

## Phylogeny, Divergence Time Estimation and Biogeography of the Genus *Onnia* (Basidiomycota, Hymenochaetaceae)

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Species of Onnia are important tree pathogens and play a crucial role in forest ecosystems. The species diversity and distribution of Onnia have been studied, however, its evolutionary history is poorly understood. In this study, we reconstructed the phylogeny of Onnia using internal transcribed spacers (ITS) and large subunit (LSU) rDNA sequence data. Molecular clock analyses developed the divergence times of Onnia based on a dataset (ITS + LSU rDNA +  $rpb1 + rpb2 + tef1\alpha$ ). Reconstruct Ancestral State in Phylogenies (RASP) was used to reconstruct the historical biogeography for the genus Onnia with a Dispersal Extinction Cladogenesis (DEC) model. Here, we provide a robust phylogeny of Onnia, with a description of a new species, Onnia himalayana from Yunnan Province, China. Molecular clock analyses suggested that the common ancestor of Onnia and Porodaedalea emerged in the Paleogene period with full support and a mean stem age of 56.9 Mya (95% highest posterior density of 35.9-81.6 Mya), and most species occurred in the Neogene period. Biogeographic studies suggest that Asia, especially in the Hengduan-Himalayan region, is probably the ancestral area. Five dispersals and two vicariances indicate that species of Onnia were rapidly diversified. Speciation occurred in the Old World and New World due to geographic separation. This study is the first inference of the divergence times, biogeography, and speciation of the genus Onnia.

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## INTRODUCTION

*Onnia* P. Karst. was proposed by Karsten and typified by *Onnia tomentosa* (Fr.) P. Karst. It is a homogeneous genus and forms a distinct clade in the Hymenochaetaceae based on phylogenetic analyses (Karsten, 1889; Wagner and Fischer, 2002; Larsson et al., 2006; Dai, 2010). Phylogenetically, *Onnia* is closely related to *Porodaedalea* Murrill, while morphologically *Porodaedalea* differs from *Onnia* by a perennial growth habit, pileate basidiocarps lacking a stipe, straight setae, and a dimitic hyphal system (Wagner and Fischer, 2002; Larsson et al., 2006; Dai, 2010; Ji et al., 2017). Almost all species of *Onnia* usually grow on gymnosperms, but one species, *Onnia vallata* (Berk.) Y.C. Dai and Niemelä, was recorded on angiosperms based on morphological features only and still without DNA data (Dai, 2010; Ryvarden and Melo, 2014; Ji et al., 2017). Some species of *Onnia* are well-known pathogens causing Tomentosus Root Rot on trees of Pinaceae, such as *Picea* and *Pinus* (Hunt and White, 1998; Germain et al., 2009; Ji et al., 2017).

Currently, eight species are accepted in Onnia, and their distribution is well defined. Onnia tomentosa is widespread in the Northern Hemisphere, including Canada, China, Czechia, Denmark, Finland, France, Germany, Italy, Norway, Poland, Russia, Spain, Sweden, the United Kingdom, Ukraine, and the United States (Table 1; Ryvarden and Gilbertson, 1993; Wagner and Fischer, 2001; Akata et al., 2009; Germain et al., 2009; Ji et al., 2017; Zhou and Wu, 2018; Wu et al., 2022). Onnia leporina (Fr.) H. Jahn is reported in Eurasia, such as China, Czechia, Finland, Italy, Norway, Sweden, and Ukraine (Ryvarden and Gilbertson, 1993; Wu et al., 2022). While O. himalayana Y.C. Dai, H. Zhao, and Meng Zhou, sp. nov., O. microspora Y.C. Dai and L.W. Zhou, and O. tibetica Y.C. Dai and S.H. He appear to be endemic to China, O. kesiyae M. Zhou and F. Wu, O. subtriquetra Vlasák and Y.C. Dai, and O. triquetra (Pers.) Imazeki occurred in Vietnam, the United States, and Europe (such as Czechia, Finland, France, Germany, Hungary, Poland, Russia, Spain, and Ukraine), respectively (Ryvarden and Gilbertson, 1993; Wu et al., 2022). Moreover, species of Onnia possessed host trees preferences, O. tomentosa and O. leporina mainly occurred on Picea, while other species commonly grow on Pinus (Ji et al., 2017; Wu et al., 2022). Indeed, species diversification and evolution of Onnia seem to inextricably interact with host trees and geographic separation, which provided niches for Onnia (Krah et al., 2018).

Recently, important research advances have been made in the studies of species diversity and divergence times of fungi (He et al., 2019; Varga et al., 2019; Wu et al., 2020; Dai et al., 2021; Wang K. et al., 2021; Zong et al., 2021). At present, more than 140,000 species of fungi were described, accounting for 3.50%-6.04% of an estimate of 2,200,000-3,800,000 (Hawksworth and Lücking, 2017; Wang et al., 2020). Hymenochaetaceae, the core family of wood-inhabiting fungi, recognizes 672 poroid species in the world (Wu et al., 2022). In addition, the determination of the divergence times within Basidiomycota based on fossil evidence has provided a robust set of age estimates for higher taxa (Zhao et al., 2017; He et al., 2019; Wang X. W. et al., 2021), with fossil species such as Quatsinoporites cranhamii S.Y. Smith et al. (2004) and Berbee and Taylor (2010) representing a minimum age of 125 Mya for Hymenochaetaceae. Meanwhile, the molecular dating studies of macrofungi widely pay attention to ectomycorrhizal fungi, saprotrophic fungi, and pathogenic fungi (Hibbett and Matheny, 2009; Chen et al., 2015; Song et al., 2016; Truong et al., 2017; Li et al., 2020; Liu et al., 2022; Wang X. W. et al., 2022). A series of studies related to the divergence time of pathogenic fungi, such as Coniferiporia L.W. Zhou and Y.C. Dai, Heterobasidion Bref., and Phytophthora ramorum Werres et al., have been published (Chen et al., 2015; Jung et al., 2021; Wang X. W. et al., 2022). However, divergence times of important coniferous pathogenic fungal Onnia have not been well resolved.

In the study of biogeography, the evolution of species is an important issue requiring reconstructing the origin, speciation, and distribution patterns of organisms (Page, 2003; Seehausen et al., 2014). To date, macrofungi, especially wood-inhabiting fungi, being closely interacted with host plants, are an interesting subject in biogeographic research (Chen et al., 2015; Song et al.,

2016; Varga et al., 2019; Li et al., 2020; Wang X. W. et al., 2022). For example, the ancestral geographic origin analyses suggested that coniferous pathogenic fungal *Coniferiporia* originated in Asia and then extend to Europe and North America (Wang X. W. et al., 2022). Regrettably, *Onnia*, a crucial member of wood-inhabiting fungi, is very much understudied in this regard.

In this article, a new species from Yunnan Province, China, *Onnia himalayana*, is phylogenetically and morphologically described. Meanwhile, a hypothesis for species diversification and origin of *Onnia* is proposed, namely, species of this genus seem to originate in the coniferous forests of southwest China.

## MATERIALS AND METHODS

## **Sample Collection**

Species, voucher specimens, and GenBank accession numbers of *Onnia* used in the present study were obtained from Asia, Europe, and North America. They are listed in **Table 1**.

## Morphology

The studied Onnia specimens are deposited in the herbarium of the Institute of Microbiology, Beijing Forestry University (BJFC). Morphological descriptions are based on field notes and herbarium specimens. Sections were studied at a magnification of up to  $1,000 \times$  using a Nikon Eclipse 80i microscope and phase contrast illumination. Microscopic features and measurements were made from slide preparations stained with Cotton Blue and Melzer's reagent. Basidiospores were measured from sections cut from the tubes. To represent variation in the size of basidiospores, 5% of measurements were excluded from each end of the range and are given in parentheses. In the description: KOH = 5% potassium hydroxide, IKI = Melzer's reagent, IKI- = neither amyloid nor dextrinoid, CB = Cotton Blue, CB + = cyanophilous in Cotton Blue, CB- = acyanophilous in Cotton Blue, L = arithmetic average of basidiospore length, W = arithmetic average of basidiospore width, Q = L/Wratios, and n = number of basidiospores/measured from given number of specimens. Color terms are from Anonymous (1969) and Petersen (1996).

# DNA Extraction, Polymerase Chain Reaction, and Sequencing

Total DNA was extracted from dried specimens with a rapid plant genome extraction kit (Aidlab Biotechnologies Co., Ltd, Beijing, China), modified following Cao et al. (2012) and Zhao and Cui (2013). The internal transcribed spacers (ITS), large subunit of nuclear ribosomal RNA gene (LSU rDNA), partial DNA-directed RNA polymerase II subunit one gene (*rpb1*) and subunit two gene (*rpb2*), and partial translation elongation factor 1-alpha gene (*tef1* $\alpha$ ) were amplified with primer pairs ITS 4 (5'-TCC TCC GCT TAT TGATAT GC-3') and ITS 5 (5'-GGA AGT AAA AGT CGT AAC AAG G-3'; White et al., 1990), LROR (5'-ACC CGC TGA ACT TAA GC-3') and LR7 (5'-TAC TAC CAC CAA GAT CT-3'), RPB1-Af (5'-GAR TGY CCD GGD CAY TTY GG-3') and RPB1-Cf (5'-CCN GCD ATN TCR TTR TCC ATR TA-3';

#### TABLE 1 | Taxa information and GenBank accession numbers used in this study.

TS     LSU r0M     pb1     pb2     terfue       Amylosofican outbervorse     HHB 2008     GU187050     GU187050     GU187769     GU187	Species	Sample	GenBank accession nos.				Country	
Amplescontransettemmerse     H=H 2688     CU187200     GU187707     GU187770     GU187770     GU187777     Carrada       Anteria andronoloa     CBS 418.72     GU187707     GU187708     GU18708			ITS	LSU rDNA	rpb1	rpb2	tef1α	
Advances     MUL 4413     GU197700     GU197570     GU197705     GU197777     GU197705     GU197705	Amylocorticium cebennense	HHB 2808	GU187505	GU187561	GU187439	GU187770	GU187675	United States
Alterida and/noblez     CBS 418.72     G1197739	Anomoloma myceliosum	MJL 4413	GU187500	GU187559	GU187441	GU187766	GU187677	Canada
Aunclarker     Xiachelmino     LT7/160/2     KY418808     KY418808     KY418082     KY418083     China       Biodnotesi kurcontenia     AFTOL 1527     D02490494     D0250249     A7218474     GUII677820     GUII677830     GUII677710	Athelia arachnoidea	CBS 418.72	GU187504	GU187557	GU187436	GU187769	GU187672	Netherlands
Bioktogowie Nacomanie AFTOL 152     DCI44004     DD151112     GU187780     GU187783     United Stat Biodramowie normania     GU18778     DD1524580     DO265604     AV28170     DD15611       Controling perminis     GU101318     KU300288     KU300224     -     -     -     -     DD1561       Controling perminis     GU101525     KU3002877     JU087977     JU087976     AV881760     -     -     United Stat       F. Impliania     MUCL 45351     FV369378     AV881567     -     AV881760     HM550680     HM55067     AV881760     HM550670     -     -     United Stat       F. Impliania     MUCL 45351     FV450808     HM550801     -     HM550170     United Stat       Gonophilum sociatium     WICL 45351     SU254571     SU87493     GU187718     GU187775     China       Gonophilum sociatium     AFTOL 701     AV851080     AV721057     AV88157     -     -     -     China       Gonophilum sociatium     GU187728     GU187728     GU187775     GU187775     China     -     Ch	Auricularia heimuer	Xiaoheimao	LT716074	KY418890	KY418982	KY419035	KY419083	China
Bondingsein montana     AFTCL 4.62     D D22003     D D23103     D D22009     AY218/74     D D0560/4     Carnada       Chyptonocous humionia     AFTCL 452     D0345615     D D045514     -     D D045571     -     Chyptonocous humionia       Chyptonocous humionia     AFTCL 452     D X8581070     M X701525     -     A7800748     Eatonia       F. moditoria     MUCL 35351     J X053778     J X053789     J X053789     -     -     -     -     United State       F. moditoria     MUCL 35351     J X053789     J X053769     -     A7803748     Eatonia       F. moditoria     M H05.388     D A785470     D C053669     GUI197269     GUI197272     Germmaly       Ginnerphalue repairwait     D C153470     D C053469     GUI197249     GUI197278     GUI19728     GUI197278     GUI19728     GUI19728     GUI19728     GUI19728     GUI19728     GUI19728     GUI19728     GU	Boletopsis leucomelaena	AFTOL 1527	DQ484064	DQ154112	GU187494	GU187820	GU187763	United States
Catholis persons     Cul 10318     KU300244     -     -     -     -     Chris       Coptococcos huminolis     APTCL 152     0.0645511     0.0645511     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645513     0.0645133     0.0645133     0.0645133	Bondarzewia montana	AFTOL 452	DQ200923	DQ234539	DQ256049	AY218474	DQ059044	Canada
Chyptococcis huminole AFTOL 1582, D0649516 D0649514 - D0649517 D0649517 D0649519 - Forentiports hartingi MLCL 5355 VA765407 VA701595 - VA780576 VA780576 VA780576 FA19291 MLCL 5355 VA765407 VA701575 - Fangelasin MLCL 53551 VA765407 VA701575 - VA780576 VA780576 VA780576 FA19291 MLCL 5355 VA780576 - F. meditamiren AFTOL 588 VA7654080 VA7654157 - VA7805718 VA785109 UN168 Stat Genephika researe MB 55.038 D05354570 D0535696 GU157459 GU157459 GU157788 GU15770 Chra Genephika researe VA785408 VA7804878 VA780507 VA780507 VA780507 VA780507 (Phydroport almonia VA785408 VA7804878 VA780507 VA780	Coltricia perennis	Cui 10318	KU360686	KJ000224	-	-	-	China
Deoryopinal synathulania     APTCL 644     AVB61020     APTC01255     -     APTC80077     AV7801020     -     -     United State       F. angolanian     MULC1.55551     LM0263287     -     -     -     -     United State       F. angolanian     MULC1.55551     EM263225     -     -     -     -     -     United State       Globag/phillarn segontum     WIB00:3688     HMM508100     HMM508100     HMM508100     HMM508107     AV780577     AV785705     AV7	Cryptococcus humicola	AFTOL 1552	DQ645516	DQ645514	-	DQ645517	DQ645519	-
FormBook     MUCL 63551     UM083789     UM083789     UM083785     UM083785     UM083785     UM083785     UM083785     UM083785     Umo83785	Dacryopinax spathularia	AFTOL 454	AY854070	AY701525	-	AY786054	AY881020	-
F. Anglossi     MUCL 40375     EF4.20242     EF4.2025     -     -     -     -     United State       Gradga (Juliar) seguritaria     WEGA:38B     HM55030     HM550301     HM550310     HM510310     HM	Fomitiporia hartigii	MUCL 53551	JX093789	JX093833	-	JX093877	JX093746	Estonia
F. madiffermania     AFTCI. 688     AFTCI. 688     AFTCI. 688     AFTCI. 688     AFTCI. 701     HMS530100     HMS530100     GUI187720     GUI187711     GUI187720     GUI187711     GUI187710     GUI187711     GUI187711     GUI187711     GUI187711     GUI187711     GUI187713     GUI18773     GUI18773     GUI18773     GUI18773     GUI187725     GUI187725     GUI187725	F. langloisii	MUCL 46375	EF429242	EF429225	-	-	-	United States
Geoephelkur segein/um     Wilcox SBB     HMS30001     HMS3001     -     HMS3010     HMS3010     United State       Grampalkur sensus     MB 95-038     APEQL 701     APS8-038     APEQL 711     APS8-038     APS8477     China       Grampalkur picrows     ZBL2015011     UT1716006     KY418982     KY418903     GU187773     China       Lappia argitece     CB3 222.74     GU187733     GU187733     GU187773     GU18773     GU18773     China       Lappia argitece     CB3 222.74     GU187738     GU187773     GU18773     GU18773     China       Lappias cristata     ZPL20151133     UT1716226     KV418914     KV418903     GU187713     GU18773     China     China issigaina     GU18773     China	F. mediterranea	AFTOL 688	AY854080	AY684157	-	AY803748	AY885149	
Gamphilise rosews     MB 95-038     COS34670     DOS34680     GUIR7459     GUIR7459     GUIR7451     GUIR7181     GUIR7181 <td>Gloeophyllum sepiarium</td> <td>Wilcox-3BB</td> <td>HM536091</td> <td>HM536061</td> <td>_</td> <td>HM536109</td> <td>HM536110</td> <td>United States</td>	Gloeophyllum sepiarium	Wilcox-3BB	HM536091	HM536061	_	HM536109	HM536110	United States
Grifois foronolosa     AFTOL 701     AV86-904     AV923118     AV964876     AV98577     AV985113       Grimoglus process     ZRL2015011     LT716006     KY419027     -     -     -     China       Introducta grissus     Dai 13436     KOG68492     K	Gomphidius roseus	MB 95-038	DQ534570	DQ534669	GU187459	GU187818	GU187702	Germany
Gymnapiles ploraus     ZPL2015011     LT716066     KV418822     KV418820     KV418027     KV418027     KV418077     Ohina       Hydroporis lamelleta     Dal 13436     HXG464802     KX384823     KX384871     HXG364819     MF97775     Ohina       Jaaqaa gillacaa     CBS 262,74     GU187524     GU187581     GU1877463     GU187774     GU187757     China       Leptota cristina     ZPL20151133     LT716006     KV418986     KV418977     GU187757     GU187758     GU187748     GU187758     GU187744     AF10779     MM950777     GU18758       Leptota cristina     Dal 13601     KT281898     -     -     -     Ohina       Leptospora     Dal 13601     KT281898     -     -     -     Ohina       Lona leporins     Dal 13601     KT281896     KT281971     -     -     Ohina       Lona leporins     Dal 13601     KT281968     KT281971     -     -     Ohina       Lopospora     Dal 13861     KT281969     KT281971     -     -     Ohina	Grifola frondosa	AFTOL 701	AY854084	AY629318	AY864876	AY786057	AY885153	
fordsports/immalized           Gui 78293           J0279603           J0279617           -           -           -           -           Guina        Jangka srgilkaca      CBS 252,74      GUI 87724      GUI 87743      GUI 8774	Gvmnopilus picreus	ZRL2015011	LT716066	KY418882	KY418980	KY419027	KY419077	China
Instructure     Dal 13/36     KO2884822     KO2844871     KO2864871     MC2864819     MF97775     China       Japaia agliacea     CBS 252.74     GU187524     GU1877245     GU1877245     GU1877245     GU1877245     GU1877246     GU1877275     China     Ch	Hydnoporia lamellata	Cui 7629	JQ279603	JQ279617	_	_	_	China
Bapita argillaces     CBS 252.7.4     GU187524     GU187758     GU187783     GU187783     GU187778     GU187771     Nethertson Lepiota cristata       Lepiota cristata     ZPL.20151133     GU187528     GU187588     GU187791     GU187791     GU1877719     GU187777     GU18777719     GU187	Inonotus ariseus	Dai 13436	KX364802	KX364823	KX364871	KX364919	MF977775	China
Lepiota cristata     ZPL20151133     LT71602/6     KY418963     KY418963     KY418962     KY419048     China       Lepiota cristata     ZPL20151133     LT71602/6     KY418963     KY418963     KY418967     -       Meurospora crassa     OR74A     H027144     AF282411     -     AF1007791     CM800827     -       Onnia kesiyae     Dai 13610     KT281568     -     -     -     OM800027     China       Onnia kesiyae     Dai 13601     KT281569     -     -     -     Omia subistication     Omia subistication     Omia subistication     Omia subistication     Omia subistication     Omia subistication     -     -     -     China     China Subistication     -     -     China     -     China     China Subistication     -     -     China     -     China     -     China     China Subistication     China     China Subistication     -     -     China     China Subistication     -     -     China     China     China Subistication     -     -     China     China	Jaapia argillacea	CBS 252 74	GU187524	GU187581	GU187463	GU187788	GU187711	Netherlands
Laposporomycos raunkiaeri HHB 7628 GL197528 GL197528 GL197579 GL19779 GL19779 GL197719 United Stat Neurospore crasse OH74A H10271348 AF228411 - AF107799 GL197719 United Stat Neurospore crasse OH74A H2271348 AF228411 - AF107799 GL197719 United Stat Onnia kejven Onnia kejven Onnia kejven Dal 19815 KT281958 OK060027 Vetra Dal 20866 OM6977245 OM677552 OK060029 Oh06029 J/V100715 KT281956 VFT281970 181a/ Onnia himateyana Dal 22820 OM677247 OM677251 ON007276 OM937018 OM60028 United Stat Onnia himateyana Dal 28886 OM677247 OM677251 ON007276 OM937018 OM600282 United Stat Dal 20867 OM6977247 OM677251 ON007276 OM937018 OM600282 United Stat M22 OM6977244 CM967335 Othra Dal 28886 OM6977247 OM697355 Othra Dal 28886 OM697724 OM697355 Othra Dal 28886 OM697724 OM697355 Othra Dal 28821 OM967275 OM967356 Othra Dal 28622 - OM697335 Othra Dal 28622 - OM697335 Othra Dal 2862 OM697274 OM697356 Othra Dal 2862 OM697275 OM967356 Othra Dal 2862 OM697274 OM697356 Othra Dal 2862 OM697274 OM697358 Othra Dal 2862 OM697274 OM697358 Othra Dal 2865 OM697279 OM697358 Othra Dal 2865 OM6972	Leniota cristata	7BL 20151133	LT716026	KY418841	KY418963	KV418992	KY419048	China
Lapusgoon Nybos Notined     In Prace     Outro Prace     OutroPrace     Outro Prace     OutroPrace <td>Leptosporomyces raunkiaeri</td> <td>HHB 7628</td> <td>GU187528</td> <td>GU187588</td> <td>GU187471</td> <td>GU187791</td> <td>GU187719</td> <td>Linited States</td>	Leptosporomyces raunkiaeri	HHB 7628	GU187528	GU187588	GU187471	GU187791	GU187719	Linited States
Nacional de construit       Onnia legonina     Dal 13601     KT281968     -     -     -     Ottoinal       Onnia legonina     Dal 20866     OM677245     OM677252     -     -     Ottoinal       JV0000/15     KT281960     -     -     -     -     Carechia       JV0000/15     KT281967     KT281970     -     -     -     Carechia       Onnia microspora     Dal 11866     KT281957     KT281971     -     -     -     China       Onnia microspora     Dal 22820     OM677244     OM677254     -     -     -     China       Onnia subtriquetra     Dal 22886     OM677244     OM677351     OM07766     OM837018     OM806028     United Stat       Onnia tiberica     Cui 1224     KT281955     KT281969     -     -     -     United Stat       JV00109/DSJ     KT281955     KT281967     -     -     -     China       Dal 23642	Neurospora crassa	OB744	HO271348	AE286411	-	ΔE107789	XM959775	-
Onna lagonina     Dal 13010     KT_000001     F     -     -     -     -     -     -     -     -     -     -     China       Dal 20666     OM677245     OM677252     -     -     OM00029     China       JV0000/15     KT281959     -     -     -     -     Cacchia       JV1007/2     KT281950     KT281970     -     -     -     Cacchia       Onnia microspora     Dal 11897     KT281957     KT281971     -     -     -     China       Onnia subtriquetra     Dal 23687     OM677247     OM677251     OM07726     OM937018     OM900228     United Stat       Onnia subtriquetra     Dal 23687     OM677244     OM677251     OM07765     OM937018     OM900288     United Stat       MB2     KT281955     KT281969     -     -     -     United Stat       MB2     KT281953     KT281967     -     -     -     China       JV04010/L2J     KT281954     KT281967     -     -	Onnia kasivaa	Dai 18/15	NR 160600	NG 068811		AI 101103	OM800827	Vietnam
Onla hgudra     Dai 20866     OMF77245     OMF77255     -     -     -     -     -     -     -     -     -     Cacha       JV0609/15     KT281950     -     -     -     -     -     Cacha       JV1207/2     KT281950     -     -     -     -     Cacha       Phaeo1     KF996514     -     -     -     -     Cacha       Onnia himatoyana     Dai 11886     KT281957     KT281971     -     -     -     China       Onnia himatoyana     Dai 26867     OM677247     OM677251     ON007276     OM937018     OM80828     United Stat       Onnia subtriquetra     Dai 26867     OM967274     OM677251     ON007276     OM937016     United Stat       JV0410/12.J     KT281958     KT281969     -     -     -     United Stat       JV0410/12.J     KT281953     KT281966     -     -     -     China       Dai 2682     0     M967236     ON007278     OM937015     OM800830	Oppia loporina	Dai 13501	KT291059	NG_000011	_	_	0111000027	Chipa
Date 2000     Onto / TS22     -     -     -     -     -     Cacchia       JV0009/15     KT281950     -     -     -     -     Cacchia       Phaeo1     KF281956     KT281972     -     -     -     Italy       Onnia microspora     Dal 11886     KT281957     KT281970     -     -     -     China       Onnia himalayana     Dal 2686     OM677247     OM677251     ON007276     OM937018     OM800828     United Stat       Onnia subtriquetra     Dal 26866     OM677247     OM677251     ON007276     OM937018     OM800828     United Stat       ME2     KT281955     KT281969     -     -     -     United Stat       ME2     KT281955     KT281967     -     -     -     United Stat       JV01010/12.1     KT281955     KT281963     -     -     -     China       Dal 26821     OM967275     OM967387     -     -     -     China       Dal 26821     OM677245     OM677253	Onna leponna	Dai 10001	OM677245	- OM677252	-	-	014800830	China
Ondown Machael     Name     Image		Dai 20000	KT281050	0101077252	-	-	0101000029	Czochia
Onla microspora     Dial 11886     KT281960     KT28197     -     -     -     -     Cubic       Onnia microspora     Dai 11887     KT281966     KT28197     -     -     -     China       Onnia himalayana     Dai 22820     OM677247     OM677254     -     -     -     China       Onnia subtriquetra     Dai 23868     OM677247     OM677255     OM037766     OM8300828     United Stat       MB2     KT281955     KT281969     -     -     -     United Stat       MB2     KT281954     KT281968     -     -     -     United Stat       JV0410/12J     KT281961     KT281967     -     -     -     China       JV0410/12J     KT281961     KT281967     -     -     -     China       Dai 23821     OM967275     OM967336     -     -     -     China       Dai 23842     OM677246     OM677253     OM07277     OM937015     OM800820     China       Dai 23843     OM967276     OM967338 <td></td> <td>1/1007/0</td> <td>KT201959</td> <td>- 1/T001070</td> <td>-</td> <td>-</td> <td>-</td> <td>Czechia</td>		1/1007/0	KT201959	- 1/T001070	-	-	-	Czechia
PrilateO1     Nr996014     P     China       Dal 11897     KT281957     KT281957     CM677247     OM677247     OM677251     ON007276     OM937018     OM800828     United Stat       Onia subtriquetra     Dal 23686     OM677244     OM677251     ON007276     OM937018     OM800828     United Stat       M82     KT281955     KT281969     -     -     -     United Stat       JV0410/12J     KT281954     KT281967     -     -     -     United Stat       JV0109/D6J     KT281953     KT281967     -     -     -     China       Dal 23621     OM967336     FT281967     -     -     -     China       Dal 23642     OM67726     OM967338     -     -     -     China       Onnia triquetra     CBS 278.55     M1857481 </td <td></td> <td>JV1207/2</td> <td>KI201900</td> <td>K12019/2</td> <td>_</td> <td>_</td> <td>_</td> <td>Czechia</td>		JV1207/2	KI201900	K12019/2	_	_	_	Czechia
Online Initiados/Jola     Dal 11880     K1281950     K1281957     -     -     -     China       Onnia himalayana     Dal 22620     OM677247     OM677254     -     -     -     China       Onnia subtriquetra     Dal 23687     OM967274     OM677254     -     -     -     United Stat       M82     KT281955     KT281956     -     -     -     United Stat       JV0410/12J     KT281954     KT281968     -     -     -     United Stat       Onnia tibetica     Cui 12254     KT281953     KT281963     -     -     -     China       Dal 23621     OM967275     OM967337     -     -     -     China       Dal 23642     OM677250     OM967337     -     -     -     China       Dal 23643     OM677276     OM967337     -     -     -     China       Dal 23643     OM677276     OM967337     -     -     -     China       Dal 23643     OM677249     OM07276     OM937015 <td></td> <td>Phaeo I</td> <td>KF990014</td> <td>-</td> <td>_</td> <td>_</td> <td>_</td> <td>Titaly</td>		Phaeo I	KF990014	-	_	_	_	Titaly
Dail 11897     K1281897     K1281971     -     -     -     -     China       Onnia himalayana     Dai 23686     OM677247     OM677251     ON007276     OM37018     OM800828     United Stat       Dai 23687     OM967274     OM967335     -     -     -     United Stat       MB2     KT281956     KT281956     KT281957     -     -     -     United Stat       JV0410/12J     KT281956     KT281967     -     -     -     United Stat       JV0199/D6J     KT281953     KT281967     -     -     -     China       Dai 23621     OM967275     OM967337     -     -     -     China       Dai 23642     OM67726     OM967338     -     -     -     China       Dai 23642     OM677276     OM967338     -     -     -     China       Dai 23642     OM67724     OM967338     -     -     -     China       Dai 23642     OM67724     OM967339     -     -     -	Onnia microspora	Dai 11000	K1281950	KT201970	_	_	_	China
Onnia minializiana     Dia / 22620     OMM 7/234     OMM 7/234     -     United Stat       MB2     KT281955     KT281968     -     -     -     -     United Stat       JV0410/12J     KT281953     KT281968     -     -     -     United Stat       JV0109/D6J     KT281953     KT281967     -     -     -     China       Dai 23621     OM967375     OM967336     -     -     -     China       Dai 23643     OM96726     OM967338     -     -     -     China       Dai 23643     OM967276     OM967338     -     -     -     China       Dai 23643     OM967274     OM967338     -     -     -     China       Dai 23643     OM967274     OM97728     OM937015     OM808		Dai 11897	KT281957	KT281971	-	-	-	China
Onnia subtriquetra     Dia 25686     Onike 7724     Onike 7724     Onike 7724     Onike 7724     Onike 7725     Onike 5735     -     -     -     -     United Stat       MB2     KT281955     KT281966     -     -     -     United Stat       JV010/12J     KT281953     KT281967     -     -     -     United Stat       JV010/0EJ     KT281953     KT281973     -     -     -     China       Dal 23621     OM967275     OM967335     -     -     -     China       Dal 23622     -     OM967336     -     -     -     China       Dal 23642     OM677246     OM677253     ON007277     OM937019     OM808030     China       Dal 23643     OM967276     OM967338     -     -     -     China       Dai 23643     OM967276     OM967338     -     -     -     China       Dia 23643     OM967276     OM967338     -     -     -     China       Onnia triquetra     CBS 278.55 <td>Onnia nimalayana</td> <td>Dai 22620</td> <td>OM677247</td> <td>OM677254</td> <td>-</td> <td>-</td> <td>-</td> <td>China</td>	Onnia nimalayana	Dai 22620	OM677247	OM677254	-	-	-	China
Dai 23887     OM96/2/4     OM96/2/4     OM96/2/35     -     -     -     -     -     -     United Stat       JV010/DEJ     KT281955     KT281967     -     -     -     United Stat       JV0109/DEJ     KT281953     KT281967     -     -     -     United Stat       Onnia tibetica     Cui 12254     KT281957     KT281967     -     -     -     China       Dai 23621     OM967275     OM967336     -     -     -     China       Dai 23622     -     OM967337     OM07777     OM937019     OM80080     China       Dai 23642     OM677266     OM967338     -     -     -     China       Dai 23643     OM967276     OM967338     -     -     -     China       Dai 23643     OM97276     OM967338     -     -     -     China       Dai 23682     OM97277     OM967339     -     -     -     China       Dai 18900     OM677243     OM677248     OM937015	Onnia subtriquetra	Dai 23686	OM6//244	OM6//251	ON007276	OM937018	OM800828	United States
MB2     K1281955     K1281965     K1281968     -     -     -     United Stat       JV0109/D6J     KT281953     KT281967     -     -     -     United Stat       Onnia tibetica     Cui 12254     KT281961     KT281967     -     -     -     China       Dai 23621     OM967375     OM967337     -     -     -     China       Dai 23622     -     OM967337     -     -     -     China       Dai 23642     OM967276     OM967338     -     -     -     China       Mai 1964     KT281962     KT281974     -     -     -     China       Yuan 1964     KT281962     KT281975     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     China       Dai 18900     OM677241     OM677248     -     OM937015     OM800824     China       Dai 28935     OM677242     OM67739     -     -     -     Uni		Dai 23687	OM967274	OM967335	-	-	-	United States
JV0110/12J     K1281954     K1281968     -     -     -     -     United Stat       JV0109/D6J     KT281961     KT281967     -     -     -     Onlia tibetica       Onnia tibetica     Cui 12254     KT281961     KT281973     -     -     -     Ochina       Dai 23621     OM967375     OM967338     -     -     -     Ochina       Dai 23622     -     OM967375     OM907275     OM937019     OM800800     China       Dai 23643     OM967276     OM967338     -     -     -     Ochina       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Carcehia       Onnia triquetra     CBS 278.55     MH857481     MH86903     -     -     -     Carcehia       Dai 14806B     KT281965     KT281975     -     -     -     China       Dai 14806B     KT281964     MK7281975     -     -     -     China       Dai 23682     OM967279     OM97739     - <td></td> <td>MB2</td> <td>K1281955</td> <td>K1281969</td> <td>-</td> <td>-</td> <td>-</td> <td>United States</td>		MB2	K1281955	K1281969	-	-	-	United States
JV0109/DGJ     K1281953     K1281957     -     -     -     -     -     -     -     -     -     -     China     China       Dal 23621     OM967275     OM967336     -     -     -     -     China       Dal 23642     OM967276     OM967337     -     -     -     China       Dal 23642     OM967276     OM967338     -     -     -     China       Dal 23642     OM967276     OM967388     -     -     -     China       Dal 23643     OM967276     OM967388     -     -     -     China       Dial 23643     OM967276     OM967383     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     China       Onnia tomentosa     Dai 14806B     KT281965     KT281975     -     -     -     China       Dai 23682     OM677241     OM677249     OM007278     OM937016     OM800822     China <td></td> <td>JV0410/12J</td> <td>KI281954</td> <td>K1281968</td> <td>-</td> <td>-</td> <td>-</td> <td>United States</td>		JV0410/12J	KI281954	K1281968	-	-	-	United States
Onnia tibetica     Cui 12254     KT281961     KT281973     -     -     -     China       Dai 23621     OM967275     OM967336     -     -     -     China       Dai 23622     -     OM967337     -     -     -     China       Dai 23642     OM677246     OM967337     -     -     -     China       Dai 23642     OM9677276     OM967338     -     -     -     China       Dai 23643     OM967726     OM967338     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Cerechia       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Czechia       Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     China       Dai 23683     OM677242     OM677248     OM007278     OM937016     OM808024     China       Dai 23683     OM967277     OM967339     -		JV0109/D6J	KT281953	KT281967	-	-	-	United States
Dal 23621     OM967275     OM967336     -     -     -     -     China       Dai 23622     -     OM967337     -     -     -     China       Dai 23642     OM977246     OM967338     -     -     -     China       Dai 23643     OM967276     OM967338     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Cerchia       Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     Cerchia       Dai 23682     OM677241     OM677248     OM007278     OM937015     OM800824     China       Dai 23682     OM967279     OM967339     -     -     -     United Stat       Dai 23682     OM967279     OM967341     -     -     -     Carada       Dai 23685     OM967279     OM967341     - <td< td=""><td>Onnia tibetica</td><td>Cui 12254</td><td>KT281961</td><td>KT281973</td><td>-</td><td>-</td><td>-</td><td>China</td></td<>	Onnia tibetica	Cui 12254	KT281961	KT281973	-	-	-	China
Dai 23622     -     OM97337     -     -     -     -     China       Dai 23642     OM977246     OM97253     ON007277     OM937019     OM800830     China       Dai 23643     OM967276     OM967388     -     -     -     China       Vuan 1964     KT281962     KT281974     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     China       Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     China       Dai 18900     OM677241     OM677248     -     -     -     China       Dai 2935     OM677242     OM677249     ON007278     OM937016     OM800825     China       Dai 23682     OM967277     OM967339     -     -     -     United Stat       Dai 23683     OM677243     OM677249     OM007279     OM937016     OM800820     China       Dai 23685     OM967277     OM967339     - <td< td=""><td></td><td>Dai 23621</td><td>OM967275</td><td>OM967336</td><td>-</td><td>-</td><td>-</td><td>China</td></td<>		Dai 23621	OM967275	OM967336	-	-	-	China
Dai 23642     OM677246     OM677253     ON007277     OM937019     OM800830     China       Dai 23643     OM967276     OM967338     -     -     -     China       Yuan 1964     KT281962     KT281974     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Carchia       Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     China       Dai 23683     OM677241     OM677248     -     OM937015     OM800824     China       Dai 23682     OM677242     OM677248     -     OM937016     OM800825     China       Dai 23682     OM967277     OM967339     -     -     -     United Stat       Dai 23682     OM967279     OM967341     -     -     -     Carada       Dai 23683     OM677243     OM967279     OM937017     OM80082     United Stat       Dai 23685     OM967279     OM967341     -     -		Dai 23622	-	OM967337	-	-	-	China
Dai 23643     OM967276     OM967338     -     -     -     -     China       Yuan 1964     KT281972     KT281974     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Germany       JV1410/3     KT281965     KT281976     -     -     -     China       Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     China       Dai 18900     OM677241     OM677248     -     OM937015     OM800824     China       Dai 23682     OM967727     OM967339     -     -     -     -     United Stat       Dai 23683     OM677243     OM677250     OM007278     OM937017     OM80082     China       Dai 23685     OM967279     OM967339     -     -     -     -     United Stat       Dai 23685     OM967279     OM967341     -     -     -     Caada       OT-Slu     KF281966     KT281976		Dai 23642	OM677246	OM677253	ON007277	OM937019	OM800830	China
Yuan 1964     KT281962     KT281974     -     -     -     -     China       Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Germany       JV1410/3     KT281963     KT281975     -     -     -     Czechia       Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     China       Dai 18900     OM677241     OM677248     -     OM937015     OM800824     China       Dai 22935     OM677242     OM677249     ON007278     OM937016     OM800825     China       Dai 23682     OM967277     OM967339     -     -     -     United Stat       Dai 23683     OM97243     OM677250     OM907279     OM937017     OM800825     United Stat       Dai 23683     OM967277     OM967341     -     -     -     Czechia       Dai 23685     OM967279     OM967341     -     -     -     Canada       OT-Slu     KF996516     -     -		Dai 23643	OM967276	OM967338	-	-	-	China
Onnia triquetra     CBS 278.55     MH857481     MH869023     -     -     -     Germany       JV1410/3     KT281963     KT281975     -     -     -     Czechia       Onnia tomentosa     Dai 14806B     KT281965     KT281975     -     -     -     China       Dai 18900     OM677241     OM677248     -     OM937015     OM800824     China       Dai 29305     OM677242     OM677268     OM07278     OM937016     OM800825     China       Dai 29365     OM677243     OM677250     OM007279     OM937017     OM800825     United Stat       Dai 23682     OM967279     OM967341     -     -     -     United Stat       Dai 23685     OM967279     OM967341     -     -     -     Czechia       Vampola 2010     KT281966     KT281977     -     -     -     Canada       OT-Slu     KF996518     -     -     -     -     -     Sweden       T. Niemela 9079     MF319075     MF319006     - <td></td> <td>Yuan 1964</td> <td>KT281962</td> <td>KT281974</td> <td>-</td> <td>-</td> <td>-</td> <td>China</td>		Yuan 1964	KT281962	KT281974	-	-	-	China
JV1410/3     KT281963     KT281975     -     -     -     -     Czechia       Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     China       Dai 18900     OM677241     OM677248     -     OM937015     OM800824     China       Dai 22935     OM677242     OM677249     ON007278     OM937016     OM800825     China       Dai 23682     OM967727     OM967339     -     -     -     United Stat       Dai 23683     OM677243     OM677250     OM007279     OM937017     OM800822     United Stat       Dai 23685     OM967279     OM967341     -     -     -     Czechia       FP-100585-5p     KF296516     -     -     -     -     Canada       OT-Slu     KF996518     -     -     -     -     Canada       OL-Slu     KF996518     -     -     -     -     Russia       Cui 9986     KT281964     -     -     -     -     China	Onnia triquetra	CBS 278.55	MH857481	MH869023	-	-	-	Germany
Onnia tomentosa     Dai 14806B     KT281965     KT281976     -     -     -     -     China       Dai 18900     OM677241     OM677248     -     OM937015     OM800824     China       Dai 22935     OM677242     OM677249     ON007278     OM937016     OM800825     China       Dai 23682     OM967277     OM967339     -     -     -     United Stat       Dai 23683     OM677243     OM677250     OM007279     OM937017     OM80082     United Stat       Dai 23683     OM967279     OM967341     -     -     -     United Stat       Dai 23685     OM967279     OM967341     -     -     -     Cacehia       Dai 23685     OM967279     OM967341     -     -     -     Cacehia       FP-100585-5p     KF996516     -     -     -     -     Caeada       OT-Slu     KF996518     -     -     -     -     Russia       Cui 9986     KT281964     -     -     -     China <		JV1410/3	KT281963	KT281975	-	-	-	Czechia
Dai 18900     OM677241     OM677248     -     OM937015     OM800824     China       Dai 22935     OM677242     OM677249     ON007278     OM937016     OM800825     China       Dai 23682     OM967277     OM967339     -     -     -     United Stat       Dai 23683     OM677243     OM677250     OM007279     OM937017     OM800822     United Stat       Dai 23685     OM967279     OM967341     -     -     -     United Stat       Vampola 2010     KT281966     KT281977     -     -     -     Czechia       FP-100585-5p     KF996518     -     -     -     -     Caaada       OT-Slu     KF996518     -     -     -     -     Sweden       T. Niemela 9079     MF319075     MF319006     -     -     -     Russia       Cui 9986     KT281964     -     -     -     -     Russia       Cui 9986     KT281964     -     -     -     -     United Stat	Onnia tomentosa	Dai 14806B	KT281965	KT281976	-	-	-	China
Dai 22935     OM677242     OM677249     ON007278     OM937016     OM800825     China       Dai 23682     OM967277     OM967339     -     -     -     United Stat       Dai 23683     OM677243     OM677250     OM007279     OM937017     OM800825     United Stat       Dai 23685     OM967279     OM967341     -     -     -     United Stat       Vampola 2010     KT281966     KT281977     -     -     -     Czechia       FP-100585-5p     KF996518     -     -     -     -     Canada       OT-Slu     KF996518     -     -     -     -     Sweden       T. Niemela 9079     MF319075     MF319006     -     -     -     Russia       Cui 9986     KT281964     -     -     -     Russia     China       HHB-18573     KT955001     -     -     -     -     China       LOO-13789-Q     KF996517     -     -     -     United Stat       LOO-13789-Q     KF96		Dai 18900	OM677241	OM677248	-	OM937015	OM800824	China
Dai 23682     OM967277     OM967339     -     -     -     -     United Stat       Dai 23683     OM677243     OM677250     OM007279     OM937017     OM80082     United Stat       Dai 23685     OM967279     OM967341     -     -     -     United Stat       Vampola 2010     KT281966     KT281977     -     -     -     Czechia       FP-100585-5p     KF996516     -     -     -     -     Czechia       OT-Slu     KF996518     -     -     -     -     Sweden       T. Niemela 9079     MF319075     MF319006     -     -     -     Russia       Cui 9986     KT281964     -     -     -     -     Russia       Cui 9986     KT281964     -     -     -     -     Othina       HHB-18573     KT955001     -     -     -     -     United Stat       LOO-13789-Q     KF996517     -     -     -     -     Germany       Phellinopsis conchata <td></td> <td>Dai 22935</td> <td>OM677242</td> <td>OM677249</td> <td>ON007278</td> <td>OM937016</td> <td>OM800825</td> <td>China</td>		Dai 22935	OM677242	OM677249	ON007278	OM937016	OM800825	China
Dai 23683     OM677243     OM677250     OM007279     OM937017     OM80082     United Stat       Dai 23685     OM967279     OM967341     -     -     -     United Stat       Vampola 2010     KT281966     KT281977     -     -     -     Czechia       FP-100585-5p     KF996516     -     -     -     -     Czechia       OT-Slu     KF996518     -     -     -     -     Sweden       T. Niemela 9079     MF319075     MF319006     -     -     -     Finland       SFC20170810-01     MT044403     -     -     -     -     Russia       Cui 9986     KT281964     -     -     -     -     Russia       LOO-13789-Q     KF996517     -     -     -     -     United Stat       LOO-13789-Q     KF996517     -     -     -     -     United Stat       LOO-13789-Q     KF996517     -     -     -     -     Germany       Phellinopsis conchata     L		Dai 23682	OM967277	OM967339	-	-	-	United States
Dai 23685   OM967279   OM967341   -   -   -   United Stat     Vampola 2010   KT281966   KT281977   -   -   -   Czechia     FP-100585-5p   KF996516   -   -   -   -   Canada     OT-Slu   KF996518   -   -   -   -   Sweden     T. Niemela 9079   MF319075   MF319006   -   -   -   Flinland     SFC20170810-01   MT044403   -   -   -   -   Russia     Cui 9986   KT281964   -   -   -   -   China     HHB-18573   KT955001   -   -   -   -   China     HHB-18573   KT996517   -   -   -   -   United Stat     LOO-13789-Q   KF996517   -   -   -   -   Germany     Phellinopsis conchata   L7601   KU139188   KU139257   -   -   -   United Stat		Dai 23683	OM677243	OM677250	OM007279	OM937017	OM80082	United States
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Phellinopsis conchata L7601 KU139188 KU139257 - - - United State		TW 445		AF311023	_	_	_	Germany
	Phellinopsis conchete	17601	KI 1130199	KI 1120257	_	_	_	Linited States
		LIUUI	10100100	10100201				

Species	Sample	GenBank accession nos.					Country
		ITS	LSU rDNA	rpb1	rpb2	tef1α	
Phellinopsis andina	MR 1203	KP347542	KP347528	_	_	_	Argentina
Phellinus igniarius	85-917	AY340048	AF311027	-	-	-	Germany
Porodaedalea chinensis	Cui 10252	KX673606	MH152358	-	MH101479	MG585301	China
P. pini	No-6170-T	JX110037	JX110081	-	-	JX109993	United States
	FP102111T	JX110036	JX110080	-	-	-	United States
P. yunnanensis	Dai 3072	MG585282	MH152380	-	-	MG585292	China
Ramaria rubella	AFTOL 724	AY854078	AY645057	-	AY786064	AY883435	United States
Sanghuangporus sanghuang	Cui 14419	MF772789	MF772810	MF972246	MF973483	MF977790	China
Suillus pictus	AFTOL 717	AY854069	AY684154	AY858965	AY883429	AY883429	-
Thelephora ganbajun	ZRL20151295	LT716082	KY418908	KY418987	KY419043	KY419093	China
Trametes versicolor	ZRL20151477	LT716079	KY418903	KY418984	KY419041	KY419091	China
Trechispora alnicola	AFTOL 665	DQ411529	AY635768	-	-	DQ059052	United States
Ustilago maydis	AFTOL 505	AY854090	AF453938	-	AY485636	AY885160	-

#### TABLE 1 | (Continued)

New sequences are in bold; "-" represents missing data.

Matheny et al., 2002), fRPB2-5F (5'-GAY GAY MGW GAT CAY TTY GG-3') and fRPB2-7cR (5'-CCC ATR GCT TGY TTR CCC AT-3'; Liu et al., 1999; Matheny, 2005), and EF1-1567R (5'-ACH GTR CCR ATA CCA CCS ATC TT-3') and EF1-983F (5'-GCY CCY GGH CAY CGT CAY TTY AT-3'; Rehner and Buckley, 2005; Matheny et al., 2007), respectively. The polymerase chain reaction (PCR) procedures were as follows: for ITS sequences, an initial denaturation at 95°C for 3 min, followed by 34 cycles at 94°C for 40 s, 54°C for 45 s, 72°C for 1 min, and a final extension of 72°C for 10 min (Zhou et al., 2021a,b); for LSU rDNA region, an initial denaturation at 94°C for 1 min, followed by 34 cycles at 94°C for 30 s, 50°C for 1 min, 72°C for 1.5 min, and a final extension of 72°C for 10 min (Shen et al., 2016); for rpb1, rpb2, and tef1a regions, an initial denaturation at 94°C for 2 min, followed by 10 cycles at 94°C for 40 s, 60°C for 40 s, and 72°C for 2 min, then followed by 37 cycles at 94°C for 45 s, 55°C for 1.5 min, 72°C for 2 min, and a final extension at 72°C for 10 min (Chen et al., 2015; Wang X. W. et al., 2021). Sequencing for PCR products was conducted by BGI Tech Solutions Beijing Liuhe Co., Ltd., Beijing, China. Sequences were assembled and proofread with Geneious (version 9.0.2<sup>1</sup>, accessed 1 May 2021) and then submitted to GenBank under the accession numbers in Table 1.

#### **Phylogenetic Analyses**

All sequences were aligned with AliView (version 3.0; Larsson, 2014) and MAFFT (version 7; Katoh and Standley, 2013), and then manually adjusted. A dataset of 30 specimens composed of ITS + LSU rDNA sequences was subjected to maximum likelihood (ML), maximum parsimony (MP), and Bayesian inference (BI) phylogenetic analyses using RAxML (version 8, Stamatakis, 2014), PAUP (version 4.0b10; Swofford, 2002), and MrBayes (version 3.2.7a; Ronquist et al., 2012), respectively, following Zhao et al. (2021, 2022a,b). The GTRGAMMA model was chosen as the substitution model for ML analysis. Obtained phylograms were viewed with FigTree (version 1.4.4).

## **Divergence Time Estimation**

In this study, a dataset with 47 specimens (Figure 2) was used to infer the divergences times of species in the genus Onnia based on a dataset composed of ITS + LSU rDNA + rpb1 + rpb2 + teflasequences. The divergence times were estimated with BEAST (version 2.6.5; Bouckaert et al., 2014), using two ribosomal RNA genes (ITS and LSU rDNA) and three protein-coding genes (rpb1, rpb2, and tef1a). An XML (Extensible Markup Language) file was generated with BEAUti (version 2). The rates of evolutionary changes at nuclear acids were estimated using ModelTest (version 3.7) with the GTR substitution model (Posada and Crandall, 1998). Divergence time and corresponding CIs were conducted with a log-normal relaxed molecular clock and the Yule speciation prior. Three fossil time points, i.e., Archaeomarasmius leggettii Hibbett et al. (1995, 1997), Quatsinoporites cranhamii S.Y. Smith et al. (2004) and Berbee and Taylor (2010), and Paleopyrenomycites devonicus Taylor et al. (1999, 2005), representing the divergence time at Agaricales, Hymenochaetaceae, and between Ascomycota and Basidiomycota, respectively, were selected for calibration. The offset age with a gamma distributed prior (scale = 20 and shape = 1) was set as 90, 125, and 400 Mya for Agaricales, Hymenochaetaceae, and Basidiomycota, respectively. After 10,000,000 generations, the first 10% were removed as burnin. The log file was checked for convergence with Tracer (version 1.5<sup>2</sup>). Consequently, a maximum clade credibility (MCC) tree was summarized with TreeAnnotator (version 2.6.5), annotating clades with more than 0.8 posterior probability (PP).

## Inferring Historical Biogeography

Reconstruct Ancestral State in Phylogenies (RASP) (version 4.2) was used to reconstruct historical biogeography for the genus *Onnia* with a dispersal-extinction-cladogenesis (DEC) model (Yu et al., 2015, 2020). For historical biogeographic analyses, the posterior distributions of the dataset (**Table 1**), including two ribosomal RNA genes (ITS and LSU rDNA) and three protein-coding genes (*rpb1*, *rpb2*, and *tef1* $\alpha$ ), were estimated with BEAST.

<sup>&</sup>lt;sup>1</sup>http://www.geneious.com

<sup>&</sup>lt;sup>2</sup>http://beast.bio.ed.ac.uk/Tracer



**FIGURE 1** Maximum likelihood (ML) phylogenetic tree of *Onnia* based on ITS and LSU rDNA sequences, with *Porodaedalea pini*, *Phellinopsis conchata*, and *P. andina* as outgroups. ML bootstrap values ( $\geq$  50%)/maximum parsimony (MP) bootstrap values ( $\geq$  50%)/Bayesian inference (BI) posterior probabilities ( $\geq$  0.8) of each clade are indicated along branches. A scale bar in the upper left indicates substitutions per site.

The geographic distributions for *Onnia* were identified in three areas: (A) Asia, (B) Europe, and (C) North America.

## RESULTS

#### Phylogeny of Onnia

The ITS and LSU rDNA sequences are provided in **Tables 1**, 30 voucher specimens represent eight species of *Onnia*, one species of *Porodaedalea* Murrill, and two species of *Phellinopsis* Y.C. Dai. The dataset had an aligned length of 2,127 characters, including 1,750 constant, 155 parsimony-uninformative, and 222 parsimony-informative characters. MP analysis yielded a tree (tree length = 495, consistency index = 0.8889, homoplasy index = 0.1111, retention index = 0.9073, and rescaled

consistency index = 0.8064). The best model of BI for the ITS and LSU rDNA dataset was GTR + I + G, and the average SD of split frequencies was less than 0.01. The topology of the ML tree was chosen to represent the phylogenetic relationship with *Porodaedalea pini* (Brot.) Murrill, *Phellinopsis conchata* (Pers.) Y.C. Dai, and *P. andina* (Plank and Ryvarden) Rajchenb. and Pildain as outgroups, since ML, MP, and BI resulted in similar topologies. The result suggests that *O. himalayana* is closely related to *O. triquetra* (Figure 1).

## Divergence Time Estimation for Onnia

The results of divergence time estimation show (**Figure 2**) that Hymenochaetaceae emerged earlier with a mean stem age of 176.3 Mya [95% highest posterior density (HPD) of 153.5–205.7



FIGURE 2 | Estimated divergence of Onnia generated from molecular clock analyses using a combined dataset of ITS, LSU rDNA, *rpb1*, *rpb2*, and *tef1*α sequences. Estimated mean divergence time (Mya) and posterior probabilities (PP) > 0.8 are annotated at the internodes. The 95% highest posterior density (HPD) interval of divergence time estimates is marked by horizontal blue bars.

Mya] and a mean crown age of 144.9 Mya (95% HPD of 136.8– 153.8 Mya), which is consistent with previous studies (Wang X. W. et al., 2021; Ji et al., 2022). In Hymenochaetaceae, *Onnia* is closely related to the genus *Porodaedalea*, which is most deeply diversified during the Paleogene, with a mean stem age of 56.9 Mya (95% HPD of 35.9–81.6 Mya) and full support (1.0 PP,

#### **TABLE 2** | Inferred divergence time of species in the genus Onnia.

Genus/Species	Means of stem age (Mya)/95% HPD (Mya)/Posterior probabilities	Means of crown age (Mya)/95% HPD (Mya)/Posterior probabilities		
Onnia	56.9/35.9-81.6/1.0	28.6/15.5-46.2/1.0		
O. tomentosa	28.6/15.5-46.2/1.0	5.8/2.0-12.0/1.0		
O. leporina	13.9/7.3-23.6/1.0	1.7/0.1-5.6/1.0		
O. kesiyae	3.9/1.4-7.6/1.0	3.9/1.4-7.6/1.0		
O. microspora	3.9/1.4-7.6/1.0	1.8/0.4-4.1/1.0		
O. triquetra	3.2/0.7-7.1/0.9	3.2/0.7-7.1/0.9		
O. himalayana	3.2/0.7-7.1/0.9	3.2/0.7-7.1/0.9		
O. tibetica	4.8/1.9-9.0/-	0.5/0-1.8/1.0		
O. subtriquetra	4.8/1.9-9.0/-	2.8/0.5-6.4/-		

Hyphen "-" represents a posterior probability (PP) < 0.8.

**Figure 2** and **Table 2**). The majority of species of *Onnia* emerged in the Neogene, especially in the Pliocene. *Onnia tomentosa* is the oldest species with a mean stem age of 28.6 Mya (95% HPD of 15.5–46.2 Mya), while *O. triquetra* and *O. himalayana* are younger than the other species with a stem age of 3.2 Mya (95% HPD of 0.7–7.1 Mya).

#### The Historical Biogeography of Onnia

Inferred historical biogeography scenarios using RASP are shown in **Figure 3**. The RASP analysis suggests that Asia is the center of origin of the genus Onnia, and suggests that five dispersal events (three from Asia to Europe, and two from Asia to North America) and two vicariance (Eurasia and North America) events occurred during the distribution of this genus. Six species are found in Asia, three in Europe, and two in North America, suggesting that Asia is still the center of Onnia species. Moreover, there are three species, O. tomentosa, O. tibetica, and O. himalayana, distributed in southwest China, which implies that this region may be a more precise center of origin within Asia. Indeed, a total of 15 specimens of O. tomentosa, namely, six in North America, five in Asia, and four in Europe, have been collected (Figure 4 and Table 1). The dataset of ancestral state reconstruction suggested that Asia is the ancestral area (Figure 4). Meanwhile, possible concealed dispersal routes were inferred (Figure 3B): (1) Asia to North America and (2) Asia to Europe.

#### Taxonomy

Onnia himalayana Y.C. Dai, H. Zhao and Meng Zhou, sp. nov. (Figure 5).

*MycoBank*: MB: 844317.

*Type*: CHINA. Yunnan Province, Dali, Cangshan Geopark, on root of *Pinus yunnanensis*, 30 VIII 2021, Dai 22620 (Holotype, BJFC037194).

*Etymology: Himalayana* (Lat.), refers to the species being found in the eastern Himalayan area.



FIGURE 3 | (A) Ancestral state reconstruction and divergence time estimation of *Onnia* using a dataset containing ITS, LSU rDNA, *rpb1*, *rpb2*, and *tef1*α sequences. A pie chart at each node indicates the possible ancestral distributions inferred from dispersal-extinction-cladogenesis (DEC) analysis implemented in RASP. A black asterisk represents other ancestral ranges. (B) Possible dispersal routes of *Onnia* in the Northern hemisphere. Regions are labeled as follows: (A) Asia, (B) Europe, (C) North America, (AB) Asia and Europe, (AC) Asia and North America, (BC) Europe and North America, and (ABC) Asia, Europe, and North America.



chart at each node indicates the possible ancestral distributions inferred from dispersal-extinction-cladogenesis (DEC) analysis implemented in RASP. A black asterisk represents other ancestral ranges. Regions are labeled as follows: (A) Asia, (B) Europe, (C) North America, (AB) Asia and Europe, (AC) Asia and North America, and (BC) Europe and North America.

Basidiocarps annual, laterally to centrally stipitate, solitary, without odor or taste and corky when fresh, becoming hard corky upon drying. Pilei dimidiate to circular, projecting up to 3 cm, 4 cm wide, and 8 mm thick at the center. Pileal surface clay buff with cream to buff margin, velutinate, and azonate when fresh, becoming cinnamon, homogeneous, distinctly velutinate, and azonate when dry; margin sharp, curving downward when dry. Pore surface clay pink when fresh, becoming fulvous when dry, sterile margin distinct, up to 2 mm wide; pores angular, 3-4 per mm; and dissepiments thin, strongly lacerate to dentate. Context duplex, upper layer fulvous, more or less spongy, up to 4 mm thick, lower layer umber, hard corky, up to 2 mm thick, no demarcation zone between the two layers. Tubes are concolorous with pores, hard corky, and up to 2 mm long. Stipe clay buff, hard corky when dry, velutinate, up to 1 cm long, 8 mm diam; pores decurrent on the stipe.

Hyphal system monomitic, generative hyphae simple septate, IKI-, CB-; tissues darkening but otherwise unchanged in KOH. Context: hyphae in the upper layer are pale yellowish to golden yellow, slightly thick-walled, occasionally branched, frequently simple septate, straight, regularly arranged, and 5–7  $\mu$ m diam; hyphae in the lower layer are yellowish to golden brown, slightly thick- to thick-walled, occasionally branched, with frequent simple septa, straight, regularly arranged, not agglutinated, and 4–5.5  $\mu$ m diam; hyphae in stipe similar to those in context. Tubes: Tramal hyphae hyaline to yellowish, thin- to slightly thick-walled, rarely branched, frequently septate, more or less flexuous, subparallel along the tubes, not agglutinated, and 2.5–4.5  $\mu$ m diam.

Hymenium: Setae hooked, sharply pointed at apex, dark brown, thick-walled, deep-rooting, embedded in trama and projecting from hymenium, and  $40-78 \times 14-20 \ \mu\text{m}$ ; cystidia and cystidioles absent; basidia clavate, with four sterigmata and a simple septum at the base,  $12-15 \times 5-6 \ \mu\text{m}$ ; and basidioles dominant, in shape similar to basidia, but slightly smaller. Basidiospores ellipsoid to oblong-ellipsoid, hyaline, thin-walled, smooth, IKI-, CB-,  $5-6 \times 3.2-4$  (-4.1)  $\mu$ m,  $L = 5.62 \ \mu$ m,  $W = 3.63 \ \mu$ m, and Q = 1.55 (n = 30/1).



## DISCUSSION

The discovery of new fungal species has rapidly increased with the development of molecular techniques, drawing attention to the huge fungal diversity that exists on earth (Cui et al., 2019; He et al., 2019; Wu et al., 2020, 2022; Dai et al., 2021; Wang K. et al., 2021; Zhang and Dai, 2021; Ji et al., 2022). Hymenochaetaceae is a core family of macrofungi that consists of approximately 670 poroid species (Wu et al., 2022) and is an interesting subject for species diversity studies (Dai, 2010; Wu et al., 2020, 2022; Dai et al., 2021; Wang X. W. et al., 2022). Although *Onnia* is a small genus in this family, some species of *Onnia* are important pathogenic fungi that cause Tomentosus Root Rot on trees of *Picea* and *Pinus* (Hunt and White, 1998; Germain et al., 2009; Dai, 2010; Ji et al., 2017). As species distribution of *Onnia* is usually closely related to host trees (Ji et al., 2017; Wu et al., 2022), the genus is ideal for studying species diversity, divergence times, and biogeography.

Currently, dating analyses have provided a deep insight into the evolution of macrofungi using multigene analyses (Zhao et al., 2017; He et al., 2019; Varga et al., 2019). Our analysis of divergence times using a dataset of two ribosomal RNA genes (ITS and LSU rDNA) and three protein-coding genes (rpb1, rpb2, and tef1a) suggests that Onnia and Porodaedalea possibly emerged in the Paleogene with a mean stem age of 56.9 Mya (95% HPD of 35.9-81.6 Mya) and full support (1.0 PP; Figure 2 and Table 2). Considering the divergence estimation of Pinaceae (206 Mya) and the fossil record of Hymenochaetaceae (125 Mya), this estimation of Onnia and Porodaedalea seems reasonable (Smith et al., 2004; Berbee and Taylor, 2010; Magallón et al., 2015; Ran et al., 2018). Moreover, the basal modern species, O. tomentosa, occurred in 28.6 Mya, which is consistent with the timing of the second pulse of rapid uplift of the Qinghai-Tibet Plateau (between 20 and 30 Mya; Wang et al., 2012, 2018). Most species of Onnia emerged about 5 Mya (Figure 2 and Table 2), i.e., late Miocene to Pliocene, and adapted to a low temperature, facilitating survival in the Quaternary Ice Age.

Biogeographic studies of macrofungi have been very successful for ectomycorrhizal fungi, such as Amanita (see Sánchez-Ramírez et al., 2015; Truong et al., 2017), saprotrophic Lentinula (see Hibbett et al., 1998), and pathogenic fungi, e.g., Heterobasidion (Chen et al., 2015) based on molecular analyses. Our results suggest that the species distribution of Onnia has a distinct biogeographical pattern, similar to other wood-decaying fungi (Sato et al., 2017; Han et al., 2018; Li et al., 2020). Species of Onnia appear to have originated in Asia, especially in the Hengduan-Himalayan region which is a global biodiversity hotspot, and this conclusion supports previous studies on the origination of wood-decaying fungi (Song et al., 2016; Li et al., 2020; Wang X. W. et al., 2022). Three species, O. himalayana, O. tibetica, and O. tomentosa, occur in the Hengduan-Himalayan region. The basal species, O. tomentosa, emerged at 28.6 Mya (Figure 2 and Table 2), and maybe dispersal occurred between East Asia and North America via the Beringia (Bering Land Bridge). However, a vicariance event, such as the opening of the Bering Strait, could limit gene flow and species dispersal in the Old World and the New World (Hibbett, 2001; Cai et al., 2014; Li et al., 2020).

## CONCLUSION

In this study, our dataset of divergence times suggests that *Onnia* and *Porodaedalea* possibly emerged in the Paleogene. Most species of *Onnia* emerged in the late Miocene to Pliocene and adapted to a low temperature, and therefore survived in the Quaternary Ice Age. Species appear to have originated in the coniferous forests of southwest China, then spread across the Northern Hemisphere with host plants. Geographic separation

led to a diversification of new species in the Old World and New World. A total of nine species are recognized, namely, eight species that grow on gymnosperms and one species that grows on angiosperms. Furthermore, a new species, *Onnia himalayana*, is proposed and illustrated based on phylogenetic and morphological evidence.

#### DATA AVAILABILITY STATEMENT

All the sequences have been deposited in GenBank; the accession numbers are listed in **Table 1**.

## **AUTHOR CONTRIBUTIONS**

HZ: data analyses, formal analyses, conceived the ideas, and original draft and review. MZ: data curation and the draft of new species. X-YL: review and editing. FW: project administration

#### REFERENCES

- Akata, I., Dogan, H. H., Cetin, B., and Isiloglu, M. (2009). Onnia tomentosa Fr. P. Karst, a new genus record for Turkey. Biol. Divers. Conserv. 2, 78–81.
- Anonymous (1969). Flora of British Fungi. Colour Identification Chart. London, UK: Her Majesty's Stationery Office, 1–3.
- Berbee, M. L., and Taylor, J. W. (2010). Dating the molecular clock in fungi how close are we? *Fungal Biol. Rev.* 24, 1–16. doi: 10.1016/j.fbr.2010.03.001
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C. H., Xie, D., et al. (2014). BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* 10:e1003537. doi: 10.1371/journal.pcbi.1003537
- Cai, Q., Tulloss, R. E., Tang, L. P., Tolgor, B., Zhang, P., Chen, Z. H., et al. (2014). Multi-locus phylogeny of lethal amanitas: implications for species diversity and historical biogeography. *BMC Evol. Biol.* 14:143. doi: 10.1186/1471-2148-14-143
- Cao, Y., Wu, S. H., and Dai, Y. C. (2012). Species clarification of the prize medicinal *Ganoderma* mushroom "Lingzhi". *Fungal Divers.* 56, 49–62. doi: 10.1007/s13225-012-0178-5
- Chen, J. J., Cui, B. K., Zhou, L. W., Korhonen, K., and Dai, Y. C. (2015). Phylogeny, divergence time estimation, and biogeography of the genus *Heterobasidion* (*Basidiomycota, Russulales*). *Fungal Divers.* 71, 185–200. doi: 10.1007/s13225-014-0317-2
- Cui, B. K., Li, H. J., Ji, X., Zhou, J. L., Song, J., Si, J., et al. (2019). Species diversity, taxonomy and phylogeny of Polyporaceae (*Basidiomycota*) in China. *Fungal Divers*. 97, 137–392. doi: 10.1007/s13225-019-00427-4
- Dai, Y. C. (2010). Hymenochaetaceae (Basidiomycota) in China. Fungal Divers. 45, 131–343. doi: 10.1007/s13225-010-0066-9
- Dai, Y. C., Yang, Z. L., Cui, B. K., Wu, G., Yuan, H. S., Zhou, L. W., et al. (2021). Diversity and systematics of the important macrofungi in Chinese forests. *Mycosystema* 40, 770–805. doi: 10.13346/j.mycosystema.21 0036
- Germain, H., Bergeron, M. J., Bernier, L., Laflamme, G., and Hamelin, R. (2009). Patterns of colonization and spread in the fungal spruce pathogen *Onnia* tomentosa. Mol. Ecol. 18, 4422–4433. doi: 10.1111/j.1365-294X.2009.04370.x
- Han, L. H., Feng, B., Wu, G., Halling, R. E., Buyck, B., Yorou, N. S., et al. (2018). African origin and global distribution patterns: evidence inferred from phylogenetic and biogeographical analyses of ectomycorrhizal fungal genus *Strobilomyces. J. Biogeogr.* 45, 201–212. doi: 10.1111/jbi.13094
- Hawksworth, D. L., and Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiol. Spectr.* 5, 1–17. doi: 10.1128/microbiolspec.FUNK-0052-2016
- He, M. Q., Zhao, R. L., Hyde, K. D., Begerow, D., Kemler, M., and Yurkov, A. (2019). Notes, outline and divergence times of *Basidiomycota. Fungal Divers*. 99, 105–367. doi: 10.1007/s13225-019-00435-4

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- Hibbett, D. S. (2001). Shiitake mushrooms and molecular clocks: historical biogeography of *Lentinula*. J. Biogeogr. 28, 231–241. doi: 10.1046/j.1365-2699. 2001.00528.x
- Hibbett, D. S., and Matheny, P. B. (2009). The relative ages of ectomycorrhizal mushrooms and their plant hosts estimated using Bayesian relaxed molecular clock analyses. *BMC Biol.* 7:13. doi: 10.1186/1741-7007-7-13
- Hibbett, D. S., Grimaldi, D., and Donoghue, M. J. (1995). Cretaceous mushrooms in amber. *Nature* 377, 487–487. doi: 10.1038/377487a0
- Hibbett, D. S., Grimaldi, D., and Donoghue, M. J. (1997). Fossil mushrooms from Miocene and Cretaceous ambers and the evolution of Homobasidiomycetes. *Am. J. Bot.* 84, 981–991. doi: 10.2307/2446289
- Hibbett, D. S., Hansen, K., and Donoghue, M. J. (1998). Phylogeny and biogeography of *Lentinula* inferred from an expanded rDNA dataset. *Mycol. Res.* 102, 1041–1049. doi: 10.1017/S0953756297005996
- Hunt, R., and White, T. (1998). First report of *Inonotus tomentosus*, the cause of tomentosus root disease, from the Yukon Territory. *Plant Dis.* 82, 264–264. doi: 10.1094/PDIS.1998.82.2.264C
- Ji, X. H., He, S. H., Chen, J. J., Si, J., Wu, F., Zhou, L. W., et al. (2017). Global diversity and phylogeny of *Onnia (Hymenochaetaceae)* species on gymnosperms. *Mycologia* 109, 27–34. doi: 10.1080/00275514.2016.127 4619
- Ji, X., Zhou, J. L., Song, C. G., Xu, T. M., Wu, D. M., and Cui, B. K. (2022). Taxonomy, phylogeny and divergence times of Polyporus (*Basidiomycota*) and related genera. *Mycosphere* 13, 1–52. doi: 10.5943/mycosphere/13/1/1
- Jung, T., Horta Jung, M., Webber, J. F., Kageyama, K., Hieno, A., Masuya, H., et al. (2021). The destructive tree pathogen *Phytophthora ramorum* originates from the laurosilva forests of East Asia. *J. Fungi* 7:226. doi: 10.3390/jof7030226
- Karsten, P. (1889). Kritisk öfversigt af Finlands Basidsvampar (Basidiomycetes; Gastero- & Hymenomycetes). Bidrag till Kännedom af Finlands Natur och Folk 48, 1–470.
- Katoh, K., and Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30, 772–780. doi: 10.1093/molbev/mst010
- Krah, F. S., Bässler, C., Heibl, C., Soghigian, J., Schaefer, H., and Hibbett, D. S. (2018). Evolutionary dynamics of host specialization in wood-decay fungi. *BMC Evol. Biol.* 18:119. doi: 10.1186/s12862-018-1229-7
- Larsson, A. (2014). AliView: a fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics* 30, 3276–3278. doi: 10.1093/bioinformatics/ btu531
- Larsson, K. H., Parmasto, E., Fischer, M., Langer, E., Nakasone, K. K., and Redhead, S. A. (2006). Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. *Mycologia* 98, 926–936. doi: 10.1080/15572536.2006.11832622
- Li, J., Han, L. H., Liu, X. B., Zhao, Z. W., and Yang, Z. L. (2020). The saprotrophic *Pleurotus ostreatus* species complex: late Eocene origin in East Asia, multiple

dispersal, and complex speciation. *IMA Fungus* 11, 1–21. doi: 10.1186/s43008-020-00031-1

- Liu, Y. J., Whelen, S., and Hall, B. D. (1999). Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. *Mol. Biol. Evol.* 16, 1799–1808. doi: 10.1093/oxfordjournals.molbev.a026092
- Liu, Z. B., Wu, Y. D., Zhao, H., Lian, Y. P., Wang, Y. R., Wang, C. G., et al. (2022). Outline, divergence Times, and phylogenetic analyses of Trechisporales (*Agaricomycetes. Basidiomycota*). Front. Microbiol. 13:818358. doi: 10.3389/ fmicb.2022.818358
- Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., and Hernández-Hernández, T. (2015). A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytol.* 207, 437–453. doi: 10.1111/ nph.13264
- Matheny, P. B. (2005). Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; *Agaricales*). *Mol. Phylogenet. Evol.* 35, 1–20. doi: 10.1016/j.ympev.2004.11.014
- Matheny, P. B., Liu, Y. J., Ammirati, J. F., and Hall, B. D. (2002). Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, *Agaricales*). Am. J. Bot. 89, 688–698. doi: 10.3732/ajb.89.4.688
- Matheny, P. B., Wang, Z., Binder, M., Curtis, J. M., Lim, Y. W., and Henrik, N. R. (2007). Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (*Basidiomycota*, Fungi). *Mol. Phylogenet. Evol.* 43, 430–451. doi: 10.1016/ j.ympev.2006.08.024
- Page, R. D. (2003). Tangled Trees: Phylogeny, Cospeciation, and Coevolution. Chicago: University of Chicago Press.
- Petersen, J. H. (1996). The Danish Mycological Society's Colour-Chart. Greve: Foreningen til Svampekundskabens Fremme, 1–6.
- Posada, D., and Crandall, K. A. (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics* 14, 817–818. doi: 10.1093/bioinformatics/14.9.817
- Ran, J. H., Shen, T. T., Wu, H., Gong, X., and Wang, X. Q. (2018). Phylogeny and evolutionary history of Pinaceae updated by transcriptomic analysis. *Mol. Phylogenet. Evol.* 129, 106–116. doi: 10.1016/j.ympev.2018.08. 011
- Rehner, S. A., and Buckley, E. (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to *Cordyceps teleomorphs*. *Mycologia* 97, 84–98. doi: 10.1080/15572536.2006. 11832842
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., et al. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61, 539–542. doi: 10.1093/sysbio/ sys029
- Ryvarden, L., and Gilbertson, R. L. (1993). European polypores 1. Synopsis Fungorum 6, 1–387.
- Ryvarden, L., and Melo, I. (2014). Poroid fungi of Europe. Synopsis Fungorum 31, 1–455.
- Sánchez-Ramírez, S., Tulloss, R. E., Amalfi, M., and Moncalvo, J. M. (2015). Palaeotropical origins, boreotropical distribution and increased rates of diversification in a clade of edible ectomycorrhizal mushrooms (*Amanita* section Caesareae). J. Biogeogr. 42, 351–363. doi: 10.1111/jbi.12402
- Sato, H., Tanabe, A. S., and Toju, H. (2017). Host shifts enhance diversification of ectomycorrhizal fungi: diversification rate analysis of the ectomycorrhizal fungal genera *Strobilomyces* and *Afroboletus* with an 80-gene phylogeny. *New Phytol.* 214, 443–454. doi: 10.1111/nph.14368
- Seehausen, O., Butlin, R. K., Keller, I., Wagner, C. E., Boughman, J. W., Hohenlohe, P. A., et al. (2014). Genomics and the origin of species. *Nat. Rev. Genet.* 15, 176–192. doi: 10.1038/nrg3644
- Shen, L. L., Chen, J. J., Wang, M., and Cui, B. K. (2016). Taxonomy and multigene phylogeny of *Haploporus (Polyporales, Basidiomycota)*. Mycol. Prog. 15, 731–742. doi: 10.1007/s11557-016-1203-y
- Smith, S. Y., Currah, R. S., and Stockey, R. A. (2004). Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia. *Mycologia* 96, 180–186. doi: 10.1080/15572536.2005.11833010
- Song, J., Chen, J. J., Wang, M., Chen, Y. Y., and Cui, B. K. (2016). Phylogeny and biogeography of the remarkable genus *Bondarzewia* (*Basidiomycota*, *Russulales*). Sci. Rep. 6, 1–10. doi: 10.1038/srep34568
- Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313. doi: 10.1093/ bioinformatics/btu033

- Swofford, D. L. (2002). PAUP\*: Phylogenetic Analysis Using Parsimony (\* and Other Methods); Version 4.0b10. Sunderland, MA: Sinauer Associates.
- Taylor, T. N., Hass, H., and Kerp, H. (1999). The oldest fossil ascomycetes. *Nature* 399, 648–648. doi: 10.1038/21349
- Taylor, T. N., Hass, H., Kerp, H., Krings, M., and Hanlin, R. T. (2005). Perithecial ascomycetes from the 400 million year old Rhynie chert: an example of ancestral polymorphism. *Mycologia* 97, 269–285. doi: 10.1080/15572536.2006.11832 862
- Truong, C., Sánchez-Ramírez, S., Kuhar, F., Kaplan, Z., and Smith, M. E. (2017). The Gondwanan connection – Southern temperate Amanita lineages and the description of the first sequestrate species from the Americas. Fungal Biol. 121, 638–651. doi: 10.1016/j.funbio.2017.04.006
- Varga, T., Krizsán, K., Földi, C., Dima, B., Sánchez-García, M., Sánchez-Ramírez, S., et al. (2019). Megaphylogeny resolves global patterns of mushroom evolution. *Nat. Ecol. Evol.* 3, 668–678. doi: 10.1038/s41559-019-0834-1
- Wagner, T., and Fischer, M. (2001). Natural groups and a revised system for the European poroid Hymenochaetales (*Basidiomycota*) supported by nLSU rDNA sequence data. *Mycol. Res.* 105, 773–782. doi: 10.1017/S0953756201004257
- Wagner, T., and Fischer, M. (2002). Proceedings towards a natural classification of the worldwide taxa. *Phellinus* sl and *Inonotus* sl, and phylogenetic relationships of allied genera. *Mycologia* 94, 998–1016. doi: 10.1080/15572536.2003.11833156
- Wang, E., Kirby, E., Furlong, K. P., van Soest, M., Xu, G., Shi, X., et al. (2012). Twophase growth of high topography in eastern Tibet during the Cenozoic. *Nat. Geosci.* 5, 640–645. doi: 10.1038/ngeo1538
- Wang, K., Chen, S. L., Dai, Y. C., Jia, Z. F., Li, T. H., Liu, T. Z., et al. (2021). Overview of China's nomenclature novelties of fungi in the new century (2000-2020). *Mycosystema* 40, 822–833.
- Wang, K., Kirk, P. M., and Yao, Y. J. (2020). Development trends in taxonomy, with special reference to fungi. J. Syst. Evol. 58, 406–412. doi: 10.1111/jse.12538
- Wang, X. W., Jiang, J. H., Liu, S. L., Gafforov, Y., and Zhou, L. W. (2022). Species diversification of the coniferous pathogenic fungal genus *Coniferiporia* (*Hymenochaetales, Basidiomycota*) in association with its biogeography and host plants. *Phytopathology* 112, 404–413. doi: 10.1094/PHYTO-05-21-0181-R
- Wang, X. W., May, T. W., Liu, S. L., and Zhou, L. W. (2021). Towards a natural classification of *Hyphodontia* sensu lato and the trait evolution of basidiocarps within Hymenochaetales (*Basidiomycota*). J. Fungi 7:478. doi: 10. 3390/jof706048
- Wang, Z. X., Shen, Y. J., and Pang, Z. B. (2018). Three main stages in the uplift of the Tibetan Plateau during the Cenozoic period and its possible effects on Asian aridification: a review. *Clim. Past Discuss.* [Preprint]. doi: 10.5194/cp-2018-64
- White, T. J., Bruns, T., Lee, S., and Taylor, J. (1990). "Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics," in *PCR Protocols:* a Guide to Methods and Applications eds M. A. Innis, D. H. Gelfand, J. J. Sninsky, and T. J. White (New York, NY: Academic Press), 315–322.
- Wu, F., Yuan, H. S., Zhou, L. W., Yuan, Y., Cui, B. K., and Dai, Y. C. (2020). Polypore diversity in South China. *Mycosystema* 39, 653–681. doi: 10.13346/j. mycosystema.200087
- Wu, F., Zhou, L. W., Josef, V., and Dai, Y. C. (2022). Global diversity and systematics of *Hymenochaetaceae* with poroid hymenophore. *Fungal Divers*. 113, 1–192.
- Yu, Y., Blair, C., and He, X. (2020). RASP 4: ancestral state reconstruction tool for multiple genes and characters. *Mol. Biol. Evol.* 37, 604–606. doi: 10.1093/ molbev/msz257
- Yu, Y., Harris, A. J., Blair, C., and He, X. (2015). RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Mol. Phylogenet. Evol.* 87, 46–49. doi: 10.1016/j.ympev.2015.03.008
- Zhang, Q. Y., and Dai, Y. C. (2021). Taxonomy and Phylogeny of the Favolaschia calocera complex (Mycenaceae) with descriptions of four new species. Forests 12:1397. doi: 10.3390/f12101397
- Zhao, C. L., and Cui, B. K. (2013). Morphological and molecular identification of four new resupinate species of *Perenniporia (Polyporales)* from southern China. *Mycologia* 105, 945–958. doi: 10.3852/12-201
- Zhao, H., Nie, Y., Zong, T. K., Dai, Y. C., and Liu, X. Y. (2022a). Three new species of *Absidia (Mucoromycota)* from China based on phylogeny, morphology and physiology. *Diversity* 14:132. doi: 10.3390/d14020 132
- Zhao, H., Nie, Y., Zong, T. K., Wang, Y. J., Wang, M., Dai, Y. C., et al. (2022b). Species diversity and ecological habitat of *Absidia (Cunninghamellaceae*,

*Mucorales*) with emphasis on five new species from forest and grassland soil in China. J. Fungi 8:471. doi: 10.3390/jof8050471

- Zhao, H., Zhu, J., Zong, T. K., Liu, X. L., Ren, L. Y., Lin, Q., et al. (2021). Two new species in the family Cunninghamellaceae from China. *Mycobiology* 49, 142–150. doi: 10.1080/12298093.2021.1904555
- Zhao, R. L., Li, G. J., Sánchez-Ramírez, S., Stata, M., Yang, Z. L., Wu, G., et al. (2017). A six-gene phylogenetic overview of *Basidiomycota* and allied phyla with estimated divergence times of higher taxa and a phyloproteomics perspective. *Fungal Divers.* 84, 43–74.
- Zhou, M., and Wu, F. (2018). A new species of *Onnia (Hymenochaetales, Basidiomycota)* from Vietnam. *Phytotaxa* 349, 73–78. doi: 10.11646/phytotaxa. 349.1.9
- Zhou, M., Dai, Y. C., Vlasák, J., and Yuan, Y. (2021a). Molecular phylogeny and global diversity of the genus *Haploporus* (*Polyporales, Basidiomycota*). J. Fungi 7:96. doi: 10.3390/jof7020096
- Zhou, M., Wang, C. G., Wu, Y. D., Liu, S., and Yuan, Y. (2021b). Two new brown rot polypores from tropical China. *MycoKeys* 82, 173–197. doi: 10.3897/ mycokeys.82.68299
- Zong, T. K., Zhao, H., Liu, X. L., Ren, L. Y., Zhao, C. L., and Liu, X. Y. (2021). Taxonomy and. phylogeny of four new species in *Absidia (Cunninghamellaceae*,

*Mucorales*) from China. *Front. Microbiol.* 12:677836. doi: 10.3389/fmicb.2021. 677836

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