetales is an order with most species as wood-inhabiting fungi that have high phylogenetic complexity and morphological diversity. Species in this order play important roles in forest ecosystems and include wood decomposers, pathogens, and those that form ectomycorrhizal associations. However, we have limited knowledge of the patterns of large-scale evolutionary history of the order. In this study, using 171 genomes, including 113 newly assembled, we reconstructed the phylogenomic relationships, divergence times, biogeographic patterns, morphological evolution of basidiomata, and patterns of speciation/extinction in the Hymenochaetales. The phylogenomic relationships of 12 families within the Hymenochaetales suggested that 10 families can be accepted, and 2 families rejected. Molecular clock dating analyses suggested that the Hymenochaetales possibly started a rapid family-wide and genus-wide radiation during the early Cretaceous to late Jurassic and Cretaceous, respectively. Reconstruction of the ancestral state implied that Hymenochaetales probably originated from the temperate regions of Asia, with the basidiomata of the common ancestor likely being a corticioid species that rapidly transformed between the early Cretaceous and late Jurassic, coinciding with radiations at the family level. Furthermore, we detected a gradually increasing trend of speciation, extinction, and net diversification rates. We provided large-scale genomes of the Hymenochaetales and revealed evolutionary history patterns, which are key to understanding the evolution of fungi.

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1. Introduction

The order Hymenochaetales Oberw. was proposed in Frey et al. (1977) with *Hymenochaete* as the type genus, and was mainly composed of wood-inhabiting fungi belonging to the class Agaricomycetes in the division Basidiomycota. Currently, approximately 1,200 species have been placed in this order (https://www.catalogueoflife.org; accessed on 12 October 2023), and 782,984 occurrences worldwide have been reported according to the GBIF database (https://www.gbif.org/; accessed on 12 October 2023). The majority of species in the order Hymenochaetales is the white-rot fungi that decompose dead wood (saprotrophic), but the order also includes some important tree pathogens (parasitic), such as species in the genera *Onnia* and *Porodaedalea* (Dai 2010; Wu et al. 2022a; Zhao et al. 2024), as well as medicinal fungi such as *Sanghuangporus* spp., and some species, e.g. *Coltricia* spp., that form mutualistic relationships with trees (ectomycorrhizal; Dai 2010; Korotkin et al. 2018; Wu et al. 2022a; Zhao et al. 2023a).

The basidiomata of species belonging to the Hymenochaetales are diverse comprising various shapes, including poroid, hydnoid, corticioid, and

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Figure 1. Basidiomata of represented taxa of Hymenochaetales. (a) *Coltricia abieticola*. (b) *Coniferiporia sulphurascens*. (c) *Fibricium rude*. (d) *Fomitiporia hartigii*. (e) *Hirschioporus fuscoviolaceus*. (f) *Hydnoporia tabacinoides*. (g) *Hymenochaete rheicolor*. (h) *Hyphodontia tropica*. (i) *Inonotus hispidus*. (j) *Leucophellinus irpicoides*. (k) *Lyoathelia laxa*. (l) *Onnia tomentosa*. (m) *Pallidohirschioporus biforme*. (n) *Peniophorella pubera*. (o) *Porodaedalea himalayensis*. (p) *Resinicium bicolor*. (q) *Rigidoporus populinus*. (r) *Sanghuangporus alpinus*. (s) *Skvortzovia pinicola*. (t) *Xylodon rhizomorphus*. Photos credit Yu-Cheng Dai.

agaricoid (Figure 1; Larsson et al. 2006; Dai 2010; Korotkin et al. 2018; Wang et al. 2021, 2022, 2023; Wu et al. 2022a; Zhou et al. 2023). A series of studies suggested that some species in the order have a high host specificity (Dai 2010; Purahong et al. 2018; Wang et al. 2021, 2022; Wu et al. 2022a; Zhao et al. 2023a; Zhou et al. 2023). The host specificity of Hymenochaetales can be divided into four types, 1) angiosperms only, 2) gymnosperms only, 3) both angiosperms and gymnosperms, and 4) bryophytes.

New families have been added to the Hymenochaetales based on morphological characteristics and molecular phylogenetic analyses (Frey et al. 1977; Julich 1981; Fiasson and Niemelä 1984; Parmasto 2000; Larsson et al. 2006; Vizzini 2010; Zmitrovich and Malysheva 2014; Ariyawansa et al. 2015; Zhou et al. 2018, 2023; Wang et al. 2021, 2023; Wang and Zhou 2023). For instance, based on seven gene markers (nSSU, ITS, nLSU, mt-SSU, *tef1α*, *rpb1*, and *rpb2*), Wang et al. (2023) accepted 14 families, namely Chaetoporellaceae, Hymenochaetaceae, Hyphodontiaceae, Odonticiaceae, Peniophorellaceae, Repetobasidiaceae, Resiniciaceae, Rickenellaceae, Rigidoporaceae, Schizocorticiaceae, Schizoporaceae,

Sideraceae, Skvortzoviaceae, and Tubulicrinaceae. Later, Zhou et al. (2023), using five genetic loci (nSSU, ITS, nLSU, mt-SSU, and *tef1α*) and morphology, accepted 11 families, viz., Chaetoporellaceae, Coltriciaceae, Hymenochaetaceae, Hirschioporaceae, Hyphodontiaceae, Oxyporaceae, Rickenellaceae, Schizoporaceae, Neoantrodiellaceae, Nigrofomitaceae, and Trichaptaceae. However, there are conflicts when reconstructing the phylogenetic relationship of the order Hymenochaetales using different gene fragments, for instance, Wang et al. (2023) rejected the families Neoantrodiellaceae and Nigrofomitaceae, while Zhou et al. (2023) accepted them.

Biogeography and molecular dating allow to reconstruct origin, speciation, and distribution patterns of different organisms, including fungi, animals, and plants, with fungal studies lagging behind the research on animals and plants (Seehausen et al. 2014; Li et al. 2020; Jin et al. 2021). Currently, in the Hymenochaetales, despite being a species-rich order of fungi, the ancestor state origin was reconstructed only for a few genera, such as *Coniferiporia*, *Onnia*, *Sanghuangporus*, and *Trichaptum s.l.* (Zhu et al. 2019; Wang et al. 2022; Zhao et al. 2022c; Zhou et al. 2023). The divergence times of the Hymenochaetales from its sister clade have been estimated 167–289 million years ago (Mya) using several molecular sequences (He et al. 2019; Varga et al. 2019; Wang et al. 2021, 2023; Zhao et al. 2022c; Zhou et al. 2023). The increase in fungal genomic data has provided better resolution and confidence in estimating phylogenetic relationships and divergence times (Floudas et al. 2012; Spatafora et al. 2016; Varga et al. 2019; Wu et al. 2022b; Zhao et al. 2023b; He et al. 2024), including a few genomic studies conducted on the order Hymenochaetales (Chung et al. 2017; Jiang et al. 2021; Zhao et al. 2023a). For example, our previous study estimated divergence times and explored the evolutionary innovation of ectomycorrhizal *Coltricia* species at the genomic level (Zhao et al. 2023a). Although more than 30 genomes of Hymenochaetales have been published (Chung et al. 2017; Jiang et al. 2021; Zhao et al. 2022a; Zhao et al. 2023a, https://www.ncbi.nlm.nih.gov/genome/, accessed on 12 October 2023), these genomic data were not sufficient to study the biogeographical origin and evolution of the order.

In this study, we therefore generated a large genome dataset of the Hymenochaetales consisting of 171 genomes to study their phylogenomic relationships, divergence times, biogeography, speciation/extinction patterns, and explored the evolution of the morphology of the basidiomata.

2. Materials and methods

2.1. Genomes collection

The 171 fungal genomes from Agaricomycetes and Dacrymycetes were analysed in this study (Table 1), including 49 genomes from the NCBI database (https://www.ncbi.nlm.nih.gov/genome; accessed on 10 May 2023), nine genomes from the JGI MycoCosm database (https://mycocosm.jgi.doe.gov; accessed on 10 May 2023), and 113 genomes newly sequenced by the authors. Among them, 141 genomes belonged to the Hymenochaetales and consisted of 12 families, 44 genera, and 102 species; 30 genomes belonged to other orders of Agaricomycetes and Dacrymycetes. All the newly sequenced genomes were generated from herbarium specimens from the Institute of Microbiology, Beijing Forestry University (BJFC, China), the National Museum Prague of Czech Republic (PRM, Czech Republic), and the private herbarium of Josef Vlasák (JV, Czech Republic).

2.2. DNA extraction, genome sequencing, assembly, and gene prediction

Total genomic DNA of the specimens was extracted using the kit O-GPLF-400 (GeneOnBio Co., Changchun, China) according to the manufacturer's protocol. The high-quality DNAs were used to generate a 350 bp library using a kit (VAHTS® Universal Plus DNA Library Prep Kit for Illumina ND617), sequenced at Beijing Biomarker Technologies Co., Ltd (Beijing, China) on the Illumina NovaSeq 6000 platform. FastQC v0.12.1 (Andrews 2010) was used to inspect the reads quality, and then Trimmomatic v0.36 (Bolger et al. 2014) was used to remove low-quality reads, including contaminations, duplications, reads shorter than 50 bp, and low-quality reads with more than 50% of unknown bases.

The high-quality reads were assembled *de novo* into fungal genomes using MaSuRCA v3.4.3b (Zimin et al. 2013) with the default parameters due to most species lacking a reference genome. The quality of the assembled genomes was assessed using the Quast v5.0.2 (Gurevich et al. 2013) and Benchmarking

Table 1. One hundred and forty-one genomes of Hymenochaetales used in this study.

Species	Strain no.	Basidiomata type	Host	Climate distributions	Geographic distributions	Family
Coltricia abieticola	Dai 22736	Poroid	Gym	Boreal to temperate	Asia	Coltriciaceae
Coltricia abieticola	Dai 22737	Poroid	Gym	Boreal to temperate	Asia	Coltriciaceae
Coltricia crassa	Dai 23069	Poroid	Ang	Subtropical to tropical	Asia	Coltriciaceae
Coltricia perennis	Dai 23027	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Coltriciaceae
Coltricia perennis	Dai 23028	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Coltriciaceae
Coltricia perennis	Dai 23736	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Coltriciaceae
Coltricia weii	Dai 23721	Poroid	Ang	Temperate to subtropical	Asia	Coltriciaceae
Coniferiporia sulphurascens	Dai 6952	Poroid	Gym	Boreal to temperate	Asia	Hymenochaetaceae
Coniferiporia sulphurascens	FP133613	Poroid	Gym	Boreal to temperate	Asia	Hymenochaetaceae
Coniferiporia sulphurascens	Wei 3309	Poroid	Gym	Boreal to temperate	Asia	Hymenochaetaceae
Coniferiporia sulphurascens	Wei 3311	Poroid	Gym	Boreal to temperate	Asia	Hymenochaetaceae
Cyanotrama rimosa	Cui 17426	Poroid	Gym	Temperate to subtropical	Africa, Asia, and North America	Incertae sedis
Fasciodontia bugellensis	He 7652	Hydnoid	Ang	Temperate	Asia and Europe	Schizoporaceae
Fibricium rude	Dai 24423	Corticioid	Ang or Gym	Boreal to tropical	Africa, Asia, Europe, North America, and South America	Incertae sedis
Fomitiporella chinensis	Dai 22675	Poroid	Ang	Temperate to subtropical	Asia	Hymenochaetaceae
Fomitiporia hartigii	Dai 23787	Poroid	Gym	Boreal to temperate	Asia, Europe and North America	Hymenochaetaceae
Fomitiporia hartigii	Dai 23795	Poroid	Gym	Boreal to temperate	Asia, Europe and North America	Hymenochaetaceae
Fomitiporia hartigii	Wei 3306	Poroid	Gym	Boreal to temperate	Asia, Europe and North America	Hymenochaetaceae
Fomitiporia hartigii	Wei 3328	Poroid	Gym	Boreal to temperate	Asia, Europe and North America	Hymenochaetaceae
Fomitiporia mediterranea	MF3-22	Poroid	Ang	Temperate	Africa and Europe	Hymenochaetaceae
Fomitiporia norbulingka	Dai 23214	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Fomitiporia punctata	Dai 23842	Poroid	Ang	Boreal to temperate	Asia, Europe and North America	Hymenochaetaceae
Fomitiporia punicata	He 7196	Poroid	Ang	Temperate	Asia, Europe, and North America	Hymenochaetaceae
Fomitiporia rhamnoides	Dai 24108	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Fomitiporia rhamnoides	He 7784	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Fomitiporia torreyae	Dai 24327	Poroid	Ang or Gym	Temperate to subtropical	Asia	Hymenochaetaceae
Fomitiporia torreyae	Dai 24462	Poroid	Ang or Gym	Temperate to subtropical	Asia	Hymenochaetaceae
Fulvoderma australe	Cui 17941	Poroid	Ang or Gym	Subtropical to tropical	Asia	Hymenochaetaceae
Fulvoderma australe	Cui 18588	Poroid	Ang or Gym	Subtropical to tropical	Asia	Hymenochaetaceae
Fuscoporia gilva	JV 2208/21-J	Poroid	Ang	Boreal to tropical	Africa, Asia, Europe, North America, and South America	Hymenochaetaceae
Fuscoporia viticola	PhevitSig-SM15	Poroid	Ang or Gym	Boreal to temperate	Europe and North America	Hymenochaetaceae
Ginnsia viticola	He 6216	Corticioid	Ang	Boreal to temperate	Asia, Australia, and North America	Incertae sedis
Hirschioporus abietinus	Dai 24212	Poroid to hydnoid	Gym	Boreal to temperate	Africa, Asia, Europe, North America, and South America	Hirschioporaceae
Hirschioporus chinensis	Dai 23074	Poroid to hydnoid	Gym	Temperate	Asia	Hirschioporaceae
Hirschioporus chinensis	Dai 23291	Poroid	Gym	Temperate	Asia	Hirschioporaceae
Hirschioporus fuscoviolaceus	Dai 22794	Poroid to hydnoid	Gym	Boreal to temperate	Asia, Europe, and North America	Hirschioporaceae
Hirschioporus fuscoviolaceus	TF100210M3	Poroid to hydnoid	Gym	Boreal to temperate	Asia, Europe, and North America	Hirschioporaceae
Hydnoporia tabacinoides	Dai 23633	Hydnoid	Ang	Temperate	Asia	Hymenochaetaceae
Hymenochaete porioides	Dai 24347	Poroid	Ang	Subtropical to tropical	Asia	Hymenochaetaceae
Hymenochaete rheicolor	Dai 23372	Corticioid	Ang	Temperate to tropical	Asia and North America	Hymenochaetaceae
Hymenochaete xerantica	Dai 24282	Poroid	Ang	Boreal to subtropical	Asia	Hymenochaetaceae
Hymenochaete xerantica	Dai 24428	Poroid	Ang	Boreal to subtropical	Asia	Hymenochaetaceae
Hyphodontia microspora	He 7707	Hydnoid	Ang or Gym	Boreal to tropical	Africa, Asia, Europe, and South America	Schizoporaceae
Hyphodontia tropica	Dai 24265	Poroid	Ang or Gym	Temperate to tropical	Asia	Schizoporaceae
Hyphodontia tropica	Dai 24350	Poroid	Ang or Gym	Temperate to tropical	Asia	Schizoporaceae
Inocutis rheades	Dai 23708	Poroid	Ang	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Inocutis tamarix	Dai 22611	Poroid	Ang	Temperate	Africa, Asia, and Europe	Hymenochaetaceae
Inonotus hispidus	Dai 24528	Poroid	Ang	Temperate	Asia, Europe, and North America	Hymenochaetaceae
Inonotus hispidus	He 7414	Poroid	Ang	Temperate	Asia, Europe, and North America	Hymenochaetaceae
Inonotus obliquus	CT5	Poroid	Ang	Boreal to temperate	Asia, Europe and North America	Hymenochaetaceae
Inonotus obliquus	Dai 24189	Poroid	Ang	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
"Inonotus ziziphicola"	Dai 24556	Poroid	Ang	Temperate	Asia	Hymenochaetaceae

(*Continued*)

Table 1. (Continued).

Species	Strain no.	Basidiomata type	Host	Climate distributions	Geographic distributions	Family
"Inonotus ziziphicola"	Dai 24562	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Kneiffiella abdita	Dai 23521	Poroid	Gym	Temperate	Africa, Asia, Europe, and North America	Schizoporaceae
Leucophellinus irpicoides	He 7783	Poroid	Ang	Temperate	Asia	Rigidoporaceae
Lyoathelia laxa	Dai 24169	Corticioid	Gym	Temperate	Asia, Europe, and North America	Incertae sedis
Mensularia radiata	Dai 24143	Poroid	Ang	Temperate	Asia, Europe, and North America	Hymenochaetaceae
Mensularia radiata	Yuan 169	Poroid	Ang	Temperate	Asia, Europe, and North America	Hymenochaetaceae
Neomensularia castanopsidis	Dai 19907	Poroid	Ang	Subtropical	Asia	Hymenochaetaceae
***Nigrohirschioporus* sp.**	JV 2103/2-J	Poroid	Ang	Temperate	North America	Hirschioporaceae
Ochrosporellus portoricensis	JV 1312/E20-J	Poroid	Ang	Tropical	South America	Hymenochaetaceae
Ochrosporellus portoricensis	JV 1504/112	Poroid	Ang	Tropical	South America	Hymenochaetaceae
Onnia himalayana	Dai 22620	Poroid	Gym	Subtropical	Asia	Hymenochaetaceae
Onnia subtriquetra	Dai 23686	Poroid	Gym	Boreal to temperate	North America	Hymenochaetaceae
Onnia subtriquetra	Dai 23687	Poroid	Gym	Boreal to temperate	North America	Hymenochaetaceae
Onnia tibetica	Dai 23621	Poroid	Gym	Boreal to temperate	Asia	Hymenochaetaceae
Onnia tomentosa	Dai 23682	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Onnia tomentosa	Dai 23683	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Onnia tomentosa	Dai 23737	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Pallidohirschioporus biformis	Dai 23006	Poroid	Ang	Temperate to subtropical	Africa, Asia, Europe, North America, and South America	Hirschioporaceae
Pallidohirschioporus biformis	Dai 23007	Poroid	Ang	Temperate to subtropical	Africa, Asia, Europe, North America, and South America	Hirschioporaceae
Pallidohirschioporus brastagii	Dai 22921	Poroid	Ang	Subtropical to tropical	Africa, Asia, and Australia	Hirschioporaceae
Peniophorella pubera	He 7454	Corticioid	Ang or Gym	Boreal to temperate	Africa, Asia, Australia, Europe, North America, and South America	Peniophorellaceae
Perennihirschioporus fumosoavellaneus	JV 2203/80-J	Poroid	Ang	Subtropical to tropical	South America	Hirschioporaceae
Phellinidium ferrugineofuscum	SpK3Phefer14	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Phellinidium pouzarii	DSM 108285	Poroid	Gym	Temperate	Europe	Hymenochaetaceae
Phellinopsis conchata	Dai 24406	Poroid	Ang	Temperate	Asia, Europe, and North America	Hymenochaetaceae
Phellinopsis helwingiae	Dai 24418	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Phellinopsis helwingiae	Dai 24425	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Phellinopsis lonicericola	Dai 24112	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Phellinus monticola	Dai 22944A	Poroid	Gym	Boreal to Temperate	Asia	Hymenochaetaceae
Phellinus monticola	Dai 24333	Poroid	Gym	Boreal to Temperate	Asia	Hymenochaetaceae
Phellinus orientoasiaticus	Dai 24464	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Phellinus orientoasiaticus	Dai 24561	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Phellinus parmastoi	Dai 23004	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Phellinus tremulae	Yuan 245	Poroid	Ang	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Phellopilus nigrolimitatus	Dai 23808	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Phellopilus nigrolimitatus	Dai 23809	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Phellopilus nigrolimitatus	Dai 23810	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Phellopilus nigrolimitatus	Dai 23970	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Phellopilus nigrolimitatus	SigPhenig9	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Hymenochaetaceae
Phylloporia crystallina	JV 2106/102	Poroid	Ang	Tropical	South America	Hymenochaetaceae
Phylloporia lianincola	JV 2109/73	Poroid	Ang	Subtropical	South America	Hymenochaetaceae
Porodaedalea alpicola	Dai 22971	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Porodaedalea cancriformans	Dai 20889	Poroid	Gym	Temperate	North America	Hymenochaetaceae
Porodaedalea chinensis	Dai 24228	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Porodaedalea himalayensis	Dai 23983	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Porodaedalea himalayensis	Dai 23986	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Porodaedalea himalayensis	Wu9	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Porodaedalea laricis	PN71-100-IP13	Poroid	Gym	Boreal to temperate	Asia and Europe	Hymenochaetaceae
Porodaedalea mongolica	Dai 20809	Poroid	Gym	Boreal to temperate	Asia	Hymenochaetaceae
Porodaedalea occidentiamericana	Dai 20887	Poroid	Gym	Temperate	North America	Hymenochaetaceae
Porodaedalea pini		Poroid	Gym	Temperate	Europe	Hymenochaetaceae
Porodaedalea qilianensis	Dai 20878	Poroid	Gym	Temperate	Asia	Hymenochaetaceae

(*Continued*)

Table 1. (Continued).

Species	Strain no.	Basidiomata type	Host	Climate distributions	Geographic distributions	Family
Porodaedalea qilianensis	Dai 20879	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Porodaedalea qilianensis	Dai 20880	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Porodaedalea schrenkiana	Dai 20232	Poroid	Gym	Temperate	Asia	Hymenochaetaceae
Pseudoinonotus tibeticus	Dai 22973	Poroid	Gym	Boreal	Asia	Hymenochaetaceae
Pseudoinonotus tibeticus	Dai 22974	Poroid	Gym	Boreal	Asia	Hymenochaetaceae
Pseudophylloporia australiana	Dai 18845	Poroid	Ang	Subtropical	Australia	Hymenochaetaceae
Pyrrhoderma nigra	MO 489730	Poroid	Ang	Tropical	Asia	Hymenochaetaceae
Pyrrhoderma sublamaensis	FFPRI411160	Poroid	Ang	Tropical	Asia, South America	Hymenochaetaceae
Resinicium bicolor	Dai 24,237	Corticioid	Ang or Gym	Boreal to temperate	Asia, Europe, and North America	Resiniciaceae
Rickenella fibula	HBK330-10	Agaricoid	Bry	Temperate	Africa, Asia, Australia, Europe, North America, and South America	Rickenellaceae
Rickenella mellea	SZMC22713	Agaricoid	Bry	Boreal	Europe	Rickenellaceae
Rigidoporus corticola	Dai 23274	Poroid	Ang or Gym	Boreal to subtropical	Asia, Europe, and North America	Rigidoporaceae
Rigidoporus cuneatus	Dai 24305	Poroid	Gym	Temperate to subtropical	Asia	Rigidoporaceae
Rigidoporus ginkgonis	Dai 24460	Poroid	Ang or Gym	Temperate to subtropical	Asia	Rigidoporaceae
Rigidoporus macroporus	Dai 23277	Poroid	Gym	Boreal to temperate	Asia	Rigidoporaceae
Rigidoporus populinus	Dai 22806	Poroid	Ang	Temperate to subtropical	Asia, Europe, and North America	Rigidoporaceae
Rigidoporus subpopulinus	Dai 24042	Poroid	Gym	Temperate	Asia	Rigidoporaceae
Sanghuangporus alpinus	Dai 24025	Poroid	Ang	Boreal to temperate	Asia	Hymenochaetaceae
Sanghuangporus baumii	821	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Sanghuangporus lonicericola	Dai 17297	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Sanghuangporus sanghuang	MS2	Poroid	Ang	Temperate	Asia	Hymenochaetaceae
Sanghuangporus weigelae	Dai 24334	Poroid	Ang	Temperate to subtropical	Asia	Hymenochaetaceae
Sidera borealis	Dai 24120	Poroid	Gym	Boreal to temperate	Asia	Sideraceae
Sidera lenis	Dai 22834	Poroid	Gym	Boreal to temperate	Asia, Europe, and North America	Sideraceae
Sidera tibetica	Dai 23819	Poroid	Gym	Boreal to temperate	Asia	Sideraceae
Skvortzovia pinicola	Dai 24517	Hydnoid	Gym	Boreal to temperate	Asia, Europe, and North America	Skvortzoviaceae
Skvortzovia qilianensis	Dai 23888	Corticioid to hydnoid	Gym	Temperate	Asia	Skvortzoviaceae
Skvortzovia qilianensis	Dai 23889	Corticioid to hydnoid	Gym	Temperate	Asia	Skvortzoviaceae
Tropicoporus boehmeriae	Dai 22566	Poroid	Ang	Tropical	Asia	Hymenochaetaceae
Tropicoporus minus	Dai 21139	Poroid	Ang	Tropical	Asia	Hymenochaetaceae
Tropicoporus substratificans	JV 1908/80	Poroid	Ang	Tropical	South America	Hymenochaetaceae
Xylodon bubalinus	Dai 24006	Hydnoid	Ang or Gym	Temperate	Asia	Schizoporaceae
Xylodon kunmingensis	Dai 24588	Hydnoid	Ang	Subtropical	Asia	Schizoporaceae
Xylodon nongravis	Dai 24342	Poroid	Ang	Subtropical	Asia	Schizoporaceae
Xylodon ovisporus	KUC8140	Hydnoid	Ang	Boreal to temperate	Asia, Australia, North America, and South America	Schizoporaceae
Xylodon spathulatus	He 7710	Hydnoid	Ang	Boreal to subtropical	Asia, Europe, North America, and South America	Schizoporaceae
Xylodon rhizomorphus	Dai 24671	Hydnoid	Ang	Temperate	Asia	Schizoporaceae

Ang, Bry, and Gym represented angiosperms, bryophytes, and gymnosperms, respectively. Genomes generated in this study are highlighted in bold. "" represented new species published in the coming paper.

Universal Single-Copy Orthologs (BUSCO) v5.2.2 (Simão et al. 2015; Fu et al. 2023) with the Agaricomycetes gene dataset downloaded from https://busco-data.ezlab.org/v5/data/lineages/agaricomycetes_odb10.2020-08-05.tar.gz. (accessed on 16 June 2022). Protein-coding gene models of the new genomes were *de novo* predicted using the program Augustus v3.3.3 (Stanke and Waack 2003) with the default parameters. Additionally, the amino acid sequences were extracted using GffRead v0.12.6 (Pertea and Pertea 2020).

2.3. Genome-based maximum likelihood phylogenetic and molecular dating analyses

In total, 192 clusters of orthologous proteins (COPs) from our dataset (File S1), including 17 orders of Agaricomycetes and one order of Dacrymycetes as outgroups, were obtained following the approach explained in detail in previous studies (Spatafora et al. 2016; Zhao et al. 2022b, 2023b). In brief, all the proteins were identified by HMMER v3.3.1 (Finn et al. 2011) and Trimal v1.4.4 (Sánchez et al. 2011) following the markers from James et al. (2013), then aligned with MAFFT v7 (Katoh and Standley 2013). The best optimum substitution model of aligned amino acid sequences was selected using ModelTest-NG v0.1.7 (Darriba et al. 2020). Maximum Likelihood (ML) phylogenetic analyses were carried out using RAxML v8.1.12 (Stamatakis 2014) with 1,000 bootstrap replications.

The molecular clock dating analyses were performed with r8s v1.71 (Sanderson 2003) based on the 192 clusters of orthologous protein sequences with the Penalized Likelihood (PL) method. Five calibrations were selected: 1) Hymenochaetales evolved 167 Mya with confidence interval (CI) of 130–180 Mya (Varga et al. 2019), 2) Boletales evolved 141 Mya with CI of 133–182 Mya (Varga et al. 2019), and 3) Agaricomycetes and Dacrymycetes diverged from the most recent common ancestor (MRCA) 298 Mya (He et al. 2019), 4) the minimum age of Agaricales diverged 90 Mya represented by *Archaeomarasmius leggetti* Hibbett, D. Grimaldi & Donoghue (Hibbett et al. 1995, 1997), 5) the minimum age of Hymenochaetaceae diverged 125 Mya represented by *Quatsinoporites cranhamii* S.Y. Sm., Currah & Stockey (Smith et al. 2004). All the trees were viewed with FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree; accessed on 1 May 2020).

2.4. Inferring historical biogeography

In the biogeographic analyses and ancestral characteristics of basidiomata, we used 105 genomes, including 102 Hymenochaetales species and three Polyporales species as outgroups. The ML phylogenetic and molecular clock dating analyses included the above listed criteria, with an additional calibration of the Hymenochaetales (167 Mya with 130 Mya of min-age and 180 Mya of max-age; Varga et al. 2019).

We studied the evolution of geographic and climatic origin of Hymenochaetales using the 105 genomes. To trace the biogeographic history of the order Hymenochaetales, an ancestral range estimation was conducted using BioGeoBEARS v1.1.3 (Matzke 2013, 2014) implemented in the R package v4.1.2 (R Core Team 2013). A time-calibrated phylogenomic tree of 105 species was generated using r8s v1.71 (Sanderson 2003). Six geographical origins, viz., a – Africa, b – Asia, c – Australia, d – Europe, e – North America, and f – South America, respectively, and four climate regions, viz., a – Boreal, b – Temperate, c – Subtropical, and d – Tropical, respectively, were defined based on previous studies (Dai 2010; Wang et al. 2021, 2023; Wu et al. 2022a; Zhou et al. 2023) and databases, such as MycoBank (https://www.mycobank.org/; accessed on 10 September 2023) and GBIF (https://www.gbif.org/; accessed on 10 September 2023). We tested two models, DEC (Dispersal Extinction Cladogenesis) model and DEC + J (random parameter) model, which consider founder-event speciation.

2.5. Ancestral state reconstruction of morphology of basidiomata

The ancestral basidiomata morphology of Hymenochaetales species was reconstructed using BioGeoBEARS v1.1.3 (Matzke 2013, 2014) with the time-calibrated phylogenomic tree of 105 species, and the Dispersal-Extinction-Cladogenesis (DEC) and DEC + J models were selected to estimate ancestral ranges and reconstruct biogeographical histories. Four basidiomata types, viz., a – poroid, b – hydnoid, c – corticioid, and d – agaricoid were defined, respectively. The diversification rate of basidiomata type was estimated with BAMM (Bayesian Analysis of Macroevolutionary Mixtures) v2.5.0 (Rabosky and Kolokotronis 2014) and the R program BAMMtools v2.1.10 (Rabosky et al.

2014) in the R package v4.1.2 (R Core Team 2013). Priors were estimated using the BAMMtools, and then setting as expectedNumberOf Shifts = 1.0, betaInitPrior = 1.0, betaShiftPrior = 0.05, useObservedMinMaxAsTraitPriors = 1, traitPriorMin = 0, traitPriorMax = 0, and betaIsTimeVariablePrior = 1 in BAMM analyses. The Maximum Clade Credibility (MCC) tree was run for 10 million generations, with every 1,000 generations recorded. The initial 20% of the MCC run were used as burn-in, and the remaining samples were checked for effective sample size (ESS) values of more than 200 using the R program coda v0.19.4 (Plummer et al. 2006) in the R package v4.1.2 (R Core Team 2013).

2.6. Speciation, extinction, and diversification rates analyses

To estimate speciation/extinction rates in the order Hymenochaetales, we used BAMM v2.5.0 (Rabosky and Kolokotronis 2014) and the R program BAMMtools v2.1.10 (Rabosky et al. 2014) in the R package v4.1.2 (R Core Team 2013) on the 171 genomes. Firstly, the R program ape v5.7.1 (Paradis et al. 2019) was used to estimate the MCMC tree. Secondly, we ran BAMMtools to obtain prior block, including expectedumberOfShifts = 1.0, lambdaInitPrior = 13.3977, lambdaShiftPrior = 0.0039, muInitPrior = 13.3977, and lambdaIsTimeVariablePrior = 1. In addition, we set the general setup and data input as modeltype = speciation-extinction, sampleFromPriorOnly = 0, runMCMC = 1, simulatePriorShifts = 0, loadEventData = 0, initialize Model = 1, useGlobalSamplingProbability = 1, and globalSamplingFraction = 0.1. Then, we ran BAMM v2.5.0 (Rabosky and Kolokotronis 2014) for 10 million generations, logging states every 1,000 generations, and estimated the ESS using the R program coda v0.19.4 (Plummer et al. 2006) with 10% as burn-in, which was also used finally to calculate the speciation, extinction, and net diversification rate using R program BAMMtools v2.1.10 (Rabosky et al. 2014). In addition, to avoid bias in sampling diversification analyses, 67 genomes of Hymenochaetaceae with poroid hymenophore (File S2; 672 species) were recognised by Wu et al. (2022a) and then performed divergence times, speciation, extinction, and net diversification rate analyses.

3. Results

3.1. Phylogenomic and divergence time of Hymenochaetales

To reconstruct the phylogenetic relationships of the order Hymenochaetales, an aligned dataset containing 192 COPs from our dataset, consisting of 141 Hymenochaetales (Table 1) and 30 other orders of Agaricomycetes and Dacrymycetes (Table S1), were used in the ML phylogenetic analysis. The aligned data included 63,855 characters (File S1), and the PROTGAMMAILGF model was used as the best optimum substitution model based on ModelTest-NG (Darriba et al. 2020).

The ML phylogenetic analyses inferred phylogenetic relationships of the class Agaricomycetes, and most of the nodes had strong bootstrap support (Figure 2 and Figure S1). The results showed that 10 families of the order Hymenochaetales, namely Coltriciaceae, Hirschioporaceae, Hymenochaetaceae, Peniophorellaceae, Resiniciaceae, Rickenellaceae, Rigidoporaceae, Schizoporaceae, Sideraceae, and Skvortzoviaceae, were accepted, while two families, Chaetoporellaceae and Hyphodontiaceae, were rejected because they were clustered together with the Schizoporaceae. Four independent species with incertae sedis, *Fibricium rude*, *Cyanotrama rimosa*, *Ginnsia viticola*, and *Lyoathelia laxa*, were included in this study. In addition, seven families of Hymenochaetales, including Nigrofomitaceae, Odonticiaceae, Repetobasidiaceae, Schizocorticiaceae, Trichaptaceae, Tubulicrinaceae, and Umbellaceae, are absent of genomic data because without samples of these families, or the samples cannot meet the requirements of genome sequencing (Wang et al. 2023; Wang and Zhou 2023; Zhou et al. 2023).

We investigated the divergence times of the Agaricomycetes using the 192 COPs and generated a robust genome-based backbone phylogeny of 17 orders (Figure 2). Estimated stem mean age of the order-level clades ranged from 90 to 241 Mya (Figure 2 and Table S2), which suggested the origin of the orders to be between the Cretaceous and Jurassic. Molecular clock dating analyses indicated that the divergence times of families, genera, and species of the Hymenochaetales occurred at 123–163 Mya, more than 49 Mya, and more

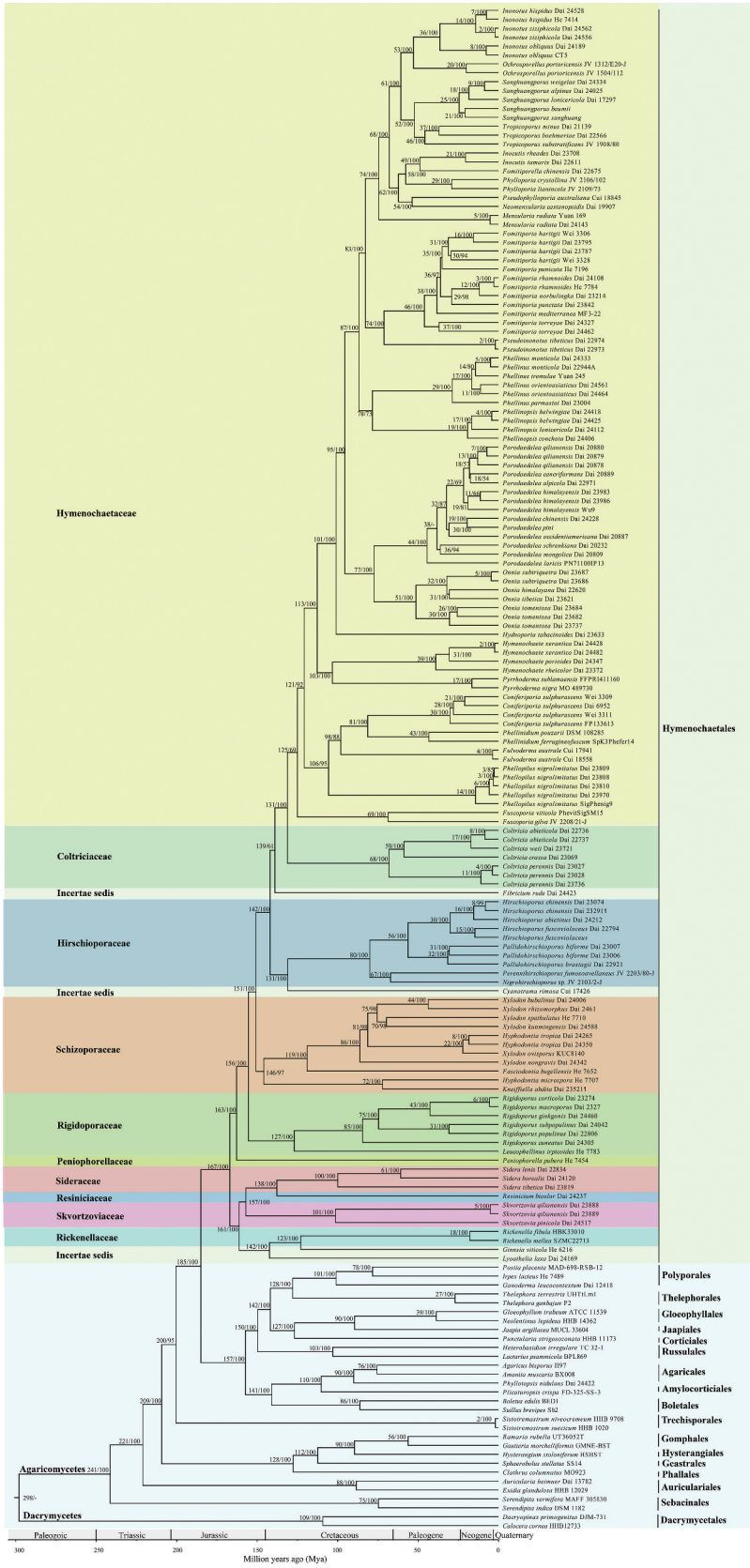

Figure 2. A time-calibrated phylogenomic tree with maximum clade credibility (MCC) chronogram and estimated divergence time of the Hymenochaetales based on 192 clusters of orthologous proteins (COPs) from the 171 genomes with divergence times (Mya)/ maximum likelihood (ML) bootstrap values (>50%) at the branch nodes.

Table 2. Inferred divergence time of taxa in the order Hymenochaetales.

Families	Genera	Species	Mean of stem age (Mya)
Coltriciaceae	*Coltricia*		134
		Coltricia abieticola	18
		Coltricia crassa	60
		Coltricia perennis	70
		Coltricia weii	18
Hirschioporaceae			144
	Hirschioporus		57
		Hirschioporus abietinus	16
		Hirschioporus chinensis	16
		Hirschioporus fuscoviolaceus	31
	Nigrohirschioporus	*Nigrohirschioporus* sp.	68
	Pallidohirschioporus		57
		Pallidohirschioporus biforme	32
		Pallidohirschioporus brastagii	32
	Perennihirschioporus	*Perennihirschioporus fumosoavellaneus*	68
Hymenochaetaceae			
	Coniferiporia	*Coniferiporia sulphurascens*	84
	Fomitiporella	*Fomitiporella chinensis*	51
	Fomitiporia		74
		Fomitiporia hartigii	37
		Fomitiporia mediterranea	40
		Fomitiporia norbulingka	13
		Fomitiporia punctata	31
		Fomitiporia punicata	37
		Fomitiporia rhamnoides	13
		Fomitiporia torreyae	41
	Fulvoderma	*Fulvoderma australe*	102
	Fuscoporia		129
		Fuscoporia gilva	71
		Fuscoporia viticola	71
	Hydnoporia	*Hydnoporia tabacinoides*	105
	Hymenochaete		107
		Hymenochaete porioides	32
		Hymenochaete rheicolor	40
		Hymenochaete xerantica	32
	Inocutis		51
		Inocutis rheades	21
		Inocutis tamarix	21
	Inonotus		55
		"*Inonotus hispidus*"	15
		Inonotus obliquus	15
		Inonotus ziziphicola	38
	Mensularia	*Mensularia radiata*	77
	Neomensularia	*Neomensularia castanopsidis*	56
	Ochrosporellus	*Ochrosporellus portoricensis*	55
	Onnia		82
		Onnia himalayana	33
		Onnia subtriquetra	34
		Onnia tibetica	33
		Onnia tomentosa	55
	Phellinidium		84
		Phellinidium ferrugineofuscum	45
		Phellinidium pouzarii	45
	Phellinopsis		82
		Phellinopsis conchata	20
		Phellinopsis helwingiae	18
		Phellinopsis lonicericola	18
	Phellinus		82
		Phellinus monticola	15
		Phellinus orientoasiaticus	17
		Phellinus parmastoi	30
		Phellinus tremulae	15
	Phellopilus	*Phellopilus nigrolimitatus*	110
	Phylloporia		60
		Phylloporia crystallina	30
		Phylloporia lianincola	30
	Porodaedalea		82
		Porodaedalea alpicola	20
		Porodaedalea cancriformans	20
		Porodaedalea chinensis	23
		Porodaedalea himalayensis	25

(*Continued*)

Table 2. (Continued).

Families	Genera	Species	Mean of stem age (Mya)
		Porodaedalea laricis	49
		Porodaedalea mongolica	40
		Porodaedalea occidentiamericana	35
		Porodaedalea pini	23
		Porodaedalea qilianensis	21
		Porodaedalea schrenkiana	40
	Pseudoinonotus	*Pseudoinonotus tibeticus*	74
	Pseudophylloporia	*Pseudophylloporia australiana*	56
	Pyrrhoderma		107
		Pyrrhoderma nigra	17
		Pyrrhoderma sublamaensis	17
	Sanghuangporus		54
		Sanghuangporus alpinus	9
		Sanghuangporus baumii	22
		Sanghuangporus lonicericola	19
		Sanghuangporus sanghuang	22
		Sanghuangporus weigelae	9
	Tropicoporus		54
		Tropicoporus boehmeriae	38
		Tropicoporus minus	38
		Tropicoporus substratificans	48
Peniophorellaceae	*Peniophorella*	*Peniophorella pubera*	163
Resiniciaceae	*Resinicium*	*Resinicium bicolor*	138
Rickenellaceae	*Rickenella*		123
		Rickenella fibula	18
		Rickenella fibula	18
Rigidoporaceae			156
	Leucophellinus	*Leucophellinus irpicoides*	128
	Rigidoporus		128
		Rigidoporus corticola	6
		Rigidoporus cuneatus	85
		Rigidoporus ginkgonis	43
		Rigidoporus macroporus	6
		Rigidoporus populinus	31
		Rigidoporus subpopulinus	31
Schizoporaceae			152
	Fasciodontia	*Fasciodontia bugellensis*	120
	Hyphodontia		73
		Hyphodontia microspora	73
		Hyphodontia tropica	22
	Kneiffiella	*Kneiffiella abdita*	73
	Xylodon		120
		Xylodon bubalinus	44
		Xylodon kunmingensis	70
		Xylodon nongravis	87
		Xylodon ovisporus	22
		Xylodon rhizomorphus	44
		Xylodon spathulatus	70
Sideraceae	*Sidera*		138
		Sidera borealis	61
		Sidera lenis	61
		Sidera tibetica	100
Skvortzoviaceae	*Skvortzovia*		157
		Skvortzovia pinicola	101
		Skvortzovia qilianensis	101
Incertae sedis	*Cyanotrama*	*Cyanotrama rimosa*	133
	Fibricium	*Fibricium rude*	142
	Ginnsia	*Ginnsia viticola*	123
	Lyoathelia	*Lyoathelia laxa*	143

"" represented new species published in the coming paper .

than 6 Mya, respectively (Table 2), providing a robust set of age estimates for the Hymenochaetales. Ten families of the Hymenochaetales originated between the Cretaceous and late Jurassic. About 61.4% of genera (27/44) originated in the Cretaceous (65–135 Mya), with the youngest genera being *Inocutis* (49 Mya) and *Fomitiporella* (49 Mya), which appeared

during the Eocene of the Palaeogene period, and 73.5% species (75/102) occurred during the Cenozoic period (later than 65 Mya).

3.2. Ancestral biogeography estimation

A total of 105 genomes, representing 102 species of Hymenochaetales and three species of Polyporales, were used to reconstruct the phylogenomic relationships based on the 192 COPs with the PROTGAMMAIVTF as the best-fit evolutionary model (Figure S2), and the divergence time estimated using the mean age of the Hymenochaetales was 167 Mya (Figure S3).

The historical biogeography inferred using DEC and DEC + J models suggested that MRCA of the order Hymenochaetales originated from the temperate regions of Asia and later spread to the boreal and tropical regions across the world (Figure 3a,b and Figure S4a,b). BioGeoBEARS analyses, allowing probabilistic inference of both biogeography and different models of range evolution, indicated that most families of the Hymenochaetales probably appeared in temperate or temperate to subtropical areas of Asia, while the family Hirschioporaceae may first have appeared in temperate to subtropical regions in Asia or South America (Figure 3a,b and Figure S4a, b). Moreover, most genera in the family Hymenochaetaceae, such as *Onnia*, *Phellinopsis*,

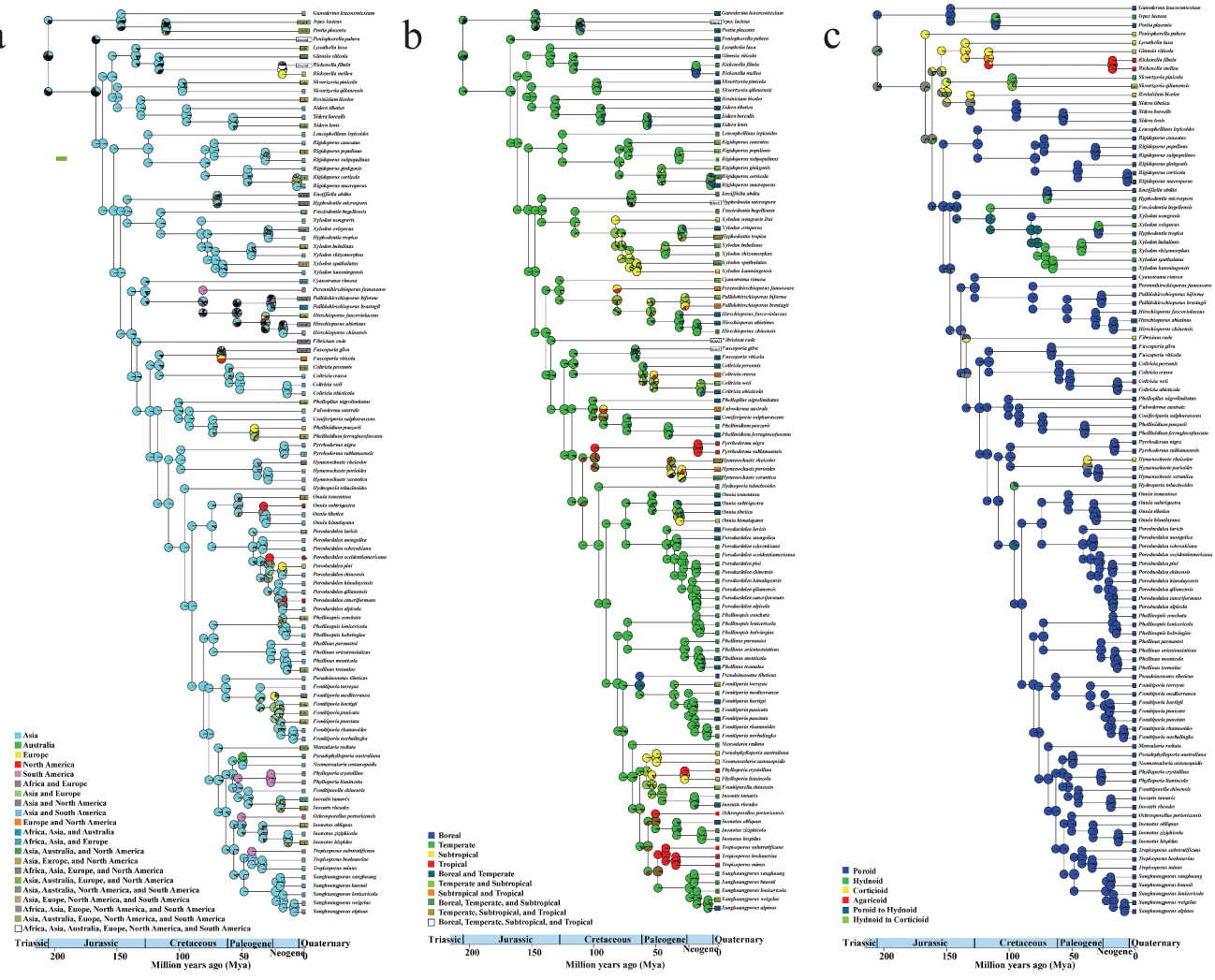

Figure 3. The evolutionary history patterns within the order Hymenochaetales. The phylogenetic trees were generated with maximum likelihood using BioGeoBEARS based on the 105 genomes under the DEC model. (a) The origin of geographical distributions of the Hymenochaetales, a – Africa, b – Asia, c – Australia, d – Europe, e – North America, and f – South America. (b) The origin of climate distributions of the Hymenochaetales, a – boreal, b – temperate, c – subtropical, and d – tropical. (c) The configuration evolution of basidiomata of the Hymenochaetales, a – poroid, b – hydnoid, c – corticioid, and d – agaricoid.

Porodaedalea, and *Sanghuangporus*, might have also first appeared in the temperate regions of Asia, but a few genera, such as *Ochrosporellus*, *Phylloporia*, and *Tropicoporus*, probably first occurred in subtropical to tropical South America.

3.3. Ancestral character evolution

We carried out the ancestral reconstruction through time to examine the configuration evolution of basidiomata using BioGeoBEARS and BAMM. BioGeoBEARS analyses suggested the corticioid morphology for most early nodes along the backbone of the Hymenochaetales as the common ancestor morphology of Hymenochaetales and Polyporales as outgroup, while basidiomata with hydnoid and agaricoid morphologies appeared later than the corticioid and poroid morphologies (Figure 3c and Figure S4c).

The early dominance of corticioid morphology was rapidly overtaken by poroid morphology during the early Cretaceous to late Jurassic (130–150 Mya; Figure 4a). The poroid type appeared as the most dominant, and the pattern may be driven by the radiation of the Hymenochaetaceae, which included the majority of poroid species. In the meantime, corticioid species also remained in some families.

Interestingly, the hydnoid morphology of diverse families probably originated from different basidiomata configurations. In some species of the family Skvortzoviaceae, the hydnoid configuration may have

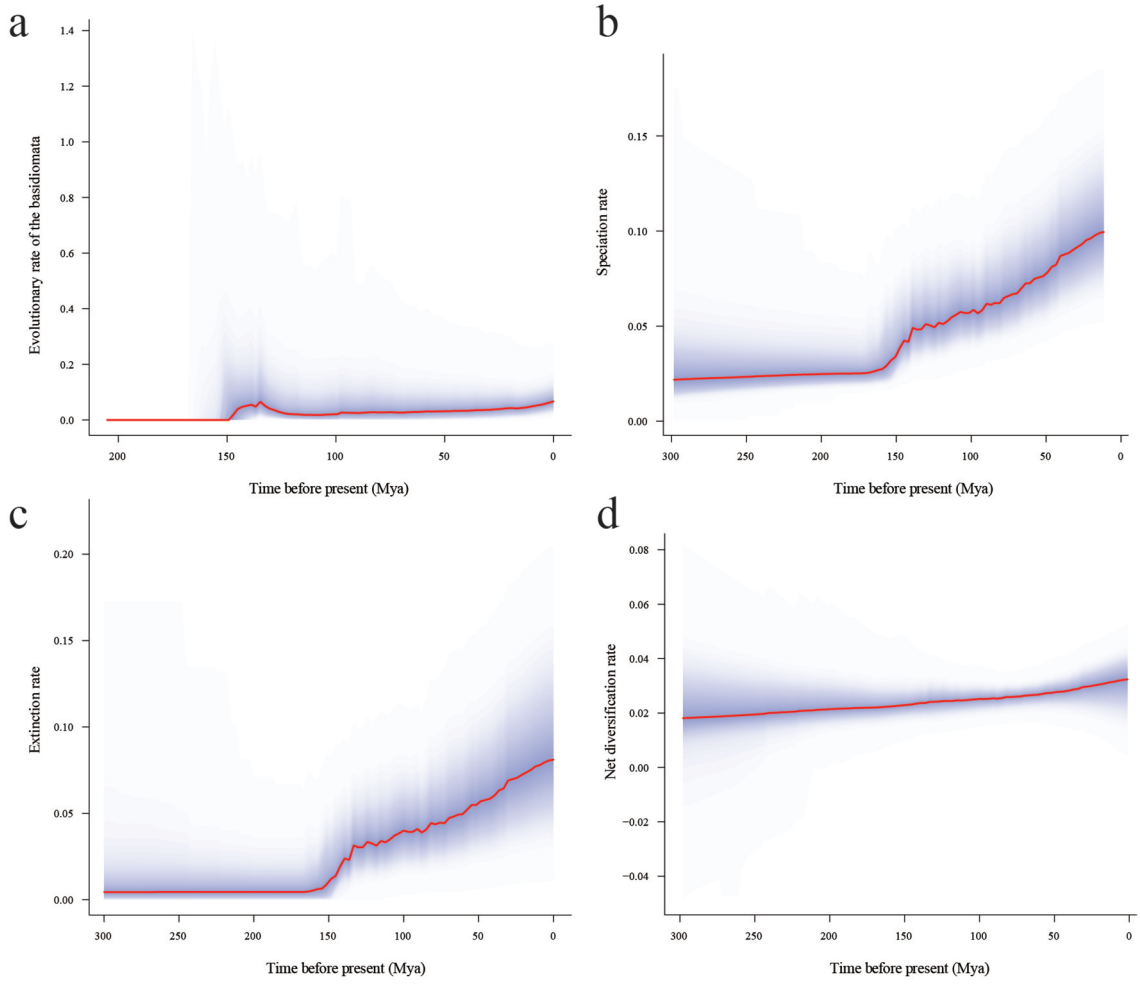

Figure 4. Patterns of diversification of the hymenochaetales through geologic time estimated by BAMM based on 192 COPs from 171 genomes. (a) Evolutionary rate of the basidiomata. (b) Speciation rate. (c) Extinction rate. (d) Net diversification rate through geologic time estimated by BAMM based on 192 COPs from 171 genomes. Shaded areas and Mya represent 95% confidence intervals and millions of years, respectively.

originated from the corticioid configuration, while the poroid configuration may be the common ancestor configuration in the family Schizoporaceae. Bayesian analysis of macroevolutionary mixtures (BAMM) analyses suggested that the diversification of basidiomata rate was relatively similar within the same morphology types, while far apart between different morphology types (Figure S5 and Figure S6).

3.4. Macroevolutionary rates

We analysed global rates of speciation, extinction, and net diversification in a macroevolution framework using BAMM based on 171 genomes. The speciation and extinction rates of the Hymenochaetales were gradually increasing during late Jurassic (approximately 150 Mya; Figure 4b,c, and Figure S7), while the extinction rate was lower than the speciation rate. Therefore, the net diversification rate of the Hymenochaetales also slightly increased (Figure 4d). However, an independent analysis using a speciation/extinction model did not detect a signal for extinction of 67 genomes of Hymenochaetaceae with poroid hymenophore (Figure S8 and Figure S9). This result is in accordance with previous studies showing that estimation of extinction rates from phylogenetic analyses can be difficult (Rabosky 2010; Beaulieu and O'Meara 2015; Varga et al. 2019). Similar trends of net diversification rates were detected using 67 genomes of Hymenochaetaceae with poroid hymenophore and all genomes of Hymenochaetales (Figure S8 and Figure S9).

4. Discussion

Although the phylogenetic relationships of the order Hymenochaetales have been extensively studied, the results are different depending on the specimens and gene sequences (Wang et al. 2021, 2023; Wu et al. 2022a; Zhou et al. 2023). Meanwhile, with the rapid development of genome sequencing technologies at more affordable costs, the study of the phylogenomic relationships of fungi is receiving widespread attention as it offers higher species resolutions (Spatafora et al. 2016; Varga et al. 2019; Li et al. 2021; Liu et al. 2022; Strassert and Monaghan 2022; Zhao et al. 2023b). Despite the considerable importance of the Hymenochaetales in the forest ecosystem, there is a significant lag in the phylogenomic research, partly because genomes were publicly available for only a few species. Recent research provided preliminary phylogenomic evolution and demonstrated the innovation of the ectomycorrhizal genus *Coltricia* at the genomic level, such as expanded transposable elements and small secreted proteins and loss of the key secreted carbohydrate-active enzymes to degrade lignin and cellulose (Zhao et al. 2023a). In the present study, we generated 113 newly sequenced genomes of the Hymenochaetales. By using a large dataset of 171 fungal genomes, we inferred the phylogenomic evolution, ancestral state reconstruction, morphological innovation, and speciation/extinction patterns of the Hymenochaetales.

Large-scale phylogenomic analysis provided a robust phylogenetic tree, and some phylogenetic conflicts were clarified or resolved. In contrast to Wang et al. (2023) who suggested that the genera *Hyphodontia* and *Kneiffiella* belong to the families Hyphodontiaceae and Chaetoporellaceae based on a combination dataset of nSSU, ITS, nLSU, *tef1α*, *rpb1*, and *rpb2* regions, respectively, we showed that *Hyphodontia* and *Kneiffiella* are more likely to belong to the Schizoporaceae. In line with previous studies, the families Coltriciaceae and Hirschioporaceae were confirmed (Wang et al. 2023; Zhou et al. 2023). Finally, we support that the genus *Fibricium* should be removed from the family Hymenochaetacea (Wu et al. 2022a; Wang et al. 2023).

Molecular clock dating has been widely used in the taxonomic framework and species diversity studies of the Hymenochaetales but has been based on just a few gene sequences (Wang et al. 2021, 2023; Hussain et al. 2022; Zhao et al. 2022c; Zhou et al. 2023). The divergence times estimated in our study using large-scale genomes provide additional solid evidence to address taxonomic problems in this order.

The origin and evolution of species is an important topic, and biogeographic studies have estimated the speciation, ancestral state origin, and distribution patterns of organisms (Wiens 2004; Seehausen et al. 2014). However, unlike animals and plants, biogeographical analyses of fungi are poor because 1) species recognition is limited (Taylor et al. 2006), 2) there are only a few fossil specimens (Taylor and Berbee 2006), and 3) sampling is incomplete (Schmit and Mueller 2007). So far biogeographical analysis has only been performed on four genera of the

Hymenochaetales, including *Coniferiporia*, *Onnia*, *Sanghuangporus*, and *Trichaptum s.l*. (Zhu et al. 2019; Wang et al. 2022; Zhao et al. 2022c; Zhou et al. 2023). To fill this gap, we studied the genomes of 102 Hymenochaetales species to identify more accurately the geographic origin, and the obtained results suggested that the temperate region of Asia has the highest possibility to be such an ancestral place, which is in agreement with the origin of genera of Hymenochaetales, such as *Coniferiporia*, *Onnia*, and *Sanghuangporus*, suggested in other studies (Zhu et al. 2019; Wang et al. 2022; Zhao et al. 2022c).

Previous studies suggest that the morphological evolution of basidiomata may have promoted species diversification in the class Agaricomycetes (Varga et al. 2019) and the resupinate (crust-like) basidiomata as the likely ancestors (Hibbett and Binder 2002; Hibbett and Lutzoni 2004; Varga et al. 2019). Meanwhile, it seems that the more complex configuration, especially the pileate-stipitate type, rapidly replaced the resupinate configuration in the late Jurassic (170–180 Mya; Varga et al. 2019). Although the Hymenochaetales (an order in the class Agaricomycetes) has a high diversity of species and basidiomata, there was a lack of research on the evolution of basidiomata morphological innovations. Wang et al. (2021) indicated that the ancestor's morphology was a poroid resupinate type, however, the ancestral state reconstructions through time conducted herein, suggest that the ancestors with corticioid type were in the early nodes of the Hymenochaetales, and then evolved the more complex configuration during the early Cretaceous to late Jurassic (130–150 Mya), which happened after the morphological innovations of the Agaricomycetes (170–180 Mya; Varga et al. 2019). Furthermore, the reconstruction results suggested that the hydnoid type originated from the corticioid or poroid configuration, instead of from the hydnoid type back to the poroid configuration (Wang et al. 2021).

In addition, we estimated the global rates of speciation, extinction, and net diversification in Hymenochaetales based on the full genome data. Varga et al. (2019) estimated the diversification rates increased abruptly at 180 Mya in the early Jurassic of mushroom-forming fungi (Agaricomycetes). Our results suggested that diversification rates of Hymenochaetales, belonging to Agaricomycetes, were increased at 150 Mya in the late Jurassic, which was later than Agaricomycetes (Varga et al. 2019). Moreover, the gradual increase in diversification rate after late Jurassic coincided with the radiation of Hymenochaetales. Although it is difficult to detect the extinction rate using the phylogenies (Rabosky 2010; Beaulieu and O'Meara 2015; Varga et al. 2019), a signal was estimated in an independent analysis (Figure 4) during the Jurassic (150 Mya), which followed the previous study of mushroom evolution (Varga et al. 2019). In addition, more fossil records and comprehensive sampling are needed to analyse global speciation/extinction patterns of the Hymenochaetales.

5. Conclusions

We have presented a comprehensive evolutionary history of Hymenochaetales based on genome-wide data. A total of 171 genomes were used to reconstruct the phylogenetic relationships of the Hymenochaetales, which provided a robust phylogenomic tree and taxonomic framework of divergence times. We identified the divergence time of major family-wide, genus-wide, and species-wide of the Hymenochaetales during early Cretaceous to late Jurassic, Cretaceous, and Cenozoic, respectively. The results revealed that the ancestral state of the Hymenochaetales originated from the temperate regions in Asia. Our analyses found the corticoid configuration of the basidiomata to be most likely ancestral morphology; nonetheless, the poroid configuration of the basidiomata has likely been a key driver of the evolutionary radiations. This study provides a wealth of genomic information, helping to elucidate the evolution of this ecologically and economically important group of fungi in the forest ecosystem.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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H.Z. developed the project concept, analysed data, and wrote the original draft; F.W., S.M., I.N.P., K.V.K., and H.G.L. provided genomic data; Y.C.D. and Y.Y. provided funding, participated in data analyses, and contributed to writing. All authors have contributed to results and discussion and edited the manuscript.

Data availability statement

All newly generated sequences have been deposited in the NCBI database under the BioProject ID: PRJNA1039714 and BioSample accessions: (SAMN38224086–SAMN38224098, SAMN38226665–SAMN38226669, SAMN38236504–SAMN38236523, SAMN38236780–SAMN38236789, SAMN38237522–SAMN38237536, SAMN38241647–SAMN38241656, SAMN38241719–SAMN38241733, SAMN38241838–SAMN38241847, and SAMN38245827–SAMN38245841).

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