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ARTICLE

Systematic revision, molecular phylogeny and divergence times of Thelephorales (Basidiomycota)

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Abstract

Thelephorales is an important order of macro-fungi belonging to Basidiomycota. Species in this order play an essential role in the biogeochemical cycle in forest ecosystems and bring an essential economic value in developing and utilizing edible and medicinal fungal resources. In this study, the classification system of Thelephorales was revised based on morphological and phylogenetic analyses. The DNA sequences of multiple loci, including the internal transcribed spacer (ITS) regions, the large subunit of nuclear ribosomal RNA gene (nLSU), the small subunit of nuclear ribosomal RNA gene (nSSU), and the second largest subunit of RNA polymerase II gene (RPB2) were used to construct phylogenetic relationships and infer the divergence time of Thelephorales. The phylogenetic analyses revealed that six clades at the family level were obtained in Thelephorales with high supports. The ancestor of Thelephorales split at about 269.07 Mya, and the mean stem ages of the families of Thelephorales were centralized differentiation in 145.95–269.07 Mya. Combined with morphological studies, Thelephorales were confirmed to comprise six families, including four new families: Lenzitopsidaceae, Polyozellaceae, Sarcodonaceae, Tomentellopsidaceae, and two existing families: Bankeraceae and Thelephoraceae. There are twelve identified genera viz. *Amaurodon*, *Boletopsis*, *Corneroporus*, *Hydnellum*, *Lenzitopsis*, *Neosarcodon*, *Odontia*, *Sarcodon*, *Phellodon*, *Polyozellus*, *Thelephora*, and *Tomentellopsis*. Furthermore, 20 new species were described, and 4 new combinations were proposed. Illustrated descriptions and scanning electron micrographs of the basidiospores of the new species were provided. Keys to Thelephorales and the accepted families, and the notes of the accepted genera in Thelephorales were also provided.

Keywords – ectomycorrhizal fungi – Thelephorales – multi-gene phylogeny – taxonomy – evolution

INTRODUCTION

Thelephorales Corn ex. Oberw., a member of the Agaricomycetes (Basidiomycota), was established by Oberwinkler in 1976. Species in Thelephorales were characterized by pileus vary in shape, including resupinate, effused-reflexed, spathulate, imbricate-spathulate, flabellate, or infundibuliform; hymenophores vary to poroid, lamellate, aculeate, or smooth; and basidiospores colorless to strongly pigmented, non-amyloid, warted to typically echinulate (Stalpers 1993, Kõljalg 1996, Yorou 2008, Hibbett et al. 2014, Vizzini et al. 2016).

Thelephorales species play a vital role in the ecosystem. Many species of Thelephorales are ectomycorrhizal (EcM) fungi, which can form an outer sheath around the root of the plant, and the

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hyphae penetrate the space between the root cortex cells and the epidermal cells form a Hartig network. (Smith & Read 2008, Vasco-Palacios 2018). In addition, most Thelephorales species, as EcM fungi, can absorb organic compounds from host plants (Smith & Read 2008), and increase the surface area of host plants to absorb nutrients, especially nitrogen and phosphorus (Agerer 2006, Smith & Read 2008). Therefore, Thelephorales species can participate in the energy flow and promote the material circulation of the ecosystem.

Some Thelephorales species are delicious edible fungi or biologically active fungi, which have substantial economic value in developing and utilizing edible and medicinal fungi resources. For example, *Sarcodon imbricatus* (L.) P. Karst. and *Thelephora ganbajun* M. Zang are staples at the edible mushroom market in southwest China and are very popular with the locals. Some species have biological activities, such as *Hydnellum concrescens* (Pers.). Banker and *Phellodon melaleucus* (Sw. ex Fr.) P. Karst., the former has an inhibitory action on syncytium formation, trafficking of glycoprotein and hemagglutinin-neuraminidase (HN) to the cell surface (Lee et al. 2012), while the latter has a unique antibiotic named Phellodonic Acid, isolated by Stadler et al. (1993).

The genera contained in Thelephorales have been much debated for a long time. Stalpers (1993) conducted a systematic study of Thelephorales and proposed that it contains 15 genera representing two families: Bankeraceae and Thelephoraceae. The first family, Bankeraceae, contains *Bankera* Coker & Beers ex Pouzar, *Boletopsis* Fayod, *Hydnellum* P. Karst., *Phellodon* P. Karst., *Sarcodon* Que´l. ex P. Karst; and Thelephoraceae contains *Botryohypochnus* Donk, *Lenzitopsis* Malencon & Bertault, *Polyozellus* Murrill, *Pseudotomentella* Svrček, *Skepperia* Berk., *Thelephora* Ehrh. Ex Willd., *Tomentella* Pers. Ex Pat., *Tomentellago* Hjortstam & Ryvarden, *Tomentellopsis* Hjortstam, *Tylospora* Donk. Recently, He et al. (2019) elucidated all valid publications of Basidiomycetes and suggested that Thelephorales contains 16 genera, of which *Bankera*, *Boletopsis*, *Corneroporus* T. Hatt., *Hydnellum*, *Sarcodon* are contained in Bankeraceae, while *Amaurodon* J. Schröt, *Gymnoderma* Humb., *Lenzitopsis*, *Parahaplotrichum* W.A. Baker & Partr., *Phellodon*, *Polyozellus*, *Pseudotomentella*, *Skepperia* Berk., *Thelephora*, *Tomentella*, *Tomentellopsis* are contained in Thelephoraceae. Compared with Stalpers (1993), He et al. (2019) eliminated three genera (*Botryohypochnus, Tylospora,* and *Tomentellago*) and added three genera (*Gymnoderma*, *Parahaplotrichum,* and *Skepperia*) in Thelephorales. However, the genera *Botryohypochnus* and *Tylospora* at present have been classified into Cantharellales and Atheliales, respectively, according to MycoBank (https://www.mycobank.org). *Bankera* and *Tomentellago* were combined into *Phellodon* and *Amaurodon*, respectively, which were still members of Thelephorales (Baird et al. 2013, Kõljalg 1996). At the same time, due to the lack of molecular sequences and descriptions of *Gymnoderma*, *Parahaplotrichum*, and *Skepperia*, further research cannot be carried out for the time being to clarify the phylogenetic relationships of the three genera. In addition, a distinct clade, "*Neosarcodon*" was informally defined in the ITS sequence analysis (Larsson et al. 2019). Moreover, the recent study of Wang et al. (2024) formally introduced *Neosarcodon* as a genus by moving nine species from *Sarcodon* to *Neosarcodon* and revised the delimitation of *Sarcodon* based on phylogenetic and morphological analyses. What's more, Kõljalg (1996) proposed the concept of "tomentelloid fungi" to cover a group of fungi that share similar morphological characteristics with *Tomentella*, including four genera: *Amaurodon*, *Odontia*, *Pseudotomentella*, and *Tomentellopsis*. However, the genus *Odontia* was not contained in the Thelephorales in the above two systematic studies (Stalpers 1993, He et al. 2019). Tedersoo et al. (2014) confirmed that *Odontia* is a non-mycorrhizal sister genus of *Tomentella* and *Thelephora* based on stable isotope analysis, field observations, and synthetic experiments. Considering the lack of evidence at the molecular level of the previous studies (Stalpers 1993, He et al. 2019), in this study, we included *Odontia* in the phylogenetic study of Thelephorales to clarify its taxonomic status.

Many genera of Thelephorales are phylogenetically paraphyletic and have been revised in recent years. Baird et al. (2013) confirmed that *Bankera* and *Phellodon* are phylogenetically paraphyletic and recombined the typified species *Bankera fuligineoalba* (J.C. Schmidt) Pouzar to

Phellodon, according to morphological studies and phylogenetic analyses. Since then, *Bankera* has been combined into *Phellodon*, and the type genus of Bankeraceae has been changed to *Phellodon*. Previously, molecular evidence has confirmed that *Hydnellum* and *Sarcodon* in Bankeraceae were paraphyletic, both genera aggregated in the same clade, named the "*Hydnellum-Sarcodon* lineage" (Binder et al. 2005). However, Baird et al. (2013) suggested that the generic limits of *Hydnellum* and *Sarcodon* need reassessment. Later, Larsson et al. (2019) conducted a systematic study to reassess the generic limits for *Hydnellum* and *Sarcodon*, and transferred twelve species from *Sarcodon* to *Hydnellum* based on ITS and nLSU sequences. Moreover, *Polyozellus* and *Pseudotomentella* were two closely related genera in Thelephoraceae (Svantesson et al. 2021). Morphologically, *Polyozellus* differs from *Pseudotomentella* by its pileate and stipitate basidiomata. Svantesson et al. (2021) redefined the generic delimitation of the two genera based on a multi-gene dataset and recombined nearly all *Pseudotomentella* species to *Polyozellus*. Recently, Kõljalg et al. (2024) merged the genus *Tomentella* into *Thelephora* and proposed 191 new combinations.

With the rapid development of molecular techniques in recent years, DNA sequence data have been widely used in the taxonomic studies of Thelephorales. Baird et al. (2013) conducted a systematic study on the species diversity and classification of stipitate hydroids in the southern region of the United States, describing 41 species and constructing phylogenetic trees using ITS fragments. Li (2017) systematically studied Bankeraceae from Korea, describing 17 species, including three new and seven uncertain species in his master's thesis. He et al. (2024) analyzed all the valid literatures of Basidiomycota and confirmed that Thelephorales included 17 genera and ca. 470 species. However, due to the lack of molecular sequences, there were no systemic phylogenetic studies for the entire Thelephorales, and only some studies on specific genera (Yorou et al. 2011a, b, Vizzini et al. 2016, Khalid & Muhammad 2017, Voitk et al. 2017, Yuan et al. 2018, Svantesson et al. 2019, 2021, 2022, Mu et al. 2021, Liu et al. 2021, Lu et al. 2022, Kuhar et al. 2022, Yang et al. 2023). So far, no phylogenetic studies have been conducted on the entire Thelephorales.

Recently, divergence time was used as an essential criterion for the classification and estimation of evolutionary time in Basidiomycota (Zhao et al. 2016, 2017, He et al. 2019; Ji et al. 2022, Liu et al. 2023b, c). Hennig (1966) proposed the divergence time to recognize different taxonomic ranks, which can be used as a standardized criterion in the systematics of all known organisms. This conception was first used to study fish, anthropoid primates and fruit flies at the end of 20th century (Avise & John 1999). Zhao et al. (2017) recently confirmed that the mean stem ages of Basidiomycota and Entorrhizomycota are ca. 530 million years ago (Mya). Liu et al. (2023b) confirmed that Polyporales appeared in the early Cretaceous (about 141.55 Mya). However, no comprehensive study focused on the divergence time of Thelephorales.

This study aims to revise the classification, phylogenetic relationships, and divergence time of the Thelephorales and describe the new taxa of *Hydnellum*, *Neosarcodon*, *Phellodon*, *Sarcodon*, and *Thelephora* based on extensive morphological examinations of more specimens from China and some other countries, combined with analyses of multi-gene sequences data. The phylogeny and divergence time of Thelephorales were reconstructed and analyzed based on DNA sequences of multiple loci, including ITS, nLSU, nSSU and RPB2 genes. Based on morphological studies and phylogenetic analyses, twelve genera belonging to six families were accepted within the Thelephorales, including four new families, 20 new species, and 4 new combinations.

MATERIALS AND METHODS

Morphological studies

The examined specimens were deposited at the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC) and the Institute of Applied Ecology, Chinese Academy of Sciences (IFP). Morphological descriptions and abbreviations used in this study following Sun et al. (2020, 2022). Samples for microscopic examination were stained in cotton blue, Melzer's reagent, and observed at magnifications up to ×100 under a light microscope (Nikon Eclipse E 80i

microscope, Nikon, Tokyo, Japan) following Sun et al. (2022). A field Emission Scanning Electron Microscope (FESEM) Hitachi SU-8010 (Hitachi, Ltd., Tokyo, Japan) was used to photograph the morphology of the basidiospores. Sections were studied at magnifications up to 2000× following Sun et al. (2022). The following abbreviations were used: L = mean spore length, W = mean spore width, Q = L/W ratio, n (a/b) = number of spores (a) measured from given number of specimens (b), IKI = Melzer's reagent, IKI– = negative in Melzer's reagent, KOH = 5% potassium hydroxide, CB = Cotton Blue, CB+ = cyanophilous, CB− = acyanophilous.

DNA extraction, PCR amplification and sequencing A CTAB plant genome rapid extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd) was employed for DNA extraction and PCR amplification from dried specimens according to the manufacturer's instructions with some modifications (Liu et al. 2023a). The primer pairs ITS5/ITS4, LR0R/LR7, NS1/NS4 and 5F/7Cr were used to amplify ITS, nLSU, nSSU and RPB2 gene loci, respectively.

The Polymerase Chain Reaction (PCR) procedure for ITS was as follows: initial denaturation at 95 ℃ for 3 min, followed by 35 cycles at 94 ℃ for 40 s, 56 ℃ for 45 s, and 72 ℃ for 1 min, and a final extension of 72 ℃ for 10 min. The PCR procedure for nLSU and nSSU was as follows: initial denaturation at 94 ℃ for 1 min, followed by 35 cycles at 94 ℃ for 30 s, 50 ℃ for 1 min, and 72 ℃ for 1.5 min, and a final extension of 72 ℃ for 10 min. The PCR procedure for RPB2 was as follows: initial denaturation at 94 ℃ for 2 min, nine cycles at 94 ℃ for 45 s, 60 ℃ for 45 s, followed by 36 cycles at 94 ℃ for 45 s, 53 ℃ for 1 min, 72 ℃ for 1.5 min and a final extension of 72 ℃ for 10 min. The PCR products were purified and sequenced with the same primers at the Beijing Genomics Institute, China. The newly generated sequences were deposited at GenBank. All sequences analyzed in this study were listed in Table 1.

Table 1. A list of species, specimens and GenBank accession numbers of the sequences used in this study.

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Agaricus campestris	LAPAG370	-	KM657927	KR006607		KT951556
Aphanobasidium pseudotsugae	CFMR: HHB-822	USA	GU187509	GU187567	GU187620	GU187781
Amaurodon angulisporus	SYN2217	Burkina Faso	-	FR823360	-	-
Amaurodon aquicoeruleus	UK 452	Australia	AM490944	AM490944	-	-
Amaurodon caeruleocaseus	PERTH06670709	Australia	MT565478	-	-	-
Amaurodon caeruleocaseus	MEL2231735	Australia	KP311335	KP311452	-	-
Amaurodon hydnoides	LR37576	Venezuela	AM490941	AM490941	-	-
Amaurodon sumatranus	TU115407	Malaysia	-	MT737304	-	OK632661
Amaurodon viridis	TAA149664	Russia	AM490942	AY586625	-	-
Amaurodon viridis	TU115739	Italy	-	OK559560	OK559673	-
Amaurodon viridis	KHLarsson14947b	Norway	MK602707	MK602707	-	-
Amylocorticium cebennense	CFMR: HHB-2808	USA	GU187505	GU187561	GU187612	GU187770
Antrodia tanakae	Cui 9743	China	KR605814	KR605753	KR605914	KR610833
Athelia epiphylla	CFMR: FP-100564	USA	GU187501	GU187558	GU187613	GU187771
Boletopsis grisea	AH42971	Spain	MN536748	MN536743	-	-
Boletopsis grisea	AH44091	Spain	MN536747	MN536742	-	-
Boletopsis grisea	Dai 23070	China	OL673003	OL672990	**OR761700**	**PP545350**
Boletopsis grisea	Cui 23076	USA	**OR761684**	**OR761804**	**OR761701**	-
Boletopsis leucomelaena	UPSF173290	Sweden	MN536739	MN536738	-	-
Boletopsis leucomelaena	UPSF575617	Sweden	MN536740	MN536739	-	-
Boletopsis macrocarpa	Dai 21780	China	OL673004	OL672991	-	-
Boletopsis macrocarpa	Dai 22727	China	OL673007	OL672994	**OR761702**	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Boletopsis macrocarpa	Dai 22728	China	OL673005	OL672992	**OR761703**	-
Boletopsis macrocarpa	Dai 22729	China	OL673006	OL672993	**OR761704**	-
Boletopsis macrocarpa	Dai 22748	China	OL673008	OL672995	**OR761705**	**PP545351**
Boletopsis mediterraneensis	AH44070	Spain	MN536724	MN535630	-	-
Boletopsis mediterraneensis	AH44080	Spain	MN536723	MN535629	-	-
Boletopsis nothofagi	PDD96007	New Zealand	JQ417193	-	-	-
Boletopsis sp.	Dai 22172	China	OL673011	OL672998	-	-
Boletopsis tibetana	Dai 20896	China	OL673012	OL672999	-	-
Boletopsis tibetana	Dai 20897	China	OL673013	OL673000	-	-
Boletopsis watlingii	Wat 28788	UK	DQ408767	-	-	-
Boletopsis watlingii	HoldenE150627	UK	DQ408766	-	-	-
Boletopsis watlingii	SMI350	Canada	FJ845401	-	-	-
Boletus edulis	HMJAU4637	-	JN563894	KF112455	-	KF112704
Bondarzewia sp.	Yu 56	China	KT693203	KT693205	-	-
Callistosporium graminicolor	AFTOL-ID 978	USA	DQ484065	AY745702	AY752974	KJ424369
Cotylidia sp.	MB5	-	AY854079	AY629317	AY705958	AY883422
Clavulicium macounii	GB: KHL12129	Sweden	-	KC203494	-	-
Geastrum recolligens	OSC41996	-	-	DQ218486	-	DQ219052
Gloeophyllum sepiarium	Wilcox-3BB	USA	HM536091	HM536061	HM536062	HM536109
Hydnellum ailaoense	HKAS 125553	China	OP602211	OP605523	-	-
Hydnellum ailaoense	HKAS 125554	China	OP602212	OP605520	-	-
Hydnellum ailaoense	Dai 19998	China	**OR761639**	**OR761762**	-	-
Hydnellum amygdaliolens	GB-0202072	France	MW144290	MW144290	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Hydnellum amygdaliolens	SC-2011	-	JN376763	-	-	-
Hydnellum atrorubrum	Wei 8315	China	MW579937	-	-	-
Hydnellum atrorubrum	Wei 8261	China	MW579936	MW579884	MW579910	-
Hydnellum atrospinosum	Yuan 6514	China	MW579940	MW579886	MW579913	-
Hydnellum atrospinosum	Dai 24519	China	**OR761640**	**OR761763**	**OR761706**	**PP545352**
Hydnellum atrospinosum	Dai 24520	China	**OR761641**	**OR761764**	**OR761707**	**PP545353**
Hydnellum aurantiacum	RGCarlsson08-105	Sweden	MK602711	MK602711	-	-
Hydnellum aurantiacum	EBendiksen177-07	Norway	MK602712	MK602712	-	-
Hydnellum aurantiacum	Cui 16276	China	**OR761696**	**-**	**OR761708**	-
Hydnellum aurantiacum	Cui 18737	China	**OR761642**	**OR761765**	**-**	**-**
Hydnellum aurantiacum	Cui 23070	USA	**OR761685**	**OR761805**	**OR761709**	**PP545354**
Hydnellum auratile	OF294095	Norway	MK602714	MK602714	-	-
Hydnellum auratile	OF242763	Norway	MK602715	MK602715	-	-
Hydnellum bomiense	Yuan 13759	China	MW579941	MW579887	MW579914	OK254206
Hydnellum bomiense	Yuan 13767	China	MW579942	-	MW579915	-
Hydnellum brunneorubrum	Yuan 14339	China	MW57994 3	MW57988 8	MW579916	OK254216
Hydnellum brunneorubrum	Yuan 14668	China	MW57994 5	MW57989 0	MW579918	OK254218
Hydnellum brunneorubrum	Chen 447	China	**OR761643**	**OR761766**	**OR761710**	**PP545355**
Hydnellum brunneorubrum	Chen 449	China	**OR761644**	**OR761767**	**OR761711**	**PP545356**
Hydnellum caeruleum	OF291490	Norway	MK602717	MK602717	-	-
Hydnellum caeruleum	Cui 17100	China	**OR761645**	**OR761768**	**OR761712**	**PP545358**
Hydnellum caeruleum	Cui 17101	China	**OR761646**	**OR761769**	**OR761713**	**PP545359**
Hydnellum caeruleum	Cui 17013	China	**OR761647**	**OR761770**	**OR761714**	**PP545357**

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Hydnellum chocolatum	Cui 18545	China	ON603657	-	-	ON605665
Hydnellum chocolatum	Cui 18543	China	ON603656	ON603638	ON603646	-
Hydnellum chrysinum	SC071	-	KJ534291	-	-	-
Hydnellum chrysinum	Dai 18981	China	**OR761648**	**-**	**OR761715**	-
Hydnellum chrysinum	Cui 18756	China	**OR761649**	**OR761771**	**-**	-
Hydnellum cinnamomea	Cui 18743	China	**OR813988**	**OR814033**	**OR814068**	**PP545336**
Hydnellum cinnamomea	Cui 18740	China	**OR813989**	**OR814034**	**OR814069**	**PP545337**
Hydnellum cinnamomea	Cui 18755	China	**OR813990**	**OR814035**	**OR814070**	-
Hydnellum cinnamomea	Cui 18744	China	**OR813991**	**OR814036**	**OR814071**	-
Hydnellum coactum	Wei 8094	China	MN846278	MN846287	-	-
Hydnellum coactum	Shi 181	China	MN846279	MN846288	-	-
Hydnellum complicatum	REB-71	USA	KC571711	-	-	-
Hydnellum complicatum	REB-329	USA	KC571712	-	-	-
Hydnellum concentricum	Cui 17017	China	ON603658	ON603639	ON603647	ON605666
Hydnellum concentricum	Cui 17098	China	-	ON603640	ON603648	-
Hydnellum concrescens	REB-385	USA	JN135182	-	-	-
Hydnellum concrescens	REB-384	USA	KC571714	-	-	-
Hydnellum crassipileatum	Cui 17021	China	ON603660	ON603641	ON603649	ON605668
Hydnellum crassipileatum	Cui 17019	China	ON603659	ON603642	ON603650	-
Hydnellum cristatum	4446	Canada	KM406974	-	-	-
Hydnellum cristatum	REB-169	USA	JN135174	-	-	-
Hydnellum cumulatum	SEW 69	USA	AY569026	-	-	-
Hydnellum cumulatum	REB-342	USA	JN135172	-	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Hydnellum cyanopodium	SEW 85	USA	AY569027	-	-	-
Hydnellum decurrata	Cui 23050	USA	**OR813993**	**OR814038**	**OR814072**	**PP545339**
Hydnellum decurrata	Cui 23049	USA	**OR813992**	**OR814037**	**OR814073**	**PP545338**
Hydnellum decurrata	Cui 23052	USA	**OR813994**	**OR814039**	**OR814074**	**PP545340**
Hydnellum decurrata	Cui 23056	USA	**OR813995**	-	**OR814075**	**PP545341**
Hydnellum diabolus	KAH13873	Canada	AF351863	-	-	-
Hydnellum diabolus	Cui 18706	China	**OR761650**	**OR761772**	**OR761716**	-
Hydnellum diabolus	Cui 18707	China	**OR761651**	**OR761773**	**OR761717**	-
Hydnellum dianthifolium	ML902162HY	-	KX619420	-	-	-
Hydnellum dianthifolium	ML61211HY	-	KX619419	-	-	-
Hydnellum earlianum	REB-375	USA	JN135179	-	-	-
Hydnellum earlianum	Cui 16958	China	**OR761652**	**OR761774**	**OR761718**	**PP545359**
Hydnellum earlianum	Cui 17154	China	**OR761653**	**OR761775**	**OR761719**	**PP545361**
Hydnellum fagiscabrosum	Cui 17228	China	**OR761654**	-	**OR761720**	**PP545362**
Hydnellum fagiscabrosum	GB-0195805	Sweden	MW144294	MW144294	-	-
Hydnellum fagiscabrosum	GB-0195625	Sweden	MW144292	MW144292	-	-
Hydnellum fennicum	OF242833	Norway	MK602738	MK602738	-	-
Hydnellum fennicum	SWesterberg110909	Sweden	MK602739	MK602739	-	-
Hydnellum ferrugineum	ELarsson 197-14	Sweden	MK602722	MK602722	-	-
Hydnellum ferrugineum	Cui 17015	China	**OR761655**	**OR761776**	**OR761721**	-
Hydnellum ferrugineum	Cui 17099	China	**OR761656**	**OR761777**	-	**PP545363**
Hydnellum ferrugipes	REB-176	USA	KC571727	-	-	-
Hydnellum ferrugipes	REB-68	USA	JN135176	-	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Hydnellum fibulatum	Yuan 14646	China	MW579957	-	MW579926	-
Hydnellum fibulatum	Yuan 14656	China	MW579927	-	MW579958	-
Hydnellum fuligineoviolaceum	LA120818	Sweden	MK602740	MK602740	-	-
Hydnellum fuligineoviolaceum	BNylen130918	Sweden	MK602741	MK602741	-	-
Hydnellum fuscoindicum	OSC 113641	USA	EU669230	EU669280	-	-
Hydnellum fuscoindicum	OSC 107844	USA	EU669229	EU669279	-	-
Hydnellum geogenium	OF66379	Norway	MK602723	MK602723	-	-
Hydnellum geogenium	EBendiksen526-11	Norway	MK602725	MK602725	-	-
Hydnellum glaucopus	RGCarlsson13-060	Sweden	MK602743	MK602743	-	-
Hydnellum glaucopus	JNitare06091	Sweden	MK602744	MK602744	-	-
Hydnellum glaucopus	Cui 17492	China	**OR761657**	-	**OR761722**	-
Hydnellum gracilipes	ELarsson 219-11	Sweden	Norway	MK602727	-	-
Hydnellum gracilipes	GB-0113779	Sweden	MK602726	MK602726	-	-
Hydnellum granulosum	Yuan 12213a	China	MW579948	MW579893	MW579921	OK254213
Hydnellum granulosum	Yuan 12213b	China	MW579947	MW579892	MW579920	OK254212
Hydnellum grosselepidotum	Wei 8120	China	MN846274	MN846283	-	-
Hydnellum grosselepidotum	Wei 8075	China	MN846276	MN846285	-	-
Hydnellum grosselepidotum	SAAS 2472	China	OP437911	-	-	-
Hydnellum illudens	OF76340	Norway	MW144334	MW144334	-	-
Hydnellum illudens	SAAS 3830	China	OP437912	OP407678	-	OP434361
Hydnellum illudens	SAAS 3844	China	OP437914	OP407680	-	OP434363
Hydnellum inflatum	Wang 80	China	MW579949	MW579949	MW579922	OK254210
Hydnellum inflatum	Shi 506	China	OK254210	MW579895	OK254210	OK254211

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Hydnellum joeides	KHjortstam17589	Sweden	MK602750	MK602750	-	-
Hydnellum joeides	Nitare110829	Sweden	MK602751	MK602751	-	-
Hydnellum lepidum	EGrundel110916	Sweden	MK602753	MK602753	-	-
Hydnellum lepidum	JNitare110829	Sweden	MK602754	MK602754	-	-
Hydnellum lidongense	Wei 8329	China	MN846281	MN846290	-	-
Hydnellum lidongense	SAAS 2435	China	OP437915	OP407681	-	OP434364
Hydnellum lidongense	Dai 24635	China	**OR761658**	**OR761778**	**OR761723**	**PP545364**
Hydnellum lundellii	OF242639	Norway	MK602759	MK602759	-	-
Hydnellum lundellii	OF295814	Norway	MK602760	MK602760	-	-
Hydnellum luteocaesia	Cui 23033	USA	**OR813996**	**OR814040**	**OR814076**	**-**
Hydnellum luteocaesia	Cui 23045	USA	**OR813997**	**OR814041**	**OR814077**	**PP545342**
Hydnellum luteocaesia	Cui 23046	USA	**OR813998**	**OR814042**	**OR814078**	**-**
Hydnellum martioflavum	OF242872	Norway	MK602761	MK602761	-	-
Hydnellum martioflavum	SAAS 2667	China	OP437917	-	-	OP434365
Hydnellum melanocarpum	Cui 18556	China	ON603661	-	ON603651	-
Hydnellum melanocarpum	Cui 18557	China	ON603662	ON603643	ON603652	-
Hydnellum melanocarpum	Cui 18559	China	ON603663	ON603644	ON603653	ON605667
Hydnellum mirabile	SLund140912	Sweden	MK602730	MK602730	-	-
Hydnellum mirabile	RGCarlsson11-119	Sweden	MK602728	MK602728	-	-
Hydnellum mirabile	ELarsson170 14	Sweden	MK602729	MK602729	-	-
Hydnellum nitida	Cui 18571	China	**OR814000**	**-**	**OR814080**	**-**
Hydnellum nitida	Cui 18572	China	**OR813999**	**OR814043**	**OR814079**	**-**
Hydnellum nemorosum	GB-0195631	Sweden	MW144373	MW144373	-	-

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			ITS	nLSU	nSSU	RPB2
Hydnellum nemorosum	OF242352	Norway	MW144372	MW144372	-	-
Hydnellum nemorosum	Cui 23073	USA	**OR761686**	**OR761806**	**OR761724**	-
Hydnellum nemorosum	Cui 23074	USA	**OR761687**	**OR761807**	**OR761725**	-
Hydnellum parvum	REB-131	USA	JN135187	-	-	-
Hydnellum parvum	REB-392	USA	KC571717	-	-	-
Hydnellum peckii	ELarsson174-14	Sweden	MK602732	MK602732	-	-
Hydnellum peckii	Yuan 13720	China	MW579967	MW579906	MW579932	OK254215
Hydnellum peckii	Cui 18703	China	-	**OR761779**	**OR761726**	**PP545365**
Hydnellum peckii	Cui 18617	China	**OR761659**	**OR761780**	-	-
Hydnellum pineticola	REB-49	USA	KC571733	-	-	-
Hydnellum pineticola	REB-43	USA	JN135175	-	-	-
Hydnellum pineticola	Cui 23041	USA	**OR761688**	**OR761808**	**OR761727**	-
Hydnellum pineticola	Cui 23042	USA	**OR761689**	-	**OR761728**	-
Hydnellum piperatum	REB-332	USA	JN135173	-	-	-
Hydnellum piperatum	REB-304	USA	KC571723	-	-	-
Hydnellum piperatum	Cui 23044	USA	**OR761690**	**OR761809**	**OR761729**	-
Hydnellum qinghaiense	Dai 18937	China	-	**OR814044**	**OR814081**	-
Hydnellum qinghaiense	Dai 18939	China	**OR814001**	**OR814045**	**OR814082**	-
Hydnellum qinghaiense	Dai 18943	China	**OR814002**	**OR814046**	-	-
Hydnellum radiatum	Cui 17130	China	ON603664	ON603645	ON603654	ON605669
Hydnellum radiatum	Cui 16254	China	ON603665	-	ON603655	-
Hydnellum regium	SEW 93	USA	AY569031	-	-	-
Hydnellum roseoviolaceum	GB-0195687	Sweden	MW144375	MW144375	-	-

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			ITS	nLSU	nSSU	RPB2
Hydnellum roseoviolaceum	GB-0195936	Sweden	MW144374	MW144374	-	-
Hydnellum rubidofuscum	Yuan 14587	China	MW579952	MW579897	MW579925	OK254208
Hydnellum rubidofuscum	Yuan 14561	China	MW579951	MW579896	MW579924	OK254207
Hydnellum scabrosellum	GB-0195791	Sweden	MW144378	MW144378	-	-
Hydnellum scabrosellum	GB-0195689	Sweden	MW144379	MW144379	-	-
Hydnellum scabrosum	OF295824	Norway	MK602764	MK602764	-	-
Hydnellum scabrosum	OF292320	Norway	MK602766	MK602766	-	-
Hydnellum scleropodium	REB-3	USA	JN135186	-	-	-
Hydnellum scleropodium	REB-352	USA	KC571740	-	-	-
Hydnellum scrobiculatum	REB-78	USA	JN135181	-	-	-
Hydnellum sp.	SAAS3824	China	OK636119	-	-	OP434357
Hydnellum spongiosipes	REB-107	USA	KC571743	-	-	-
Hydnellum spongiosipes	REB-52	USA	JN135184	-	-	-
Hydnellum spongiosipes	Cui 23109	USA	**OR761691**	**OR761810**	**OR761730**	-
Hydnellum squamulosum	Yuan 13625	China	MW579956	MW579899	-	OK254204
Hydnellum squamulosum	Cui 18686	China	**OR761661**	**OR761782**	**OR761732**	-
Hydnellum squamulosum	Cui 18685	China	**OR761660**	**OR761781**	**OR761731**	-
Hydnellum suaveolens	ELarsson 139-09	Norway	MK602734	MK602734	-	-
Hydnellum suaveolens	ELarsson 8-14	Sweden	MK602735	MK602735	-	-
Hydnellum suaveolens	Cui 18671	China	**OR761662**	**OR761783**	**OR761733**	**PP545366**
Hydnellum suaveolens	Cui 18610	China	**OR761663**	**OR761784**	**OR761734**	-
Hydnellum subalpinum	SAAS2778	China	OP437919	OP407685	-	OP434369
Hydnellum subalpinum	SAAS2961	China	OP437922	OP407688	-	OP434372

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Hydnellum subalpinum	SAAS2923	China	OP437921	OP407687	-	OP434371
Hydnellum subalpinum	Cui 18710	China	**OR804330**	**OR793838**	**OR793841**	-
Hydnellum subalpinum	Cui 18711	China	**OR804331**	**OR793839**	**OR793842**	-
Hydnellum subcaeruleum	Dai 18976	China	**OR814003**	**OR814047**	**OR814083**	-
Hydnellum subcaeruleum	Dai 18979	China	**OR814004**	**OR814048**	**OR814084**	-
Hydnellum subcaeruleum	Dai 18980	China	**OR814005**	**OR814049**	**OR814085**	-
Hydnellum subailaoensis	Dai 24634	China	**OR814006**	**OR814050**	**OR814086**	**PP545343**
Hydnellum subscabrosellum	SAAS 3833	China	OK636110	OP407683	-	OP434367
Hydnellum subscabrosellum	SAAS3842	China	OK636111	OK636111	-	OP434368
Hydnellum subsuccosum	SEW 55	USA	AY569033	-	-	-
Hydnellum subsuccosum	REB-10	USA	JN135178	-	-	-
Hydnellum succulentus	Dai 19953	China	**OR814007**	**OR814051**	**OR814087**	-
Hydnellum succulentus	Cui 22876	China	**OR814008**	**OR814052**		
Hydnellum sulcatum	Yuan 14521	China	MW579961	MW579902	MW579930	OK254202
Hydnellum sulcatum	Cui 16954	China	-	**OR761785**	**OR761735**	-
Hydnellum sulcatum	Cui 16965	China	**OR761664**	**OR761786**	**OR761736**	-
Hydnellum sp.	Cui 16459	Vietnam	-	PP087925	OR814103	-
Hydnellum sp.1	Shi 164	China	MW579969	-	-	-
Hydnellum sp.2	Yuan 14387	China	MW579970	MW579908	MW579934	-
Hydnellum sp.3	Yuan 14388	China	MW579971	-	-	-
Hydnellum sp.4	Wang 295	China	MW579972	-	-	-
Hydnellum sp.5	Yuan 14594	China	MW579973	MW579909	MW579935	OK254205
Hydnellum tarda	Dai 19925	China	**OR814009**	**OR814053**	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Hydnellum tarda	Dai 19974	China	**OR814010**	**OR814054**	**OR814088**	-
Hydnellum tarda	Dai 19975	China	**OR814011**	-	**OR814089**	-
Hydnellum yunnanense	Yuan 14386	China	MW579962	MW579903	-	OK254199
Hydnellum yunnanense	Yuan 14396	China	MW579963	MW579904	-	OK254200
Hydnellum yunnanense	Dai 20399	China	**OR761665**	-	-	-
Hydnellum underwoodii	REB-358	USA	JN135189	-	-	-
Hydnellum underwoodii	REB-50	USA	KC571781	-	-	-
Hydnellum versipelle	REB242	USA	JN135188	-	-	-
Hydnellum versipelle	SAAS 2841	China	OP437923	OP407689	-	OP434373
Hydnellum versipelle	SAAS 2905	China	OP437924	OP437924	-	OP434373
Hydnellum xanthopus	Cui 18618	China	**OR814012**	**OR814055**	**OR814090**	-
Hydnochaete duportii	AFTOL-ID 666	-	DQ404386	AY635770	-	AY662669
Hyphoderma praetermissum	AFTOL-ID 518	-	AY854081	AY700185	AY707094	AY787221
Jaapia argillacea	CBS:252.74	Netherlands	GU187524	GU187581	-	GU187788
Lactarius deceptivus	AFTOL-ID 682	USA	AY854089	AY631899	AY707093	AY803749
Lenzitopsis daii	Yuan 2959	China	JN169799	JN169795	MT732087	MT724774
Lenzitopsis daii	Yuan 2952	China	JN169798	JN169794	-	-
Lenzitopsis daii	Dai 18892	China	**OR761666**	**OR761787**	**OR761743**	**PP545370**
Lenzitopsis daii	He 7135	China	**OR761667**	**OR761788**	**OR761744**	
Lenzitopsis daii	Dai 22612	China	**OR761668**	**OR761789**	**OR761745**	
Lenzitopsis oxycedri	KHLarsson15304	Spain	MK602774	MK602774	-	-
Lenzitopsis oxycedri	UK635	-	JN169800	JN169796	-	-
Leptosporomyces raunkiaeri	CFMR: HHB-7628	USA	GU187528	GU187588	GU187640	GU187791

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Neolentinus adhaerens	DAOM 214911	-	HM536096	HM536071	HM536072	HM536116
Neosarcodon atroviridis	REB-104	USA	JN135190	-	-	-
Neosarcodon atroviridis	REB-109	USA	KC571769	-	-	-
Neosarcodon atroviridis	REB-61	USA	KC571768	-	-	-
Neosarcodon bairdii	AV990	Colombia	KR698938	-	-	-
Neosarcodon colombiensis	AG-2015	Colombia	KP972654	-	-	-
Neosarcodon melanocarpus	Dai 19964	China	-	**OR814056**	**OR814091**	-
Neosarcodon melanocarpus	Dai 19978	China	**OR814013**	**OR814057**	**OR814092**	-
Neosarcodon pallidogriseus	AV989	Colombia	KR698939	-	-	-
Neosarcodon pakaraimensis	TH9554	Guyana	KM668103	-	-	-
Neosarcodon pakaraimensis	TH9513	Guyana	KC155390	-	-	-
Neosarcodon portoricensis	Baroni 8776	Puerto Rico	KM668100	-	-	-
Neosarcodon quercophilus	CFMR-BZ-3833	BELIZE	KM668101	-	-	-
Neosarcodon rufobrunneus	AV1989	Colombia	KR698937	-	-	-
Neosarcodon umbilicatus	Baroni 10201	Belize	KM668102	-	-	-
Neosarcodon umbilicatus	-	Belize	NR137923	-	-	-
Odontia aculeata	Yuan 10793	China	MG719981	-	-	-
Odontia aculeata	Yuan 10767	China	MG719982	-	-	-
Odontia duemmeri	TU103876	Cameroon	UDB013978	-	-	-
Odontia ferruginea	TAAM149492	Estonia	UDB000285	-	-	-
Odontia ferruginea	TU110988	Estonia	UDB025793	-	-	-
Odontia fibrosa	TU115028	China	MK602775	MK602775	-	-
Odontia fibrosa	SSvantesson38	Norway	MH310788	-	OK586799	OK632664

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Odontia sparsa	Yuan 10718	China	MG719980	-	-	-
Odontia sparsa	Yuan 10780	China	MG719980	-	-	-
Odontia parvispina	Yuan 10652	China	MW033328	-	-	-
Odontia parvispina	Yuan 10716	China	MW033329	-	-	-
Odontia huanrenensis	Yuan 10663	China	MW033326	-	-	-
Odontia huanrenensis	Yuan 10741	China	MW033327	-	-	-
Odontia parvospora	Yuan 13073	China	MK883038	MK883038	-	-
Odontia parvospora	Yuan 13071	China	MK883037	MK883037	-	-
Phellodon albomarginatus	Dai 19880	China	**OR814014**	**OR814058**	-	-
Phellodon alboniger	REB-70	USA	KC571749	-	-	-
Phellodon alboniger	REB-57	USA	JN135206	-	-	-
Phellodon alboniger	Cui 23062	USA	**OR761692**	**OR761811**	**OR761737**	-
Phellodon arcularius	Cui 17127	China	**OR814015**	**OR814059**	**OR814093**	-
Phellodon atratus	CL-72	Canada	MK281471	-	-	-
Phellodon atratus	DAVFP 28189	Canada	HQ650766	-	-	-
Phellodon atroardesiacus	Cui 18449	China	MZ221189	MZ225598	MZ225636	-
Phellodon atroardesiacus	Cui 16951	China	MZ225632	MZ225597	MZ225635	MZ343197
Phellodon brunneoolivaceus	REB-166	USA	KC571752	-	-	-
Phellodon caesius	Cui 18734	China	OP751005	OP751407	OP751414	OP755305
Phellodon caesius	Cui 18735	China	-	OP751408	OP751415	-
Phellodon cinereofuscus	Cui 16944	China	MZ225581	MZ225603	MZ225641	MZ343199
Phellodon cinereofuscus	Cui 16962	China	MZ225583	MZ225605	MZ225643	MZ343200
Phellodon cinereofuscus	Cui 16963	China	MZ225584	MZ225606	MZ225644	MZ343201

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Phellodon concentricus	Dai 20401	China	-	OP751406	OP751413	-
Phellodon concentricus	Dai 20403	China	OP751004	OP751405	OP751412	-
Phellodon confluens	WAT 28574	UK	EU622361	-	-	-
Phellodon confluens	E00 186901	UK	EU622362	-	-	-
Phellodon crassipilieatus	Cui 18532	China	OL449267	OL439037	OL439027	-
Phellodon crassipilieatus	Cui 18533	China	OL449268	OL439038	OL439028	-
Phellodon ellisianus	REB-264	USA	KC571757	-	-	-
Phellodon ellisianus	REB-407	USA	KC571759	-	-	-
Phellodon fibulatus	REB-168	USA	JN135205	-	-	-
Phellodon fibulatus	REB-34	USA	KC571761	-	-	-
Phellodon fuligineoalbus	REB-271	USA	KC571760	-	-	-
Phellodon fuligineoalbus	REB-285	USA	JN135196	-	-	-
Phellodon fuligineoalbus	Cui 23048	USA	**OR761693**	-	**OR761738**	**PP545371**
Phellodon longipes	Cui 18542	China	**OR814016**	-	-	**PP545344**
Phellodon griseofuscus	Cui 18544	China	OL449265	OL439035	OL439025	OL449087
Phellodon griseofuscus	Cui 18561	China	OL449266	OL439036	OL439026	-
Phellodon henanensis	Chen 463	China	OP751002	-	OP751410	-
Phellodon henanensis	Chen 465	China	OP751003	OP751404	OP751411	-
Phellodon melaleucus	LH4	UK	EU622368	-	-	-
Phellodon melaleucus	E00219373	UK	EU622369	-	-	-
Phellodon mississippiensis	MS-1	USA	JN247563	-	-	-
Phellodon mississippiensis	MS-3	USA	JN247564	-	-	-
Phellodon niger	REB-46	USA	JN135202	-	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Phellodon niger	REB-282	USA	KC571766	-	-	-
Phellodon cf. *nothofagi*	MES-175	Chile	MH930224	-	-	-
Phellodon perchocolatus	Cui 18534	China	OL449259	OL439029	OL439020	-
Phellodon perchocolatus	Cui 18536	China	OL449260	OL439030	-	-
Phellodon perchocolatus	Cui 18540	China	OL449261	OL439031	OL439021	-
Phellodon putidus	REB-8	USA	JN135200	-	-	-
Phellodon secretus	0097	Russia	MG597404	-	-	-
Phellodon setulosus	Cui 23031	USA	**OR814017**	-	**OR814094**	-
Phellodon setulosus	Cui 23040	USA	**OR814018**	-	**OR814095**	**PP545345**
Phellodon setulosus	Cui 23058	USA	**OR814019**	-	**OR814096**	**PP545346**
Phellodon setulosus	Cui 23059	USA	**OR814020**	-	**OR814097**	**PP545347**
Phellodon sinclairii	PDD 89028	New Zealand	GU222291	-	-	-
Phellodon stramineus	Cui 16956	China	MZ225587	MZ225609	MZ225647	MZ343203
Phellodon stramineus	Cui 16959	China	MZ225588	MZ225610	MZ225648	MZ343204
Phellodon stramineus	Cui 16961	China	MZ225589	MZ225611	MZ225649	MZ343205
Phellodon subconfluens	Yuan 11123	China	MK677464	-	-	-
Phellodon subconfluens	Yuan 11150	China	MK677465	-	-	-
Phellodon subgriseofuscus	Dai 18982	China	OP751000	-	-	-
Phellodon subgriseofuscus	Dai 18993	China	OP751001	OP751403	OP751409	OP755301
Phellodon submelaleucus	Cui 18614	China	OL449262	OL439032	OL439022	-
Phellodon submelaleucus	Cui 18620	China	OL449263	OL439033	OL439023	-
Phellodon submelaleucus	Cui 18623	China	OL449264	OL439034	OL439024	-
Phellodon substramineus	Dai 24629	China	**OR814021**	**OR814060**	**OR814098**	**PP545348**

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Phellodon substramineus	Dai 24630	China	**OR814022**	**OR814061**	**OR814099**	**PP545349**
Phellodon substramineus	Dai 24631	China	**OR814023**	**OR814062**	**OR814100**	-
Phellodon sp.1	REB-83	USA	KC571747	-	-	-
Phellodon sp.1	REB-325	USA	KC571748	-	-	-
Phellodon tomentosus	SL70	UK	EU622381	-	-	-
Phellodon tomentosus	LH22	UK	EU622382	-	-	-
Phellodon yunnanensis	Cui 17097	China	MZ225593	MZ225613	MZ225651	MZ343206
Phellodon yunnanensis	Cui 17129	China	MZ225594	MZ225614	MZ225652	MZ343207
Phellodon yunnanensis	Cui 17131	China	MZ225595	MZ225615	MZ225653	MZ343208
Phellodon violascens	2359-QFB-25626	-	KM406977	-	-	-
Phellodon violascens	Cui 23047	USA	**OR761694**	**OR761812**	**OR761739**	-
Phellodon violascens	Cui 23061	USA	**OR761695**	**OR761813**	-	-
Picipes atratus	Cui 11289	China	KX900043	KX900159	KX900271	KX900307
Podoserpula ailaoshanensis	ZJL2015015	China	KU324484	KU324487	KU324491	-
Polyporus austrosinensis	Cui 11126	China	KX900045	KX900161	KX900272	KX900308
Polyozellus abundilobus	OF110312	Norway	MK290731	MK290731	-	-
Polyozellus alnophilus	OF110313	Norway	MK290715	MK290715	-	-
Polyozellus alobatus	OF110315	Norway	MK290695	MK290695	-	-
Polyozellus alobatus	SSvantesson425	Sweden	MK290696	MK290696	-	-
Polyozellus atrofuscus	ML7553	USA	MK290732	-	-	-
Polyozellus atrofuscus	1859RD	China	HQ850125	-	-	-
Polyozellus atrolazulinus	TU117559	Canada	MG214657	MT737307	MT732090	MT724777
Polyozellus atrolazulinus	TU102998	USA	MF100819	-	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Polyozellus flavovirens	KHLarsson16727	Sweden	-	OK559566	OK559682	OK632648
Polyozellus flavovirens	KHL16310	Sweden	MK290723	MK290723	-	-
Polyozellus	SSvantesson401	Sweden	MK290720	-	-	OK632653
Polyozellus	T883	Norway	MK290721	MK290721	MK290649	-
Polyozellus humicola	SSvantesson345	Sweden	MK290724	MK290724	MK290724	OK632649
Polyozellus humicola	SSvantesson539	USA	-	OK559565	OK559680	OK632650
Polyozellus mariae	TU117348	Canada	MF100831	MF100831	-	-
Polyozellus mariae	TU117235	Canada	MF100826	-	-	-
Polyozellus marymargaretae	TU117347	USA	MF100841	MT737308	MT732089	MT724778
Polyozellus medius	TU115609	Estonia	MK290714	MK290714		
Polyozellus medius	MBN021322	Canada	KC840631	-		
Polyozellus mucidulus	T1155	Norway	MK290725	MK290726		
Polyozellus mucidulus	T1123	Norway	MK290726	MK290718		
Polyozellus multiplex	TU115322	Canada	MF100814	MT737306	MT732095	MT724779
Polyozellus multiplex	TU117350	USA	MF100830	MF100830	-	-
Polyozellus multiplex	TU115049	China	MF100812	MF100812	-	-
Polyozellus nigra	KHL16273	Finland	MK290718	MK290718	-	-
Polyozellus nigra	T838	Norway	MK290719	MK290719	-	-
Polyozellus pinophilus	SSvantesson358	Sweden	MK290708	MK290708	-	-
Polyozellus pinophilus	OF110328	Norway	MK290709	MK290709	-	-
Polyozellus plurilobus	US 4263	Finland	MK290698	-	-	-
Polyozellus plurilobus	SSvantesson439	Sweden	MK290699	-	-	-
Polyozellus purpureoniger	H7021198	Russia	MF100842	-	-	-

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			ITS	nLSU	nSSU	RPB2
Polyozellus purpureoniger	TU103000	USA	MF100821	-	-	-
Polyozellus rhizopunctatus	SSvantesson129	Sweden	MK290717	MK290717	OK559677	OK632669
Polyozellus rhizopunctatus	EMartini 10413	Switzerland	-	OK559563	OK559678	OK632668
Polyozellus rotundisporus	SSvantesson413	Sweden	MK290674	MK290674	-	-
Polyozellus rotundisporus	SSvantesson394	Sweden	MK290728	MK290728	-	-
Polyozellus sciastrus	OF110317	Norway	MK290684	MK290684	-	-
Polyozellus sciastrus	OF110318	Norway	MK290688	MK290688	-	-
Polyozellus tristis	SSvantesson193	Sweden	MK290679	MK290679	OK559676	OK632658
Polyozellus tristis	OF110300	Norway	MK290676	MK290676	-	-
Polyozellus tristoides	OF110306	Norway	MK290692	MK290692	-	-
Polyozellus tristoides	R60p6	Czechia	GU327494	-	-	-
Polyozellus umbrinus	SSvantesson 351	Sweden	MK290700	-	-	-
Polyozellus umbrinus	OF110268	Norway	MK290702	MK290702	-	-
Polyozellus umbrinascens	SSvantesson 335	Sweden	MK290697	MK290697	-	-
Polyozellus umbrinascens	UE31	Italy	HM370480	-	-	-
Polyozellus vepallidosporus	5182-1201	Germany	HM146848	-	-	-
Stereopsis radicans	O: KHL15528	Brazil	-	KC203497	KC203497	KC203503
Sarcodon aspratus	-	-	DQ448877	-	-	-
Sarcodon aspratus	-	-	AF335110	-	-	-
Sarcodon flavidus	SAAS 3819	China	OK636116	OP407698	-	OP434380
Sarcodon flavidus	SAAS 3832	China	OK636112	OP407699	-	OP434381
Sarcodon flavidus	SAAS 3923	China	OK636113	OP407700	-	OP434382
Sarcodon giganteus	SAAS 3974	China	OK636122	OP407702	-	OP434384

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Sarcodon giganteus	SAAS 3576	China	OK636121	OP407701	-	OP434383
Sarcodon imbricatus	ELarsson 384-10	Norway	MK602747	MK602747	-	-
Sarcodon imbricatus	SSvantesson355	Norway	MK602748	MK602748	-	-
Sarcodon imbricatus	SAAS 2681	China	OK636080	OP407703	-	OP434385
Sarcodon imbricatus	Cui 16834	China	**OR761669**	**OR761790**	**OR761740**	**PP545367**
Sarcodon imbricatus	Cui 16835	China	**OR761670**	**OR761791**	**OR761741**	**PP545368**
Sarcodon leucopus	OF 296944	Norway	MK602756	MK602756	-	-
Sarcodon leucopus	OF 296099	Norway	MK602755	MK602755	-	-
Sarcodon leucopus	SAAS 2873	China	OK636090	OP407706	-	OP434389
Sarcodon leucopus	SAAS 2875	China	OK636087	OP407707	-	OP434388
Sarcodon leucopus	Cui 17596	China	**OR761671**	**OR761792**	**OR761742**	**PP545369**
Sarcodon neosquamosus	SAAS 2914	China	OK636095	OP407712	-	OP434390
Sarcodon neosquamosus	SAAS 2919	China	OK636096	OP407713	-	OP434391
Sarcodon neosquamosus	SAAS 2926	China	OP437932	-	-	OP434392
Sarcodon nigrosquamosus	SAAS 2704	China	OK636106	OP407709	-	-
Sarcodon nigrosquamosus	SAAS 2938	China	OK636101	OP407710	-	-
Sarcodon nigrosquamosus	SAAS 3922	China	OK636103	OP407711	-	-
Sarcodon pseudoimbricatus	Cui 16969	China	**OR804332**	**OR793840**	**OR793843**	-
Sarcodon pseudoimbricatus	SAAS 2944	China	OK636099	OP407694	-	-
Sarcodon pseudoimbricatus	SAAS 2962	China	OK636098	OP407695	-	OP434378
Sarcodon quercinofibulatus	JC-20090718.2	Italy	JX271818	MK602773	-	-
Sarcodon quercinofibulatus	RMA8	USA	MG663244	-	-	-
Sarcodon scabripes	REB-351	USA	JN135191	-	-	KF007970

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Sarcodon scabripes	FCME:23240	Mexico	EU293829	-	-	-
Sarcodon squamosus	ELarsson 248-12	Sweden	MK602767	MK602767		-
Sarcodon squamosus	OF295554	Norway	MK602769	MK602769	-	-
Sarcodon subquercinofibulatus	SAAS 2904	China	OK636123	OP407691	-	OP434375
Sarcodon subquercinofibulatus	SAAS 3780	China	OP434375	OP407692	-	OP434376
Sarcodon subquercinofibulatus	SAAS 3976	China	OK636124	OP407693	-	OP434377
Sarcodon subquercinofibulatus	Dai 20315	China	**OR814024**	**OR814063**	**OR814101**	-
Sarcodon yunnanensis	He 1078	China	**OR814025**	-	-	-
Sarcodon yunnanensis	SAAS 2471	China	OP437909	-	-	-
Schenella pityophilus	OSC59743	-	-	DQ218519		DQ219057
Schizophyllum radiatum	AFTOL-ID-516	Panama	AY571060	AY571023	AY705952	DQ484052
Serpula himantioides	MUCL:30528	Belgium	GU187545	GU187600	GU187651	GU187808
Steccherinum murashkinskyi	X449	Russia	JN710588	JN710588	-	-
Steccherinum ochraceum	KHL11902	Sweden	JQ031130	JQ031130	-	-
Stereopsis radicans	O: KHL15528	Brazil	-	KC203497	KC203497	KC203503
Thelephora africana	SYN 991	Benin	EF507254	-	-	-
Thelephora africana	SYN890	Benin	EF507256	-	-	-
Thelephora afrostuposa	SYN 2292	Guinea	JF520431	-	-	-
Thelephora afrostuposa	MSYN 2292	Guinea	NR119954	-	-	-
Thelephora agbassaensis	SYN 981	Benin	EF507257	-	-	-
Thelephora agbassaensis	MSYN 981	Benin	NR119638	-	-	-
Thelephora agereri	MRA 13793	Benin	NR119641	-	-	-
Thelephora albomarginata	NF20010	Denmark	UDB016649	-	-	-

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Thelephora alnii	TUF115341	Finland	UDB011639	-	-	-
Thelephora alnii	TH034568	Estonia	UDB002958	-	-	-
Thelephora alpina	IB 20060231	Austria	EF655702	-	-	-
Thelephora alpina	B 20060231	Austria	NR121330	-	-	-
Thelephora americana	BMJ01	USA	MT196971	-	-	-
Thelephora amyloapiculata	MSYN 893	Benin	EF507263	-	-	-
Thelephora anthocephala	src614	USA	DQ974771	-	-	-
Thelephora anthocephala	NSK1014540	Russia	MT773612	MT773612	-	-
Thelephora asiae-orientalis	Yuan 12022	China	MK211711	MK446334	-	-
Thelephora asiae-orientalis	Yuan 11918	China	MK211710	MK446333	-	-
Thelephora asperula	MT7	Germany	KF498576	-	-	-
Thelephora atra	TAAM149211	Russis	UDB000235	UDB018697	-	-
Thelephora atramentaria	TUF123496	Germany	UDB000236		-	-
Thelephora atramentaria	TUF108866	Estonia	UDB000955		-	-
Thelephora atroarenicolor	TU115438	Estonia	-	UDB016303	-	-
Thelephora atrobadia	Yuan 11099	China	KY686248	MK446335	-	-
Thelephora atrobadia	Yuan 11114	China	KY686249	MK446336	-	-
Thelephora atrocastanea	Yuan 12179	China	MK211743	MK446338	-	-
Thelephora atrocastanea	Yuan 12170	China	MK211742	MK446337	-	-
Thelephora atrocitrina	SH1502461	Italy	UDB023357	-	-	-
Thelephora atrocitrina	SH1213711	Italy	UDB023355	-	-	-
Thelephora aquila	Wei 8831	China	OP793743	OP793698	-	-
Thelephora aquila	Wei 8833	China	OP793744	OP793699	-	-

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			ITS	nLSU	nSSU	RPB2
Thelephora aurantiotincta	520625MF420	China	MZ057686	-	-	-
Thelephora aureomarginata	Yuan 10671	China	MK211744	MK446339	-	-
Thelephora aureomarginata	Yuan 10683	China	MK211745	MK878395	-	-
Thelephora austrosinensis	GDGM 48891	China	MF593266	MH620354	-	-
Thelephora austrosinensis	Dai 19706	China	**OR761672**	**OR761793**	**OR761746**	
Thelephora badia	TUF108893	Estonia	UDB000952	-	-	-
Thelephora badia	TAA159022	Russia	UDB000238	-	-	-
Thelephora beaverae	TU105060	Seychelles	-	UDB015002	-	-
Thelephora beaverae	TU103595	Seychelles	-	UDB017787	-	-
Thelephora bidoupensis	Yuan 12707	Vietnam	MK775477	MN684329	-	-
Thelephora bidoupensis	Yuan 12685	Vietnam	MK775476	MN684330	-	-
Thelephora botryoides	KHL8453	Sweden	UDB000255	AY586717	-	-
Thelephora bresadolae	TU115616	Slovenia	UDB020335	-	-	-
Thelephora bresadolae	TU115447	Estonia	UDB016311	-	-	-
Thelephora brevis	Yuan 11328	China	MK211746	MK446340	-	-
Thelephora brevis	Yuan 11332	China	MK211747	MK878396	-	-
Thelephora brevisterigmata	Yuan 12700	Vietnam	MK775472	MK775472	-	-
Thelephora brevisterigmata	Yuan 12701	Vietnam	MK775473	MK850203	-	-
Thelephora brunneocystidia	SYN 839 (M)	Benin	DQ848613	-	-	-
Thelephora brunneocystidia	RA 13779	Benin	DQ848610	-	-	-
Thelephora brunneoflava	Yuan 12162	China	MK211749	MK850194	-	-
Thelephora brunneoflava	Yuan 12161	China	MK211748	MK446341	-	-
Thelephora brunneogrisea	Yuan 12147	China	MK211751	MK446343	-	-

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			ITS	nLSU	nSSU	RPB2
Thelephora brunneogrisea	Yuan 12146	China	MK211750	MK446342	-	-
Thelephora brunneorufa	TAAM159857	Australia	UDB000274	-	-	-
Thelephora bubalinomarginata	Dai 20606	China	**OR814026**	**OR814064**	-	-
Thelephora bubalinomarginata	Dai 20608	China	**OR814027**	**-**	-	-
Thelephora bubalinomarginata	Dai 19919	China	**OR814028**	**OR814065**	-	-
Thelephora bubalinomarginata	Dai 19931	China	**OR814029**	**OR814066**	-	-
Thelephora bubalinomarginata	Dai 19932	China	**OR814030**	**OR814067**	-	-
Thelephora caryophyllea	ELarsson89-09	Sweden	MK602776	MK602776	-	-
Thelephora caryophyllea	He 6816	China	**OR761675**	**OR761794**	**OR761747**	-
Thelephora caryophyllea	Dai 20119	China	**OR761673**	**OR761795**	**OR761748**	-
Thelephora caryophyllea	Dai 21741	China	**OR761674**	**OR761796**	**OR761749**	-
Thelephora castanea	B923	Iran	UDB005597	-	-	-
Thelephora castanea	TL-6886	Denmark	UDB000120	-	-	-
Thelephora changbaiensis	Yuan 11496	China	MK211739	MK446347	-	-
Thelephora changbaiensis	Yuan 11477	China	MK211738	MK446346	-	-
Thelephora cinerascens	TU108037	Estonia	-	UDB016193	-	-
Thelephora cinerascens	TU111378	Italy	-	UDB016498	-	-
Thelephora cinereobrunnea	Yuan 12703	Vietnam	MK775478	MK850198	-	-
Thelephora cinereobrunnea	Yuan 12705	Vietnam	MK775479	MK850199	-	-
Thelephora cinereoumbrina	TU115342	Finland	UDB011602	-	-	-
Thelephora citrinocystidiata	Yuan 10680	China	KY686246	MK446348	-	-
Thelephora citrinocystidiata	Yuan 10743	China	KY686247	MK446349	-	-
Thelephora clavigera	TU115532	Estonia	UDB016389	-	-	-

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			ITS	nLSU	nSSU	RPB2
Thelephora coerulea	TU115602	Estonia	UDB016469	-	-	-
Thelephora coerulea	TAAM153804	Estonia	UDB000266	-	-	-
Thelephora coffeae	Yuan 10629	China	KY686254	MK446350	-	-
Thelephora coffeae	Yuan 11100	China	MK446350	MK446350	-	-
Thelephora conclusa	Yuan 12086	China	MK211703	MK850195	-	-
Thelephora conclusa	Yuan 11986	China	MK211702	MK446352	-	-
Thelephora cuticularis	MCVE23531	Italy	UDB023363	-	-	-
Thelephora cuticularis	MICH139821	Italy	UDB023383	-	-	-
Thelephora cystidiata	Yuan 10620	China	KY686219	MK446353	-	-
Thelephora dimidiata	Yuan 11205	China	MK211704	MK446355	-	-
Thelephora dimidiata	Yuan 11267	China	MK211705	MK211705	-	-
Thelephora dominicana	JBSD126510	Dominican	KX216400	KX216399	-	-
Thelephora duplexa	Yuan 12207	China	MK211707	MK446358	-	-
Thelephora duplexa	Yuan 12202	China	MK211706	MK446357	-	-
Thelephora efibulata	Yuan 10699	China	KY686228	MK446359	-	-
Thelephora efibulata	Dai 21669	China	**OR761697**	-	-	-
Thelephora efibulis	Yuan 11241	China	MK211708	MK446361	-	-
Thelephora efibulis	Yuan 11329	China	MK211709	MK446362	-	-
Thelephora ellisii	TU115347	Finland	UDB011603	-	-	-
Thelephora ellisii	TU123494	Germany	UDB000226	-	-	-
Thelephora farinosa	Yuan 10656	China	KY686251	-	-	-
Thelephora farinosa	Yuan 10666	China	KY686250	-	-	-
Thelephora flavidobadia	Yuan 11044	China	KY686231	MK446364	-	-

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Thelephora flavidobadia	Yuan 11061	China	KY686230	MK446365	-	-
Thelephora fuscocinerea	TAAM149918	Estonia	UDB000240	UDB018703	-	-
Thelephora fuscocrustosa	Yuan 11420	China	MK211713	MK446367	-	-
Thelephora fuscocrustosa	Yuan 11399	China	MK211712	MK446366	-	-
Thelephora fuscofarinosa	Yuan 12142	China	MK211715	MK446369	-	-
Thelephora fuscofarinosa	Yuan 12125	China	MK211714	MK446368	-	-
Thelephora fuscogranulosa	Yuan 10733	China	KY686232	MK446370	-	-
Thelephora fuscogranulosa	Yuan 10725	China	KY686233	MK446371	-	-
Thelephora fuscopelliculosa	Yuan 11305	China	MK211716	MK446372	-	-
Thelephora fuscopelliculosa	Yuan 11316	China	MK211717	MK446373	-	-
Thelephora fuscus	T1180	China	AB634268	-	-	-
Thelephora fuscus	He 6923	China	**PP573019**	**PP573018**	-	-
Thelephora galzinii	RS27093	Finland	UDB000264	-	-	-
Thelephora galzinii	2007BBF2	France	HQ204743	-	-	-
Thelephora ganbajun	HKAS 14735	China	KY245240	-	-	-
Thelephora ganbajun	Yuan16715	China	OP793760	OP793685	-	-
Thelephora glaucoflora	Dai 19753	China	OP793755	OP799736	**OR761750**	-
Thelephora glaucoflora	Dai 20462	China	**OR761677**	-	**OR761751**	
Thelephora glaucoflora	Cui 13840	China	**OR761676**	-	**OR761752**	
Thelephora globosa	Yuan 11618	Finland	MG136838	MH201367	-	-
Thelephora globosa	Yuan 11603	Finland	-	MN684328	-	-
Thelephora globospora	Yuan 10668	China	KY686242	MK446374	-	-
Thelephora globospora	Yuan 10748	China	KY686243	MK446375	-	-

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			ITS	nLSU	nSSU	RPB2
Thelephora gloeocystidiata	Yuan 11171	China	KY686220	MK446376	-	-
Thelephora gloeocystidiata	Yuan 11200	China	KY686221	MK446377	-	-
Thelephora grandinioides	CLZhao 3406	China	MZ400675	MZ400673	-	-
Thelephora grandinioides	CLZhao 3408	China	MZ400676	MZ400674	-	-
Thelephora griseocastanea	Yuan 11409	China	MK211719	MK446379	-	-
Thelephora griseocastanea	Yuan 11401	China	MK211718	MK446378	-	-
Thelephora griseofusca	Yuan 11094	China	KY686252	MK446380	-	-
Thelephora griseofusca	Yuan 11104	China	KY686253	MK446381	-	-
Thelephora griseomarginata	Yuan 11468	China	MK211721	MK446383	-	-
Thelephora griseomarginata	Yuan 11458	China	MK211720	MK446382	-	-
Thelephora guineensis	SYN 2331	-	JF520432	-	-	-
Thelephora guineensis	M SYN 2331	-	NR119955	-	-	-
Thelephora hjortstamiana	TU103641	Seychelles	AM412303	-	-	-
Thelephora hjortstamiana	Toohyp24	Australia	KC222770	-	-	-
Thelephora inconspicua	Yuan 11107	China	KY686234	MK446385	-	
Thelephora inconspicua	Yuan 11060	China	KY686235	MK446384	-	-
Thelephora incrustata	Yuan 12189	China	MK211723	MK446387	-	-
Thelephora incrustata	Yuan 11158	China	MK211722	MK446386	-	-
Thelephora interrupta	Yuan 10775	China	KY686236	MK446388	-	-
Thelephora interrupta	Yuan 11203	China	KY686237	MK446389	-	-
Thelephora intsiae	TAA195077	Seychelles	AM412296	-	-	-
Thelephora iqbalii	MH810	Pakistan	JX241471	-	-	-
Thelephora lammiensis	Yuan 11617	Finland	MG136840	MH201366	-	-

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			ITS	nLSU	nSSU	RPB2
Thelephora lapida	TU115604	Estonia	-	UDB016370	-	-
Thelephora lapida	TU115440	Estonia	-	UDB016305	-	-
Thelephora larssoniana	TU105082	Seychelles	UDB017790	-	-	-
Thelephora lateritia	NF S045	Norway	UDB000963	-	-	-
Thelephora lateritia	TU108551	Estonia	UDB000954	-	-	-
Thelephora liaoningensis	Yuan 10681	China	MK250814	-	-	-
Thelephora liaoningensis	Yuan 10707	China	KY686257	-	-	-
Thelephora lilacinogrisea	TU108189	Estonia	-	UDB018468	-	-
Thelephora lilacinogrisea	TU111381	Italy	-	UDB016500	-	-
*Thelephora_longechinulata_*	Yuan11979	China	MK211726	MK446393		-
*Thelephora_longechinulata_*	Yuan12083	China	MK211727	MK446394		-
Thelephora longiaculeifer	Yuan 10744	China	KY686238	MK446391	-	-
Thelephora longiaculeifer	Yuan 11119	China	KY686239	MK446392	-	-
Thelephora longiechinula	Yuan 12687	Vietnam	MK775474	MK850201	-	-
Thelephora longiechinula	Yuan 12720	Vietnam	MK775475	MK850200	-	-
Thelephora longisterigmata	Yuan 11610	Finland	MG136836	MG136836	-	-
Thelephora longisterigmata	Yuan 11602	Finland	-	MH201365	-	-
Thelephora maroana	SYN 878	Benin	EF507250	-	-	-
Thelephora maroana	MSYN 878	Benin	NR119636	-	-	-
Thelephora macrospora	Cui 23037	USA	**OR814031**	-	-	-
Thelephora macrospora	Cui 23038	USA	**OR814032**	-	**OR814102**	-
Thelephora megaspora	Yuan 11326	China	MK211724	MK446395	-	-
Thelephora megaspora	Yuan 11472	China	MK211725	MK446396	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Thelephora minispora	SYN 2273	Guinea	JQ814474	-	-	-
Thelephora mollissima	MCVE21287	Italy	UDB023356	-	-	-
Thelephora muricata	TU100771	Estonia	UDB003303	-	-	-
Thelephora muricata	TU100729	Finland	UDB003310	-	-	-
Thelephora nebula	He 4452	China	OP793748	OP793693	**OR761753**	-
Thelephora nebula	He 4456	China	OP793749	**OR761803**	**OR761754**	-
Thelephora nitellina	L2AA1	USA	EF411085		-	-
Thelephora nitellina	src675	USA	DQ974778		-	-
Thelephora olivacea	Yuan 11043	China	KY686224	MK446397	-	-
Thelephora olivacea	Yuan 11139	China	KY686225	MK446398	-	-
Thelephora olivaceobrunnea	Yuan 11194	China	MK211728	MK446399	-	-
Thelephora olivaceobrunnea	Yuan 12148	China	MK211729	MK446400	-	-
Thelephora pallidobrunnea	Yuan 11493	China	MK211731	MK446402	-	-
Thelephora pallidobrunnea	Yuan 11481	China	MK211730	MK446401	-	-
Thelephora pallidocastanea	Yuan 11416	China	MG799183	MN684323	-	-
Thelephora pallidocastanea	Yuan 12034	China	MG816514	MN684324	-	-
Thelephora pallidomarginata	Yuan 11474	China	MK211733	MK446404	-	-
Thelephora pallidomarginata	Yuan 11404	China	MK211732	MK446403	-	-
Thelephora palmata	AT2005162	Sweden	UDB018570	-	-	-
Thelephora palmata	TU115271	Sweden	MH310778	-	-	-
Thelephora parmastoana	TU105091	Seychelles	-	UDB016713	-	-
Thelephora parmastoana	TU103691	Seychelles	-	UDB017782	-	-
Thelephora parvispora	Yuan 11144	China	KY686226	MK446405	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Thelephora parvispora	Yuan 11196	China	KY686227	-	-	-
Thelephora patagonica	BAFC52373	Argentina	KT032091	KT032103	-	-
Thelephora patagonica	BAFC52372	Argentina	KT032090	KT032102	-	-
Thelephora penicillata	X618	Prague	OL469898	OL469898	-	-
Thelephora penicillata	X536	Czech Republic	OL469887	-	-	-
Thelephora pertenuis	Yuan 11064	China	KY686240	MK446407	-	-
Thelephora pertenuis	Yuan 11131	China	KY686241	MK446408	-	-
Thelephora pileocystidiata	TU105068	Seychelles	UDB015029	-	-	-
Thelephora pileocystidiata	TU105054	Seychelles	UDB017789	-	-	-
Thelephora pilosa	TU124234	Estonia	-	UDB028227	-	-
Thelephora pisoniae	TU103655	Seychelles	UDB017778	-	-	-
Thelephora pseudoganbajun	Yuan 16771	China	OP793765	OP793705	-	-
Thelephora pseudoganbajun	Yuan 16780	China	OP793766	OP793703	-	-
Thelephora pseudoterrestris	TAA159625	-	AF272907	-	-	-
Thelephora pseudoversatilis	FCME26232	Mexico	JX075890	JX514167	-	-
Thelephora pseudoversatilis	FCME26152	Mexico	KJ462486	-	-	-
Thelephora pulvinulata	BAFC52371	Argentina	KT032089	-	-	-
Thelephora pulvinulata	BAFC52370	Argentina	KT032088	KT032101	-	-
Thelephora punicea	KHL11908	Sweden	UDB000959	-	-	-
Thelephora pyrolae	TAAM005998	Switzerland	UDB000262	-	-	-
Thelephora qingyuanensis	Yuan 10616	China	KY686223	MK446409	-	-
Thelephora qingyuanensis	Yuan 11109	China	KY686222	MK446410	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Thelephora radiosa	P35	Mexico	MT668616	-	-	-
Thelephora radiosa	P37	Mexico	MT668618	-	-	-
Thelephora regularis	JMT17371	USA	U83485	-	-	-
Thelephora scissilis	MUOB:324045	USA	OK376730	-	-	-
Thelephora segregata	Yuan 11256	China	MK211735	MK446412	-	-
Thelephora segregata	Yuan 10650	China	MK211734	MK446411	-	-
Thelephora separata	Yuan 10664	China	MK211737	MK850196	-	-
Thelephora separata	Yuan 10654	China	MK211736	MK850197	-	-
Thelephora sikkimensis	KD 16-003	India	MF684017	-	-	-
Thelephora sikkimensis	KD 16-042	India	MF684018	-	-	-
Thelephora stipitata	Yuan 11160	China	MK211740	MK446413	-	-
Thelephora stipitata	Yuan 12143	China	MK211741	MK446414	-	-
Thelephora stipitobasidia	Yuan 12713	Vietnam	MK775470	MK850204	-	-
Thelephora stipitobasidia	Yuan 12691	Vietnam	MK775471	MK850205	-	-
Thelephora storea	Yuan 10623	China	KY686244	MK446415	-	-
Thelephora stuposa	Th0764	Norway	-	MK602778	-	-
Thelephora stuposa	TU115328	Estonia	-	UDB016174	-	-
Thelephora subclavigera	TU115594	Finland	-	UDB031979	-	-
Thelephora sublilacina	UP161	Sweden	EF493288	-	-	-
Thelephora subtestacea	TU115374	Ukraine	-	UDB016180	-	-
Thelephora subtestacea	Dai 21659	China	**OR761699**	-	-	-
Thelephora subtestacea	He 6952	China	**OR761698**	-	**OR761761**	
Thelephora tedersooi	TU103673	Seychelles	UDB017781	-	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Thelephora tedersooi	TU103664	Seychelles	UDB002644	-	-	-
Thelephora tenuirhizomorpha	Yuan 11964	China	MG799184	MN684326	-	-
Thelephora tenuirhizomorpha	Yuan 12059	China	MG799185	MN684327	-	-
Thelephora tenuissima	FK15011	Argentina	KT032083	-	-	-
Thelephora tenuissima	BAFC52369	Argentina	KT032082	KT032100	-	-
Thelephora terrestris	DM1100	Denmark	MT644883	MT644883	-	-
Thelephora terrestris	Dai 20983	China	**OR761678**	**OR761797**	**OR761756**	-
Thelephora terrestris	Dai 20981	China	**OR761679**	**OR761798**	**OR761755**	-
Thelephora terrestris	Dai 21649	China	**OR761680**	**OR761799**	**OR761757**	-
Thelephora terrestris	He 4990	China	**OR761681**	**OR761800**	**OR761758**	-
Thelephora umbrinospora	TAAM149462	Estonia	UDB000233	-	-	-
Thelephora vialis	TENN-F-072281H2	USA	MN121029	MN121029	-	-
Thelephora vialis	TENN-F-072094	USA	MN121022	MN121022	-	-
Thelephora verruculata	Yuan 12684	Vietnam	MK775469	MN684332	-	-
Thelephora verruculata	Yuan 12680	Vietnam	MK775468	MN684331	-	-
Thelephora versatilis	FCME 26149	Mexico	KC595625	-	-	-
Thelephora versatilis	MEXU 26351	Mexico	KC595626	-	-	-
Thelephora viridula	TU115536	Estonia	UDB016392	-	-	-
Thelephora wakefieldiae	TU115353	Finland	UDB011601	-	-	-
Thelephora wakefieldiae	TU115350	Finland	UDB011599	-	-	-
Thelephora wuliangshanensis	CLZhao 21020	China	MZ400677	MZ400671	-	-
Thelephora wuliangshanensis	CLZhao 4107	China	MZ400678	MZ400672	-	-
Tomentellopsis bresadoliana	JEH 031011	Sweden	EU118674	EU118674	-	-

Species	Specimen no.	Locality	GenBank accession no.			
			ITS	nLSU	nSSU	RPB2
Tomentellopsis bresadoliana	H. G-B 5388	Germany	AJ410769	-	-	-
Tomentellopsis echinospora	TUF110333	Estonia	-	MT737310	MT732086	MT724780
Tomentellopsis pulchella	KHLarsson16366	Norway	MK602779	MK602779	-	-
Tomentellopsis pusilla	GB (KHL8459)	Sweden	-	AY586718	-	-
Tomentellopsis submollis	RS-22498	Finland	AJ410774	-	-	-
Tomentellopsis submollis	P24-F	UK	AM086447	-	-	-
Tomentellopsis zygodesmoides	TUF124075	Estonia	-	MT737311	MT732091	MT724781

Note: New sequences are shown in bold, ITS: the internal transcribed spacer regions, nLSU: the large subunit of nuclear ribosomal RNA gene, nSSU: the small subunit of nuclear ribosomal RNA gene, RPB2: the second largest subunit of RNA polymerase II gene.

Phylogenetic analyses

In this study, 1,426 sequences derived from 718 fungal samples representing 340 species were used to reconstruct phylogenetic trees, including 681 sequences of ITS, 460 sequences of nLSU, 171 sequences of nSSU, and 116 sequences of RPB2. Among them, 339 sequences were newly generated, including 108 sequences of ITS, 90 sequences of nLSU, 101 sequences of nSSU, and 40 sequences of RPB2.

The phylogenetic relationships of Thelephorales were analyzed by the datasets of combined ITS+nLSU sequences and ITS+nLSU+nSSU+RPB2 sequences. *Steccherinum ochraceum* (Pers. ex J.F. Gmel.) Gray and *Steccherinum murashkinskyi* (Burt) Maas Geest. were used as outgroups in the above two phylogenetic analyses, according to Larsson et al. (2019).

Comprehensive phylogenetic analyses of *Hydnellum*, *Phellodon,* and *Thelephora* were carried out, respectively, since these three groups contain most species of Thelephorales. The phylogenetic relationships of *Hydnellum* and *Phellodon* were analyzed by the datasets of combined ITS+nLSU+nSSU+RPB2 sequences. In addition, due to the lack of multi-gene molecular sequences, the combined dataset of ITS+nLSU sequences was used to rebuild the phylogenetic relationships of *Thelephora*. *Amaurodon aquicoeruleus* Agerer (UK 452) and *A. viridis* (Alb. And Schwein.) J. Schröt (TAA 149664) were used as the outgroups in the above three phylogenetic analyses, according to Song et al. (2023).

The DNA sequences were aligned by MAFFT v.7 with the G-INI-I option (Katoh & Standley 2013). Alignments were optimized manually in BioEdit v. 7.0.9 (Hall 1999) and spliced in Mesquite v. 3.2. (Maddison & Maddison 2017). The partition homogeneity test (PHT) (Farris et al. 1994) of the four-gene dataset was tested by PAUP v. 4.0b10 (Swoford 2002) under 1,000 homogeneity replicates. The best-fit evolutionary model was selected with AIC (Akaike Information Criterion) using MrModeltest v. 2.3 (Nylander 2004). The dataset was deposited in TreeBase (http://treebase.org/treebase-web/home.html, submission lD: 31287).

The Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were performed based on the four-gene dataset. RAxML-HPC2 v. 8.2.3 (Stamatakis 2014) was used to construct the maximum likelihood (ML) analyses with the GTRGAMMA model. All model parameters were estimated by the program, and only the best ML tree from all searches was kept. The ML bootstrap values were performed using rapid bootstrapping with 1,000 replicates. All model parameters were estimated by the program, and only the best ML tree from all searches was kept. The ML bootstrap values were performed using rapid bootstrapping with 1,000 replicates. BI analyses were conducted using MrBayes 3.2.6 with four Markov chains (MCMC), performing ten million generations until the split deviation frequencies < 0.01. The trees were saved every 100 generations, and the first 25% of the sampled trees were discarded as burn-in. Then, the remaining trees were kept and estimated with BI bootstrap.

The phylogenetic trees obtained from the Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were modified by FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/, accessed on 20 September 2023) and Adobe Illustrator CS6. In this study, the tree topology of ML was used as a representative, and the bootstrap values marked on the clade were significantly credible: the ML bootstrap was 50% or above, and the BI bootstrap was 0.95 or above.

Divergence time estimation

Two fossil calibrations, *Archaeomarasmius leggetti* Hibbett, D. Grimaldi & Donoghue, and *Quatsinoporites cranhamii* S.Y. Sm., Currah & Stockey, were used in the divergence time estimation. *A. leggetti*, an agaricoid fungus dated to 94–90 Mya (Hibbett et al. 1997), was treated as the representative of the minimum age of Agaricales. *Q. cranhamii*, was dated at 125 Mya, which is the minimum divergence time of Hymenochaetales (Smith et al. 2004).

Divergence time was estimated with the BEAST v2.6.5 software package (Bouckaert et al. 2019) using the ITS, nLSU, nSSU, and RPB2 sequences of Thelephorales species. Four species of Agaricales viz. *Agaricus campestris* L., *Aphanobasidium pseudotsugae* (Burt) Boidin & Gilles, *Callistosporium graminicolor* Lennox and *Schizophyllum radiatum* Fr. were used to represent the

Agaricales clade, while *Hydnochaete duportii* Pat., *Hyphoderma praetermissum* (P. Karst.) J. Erikss. & Å. Strid and an undescribed species of *Cotylidia* were used to represent the Hymenochaetales clade. Amylocorticiales was treated as a sister clade of Agaricales Zhao et al. (2017), and the main species of Atheliales, Boletales, Russulales, Thelephorales, Stereopsidales, and other three orders were also included in our analyses. All the DNA sequences were aligned in MAFFT 7 and manually adjusted in BioEdit (Hall 1999). The rates of evolutionary changes in nuclear acids were estimated with ModelTest version 3.7 using the GTR substitution model (Posada & Crandall 1998). The XML file was executed in BEAUti v2. A log-normal distribution was employed for molecular clock analyses (Drummond & Rambaut 2007). The clock model was set to an uncorrelated lognormal relaxed clock (Drummond et al. 2006, Lepage et al. 2007). A Yule speciation model was selected prior, assuming a constant speciation rate per lineage. Gamma priors distribution was used for fossil node calibrations, set shape = 1.0, scale = 20.0, offset = 90.0 for Agaricales clade and 125.0 for Hymenochaetales clade. After 10,000,000 generations, the first 10% were removed as burn-in. The log file was checked for convergence with Tracer (version 1.54). Consequently, a Maximum Clade Credibility (MCC) tree was summarized with TreeAnnotator (version 2.6.5), annotating the clades with more than 0.8 posterior probability (PP).

RESULTS

Molecular phylogeny

The phylogenetic relationships of Thelephorales based on the combined dataset of ITS+nLSU sequences contained the sequences from 232 fungal samples of 125 species. The best-fit evolutionary models applied in Bayesian analyses were selected by MrModeltest v. 2.3 for each region of the two genes. The models for ITS and nLSU were GTR+I+G with equal frequency of nucleotides. Bayesian analyses resulted in a topology similar to that from ML analysis, with an average standard deviation of split frequencies = 0.004630. The ML topology was presented and annotated with ML bootstraps ≥50% and BI bootstraps ≥0.95.

The phylogenetic relationships of Thelephorales based on the combined dataset of ITS+nLSU+nSSU+RPB2 sequences contained the sequences from 232 fungal samples of 125 species. The best-fit evolutionary models applied in Bayesian analyses were selected by MrModeltest v. 2.3 for each region of the four genes. The models for ITS, nLSU, nSSU, and RPB2 were GTR+I+G with equal frequency of nucleotides. Bayesian analyses resulted in a topology similar to that from ML analysis, with an average standard deviation of split frequencies = 0.004729. The ML topology was presented and annotated with ML bootstraps ≥50% and BI bootstraps ≥0.95.

The phylogenetic relationships of *Hydnellum* based on the combined dataset of ITS+nLSU+nSSU+RPB2 sequences contained the sequences from193 fungal samples of 83 species. The best-fit evolutionary models applied in Bayesian analyses were selected by MrModeltest v. 2.3 for each region of the four genes; the models for ITS, nLSU, nSSU, and RPB2 were GTR+I+G with equal frequency of nucleotides. Bayesian analysis resulted in a topology similar to that from ML analysis, with an average standard deviation of split frequencies = 0.002120. The ML topology was presented and annotated with ML bootstraps ≥50% and BI bootstraps ≥0.95.

The phylogenetic relationships of *Phellodon* based on the combined dataset of ITS+nLSU+nSSU+RPB2 sequences contained the sequences from 73 fungal samples of 35 species. The best-fit evolutionary models applied in Bayesian analyses were selected by MrModeltest v. 2.3 for each region of the four genes; the models for ITS, nLSU, nSSU, and RPB2 were GTR+I+G with equal frequency of nucleotides. Bayesian analysis resulted in a topology similar to that from ML analysis, with an average standard deviation of split frequencies = 0.006860. The ML topology was presented and annotated with ML bootstraps ≥50% and BI bootstraps ≥0.95.

The phylogenetic relationships of *Thelephora* based on the combined dataset of ITS+nLSU sequences contained the sequences from 284 fungal samples of 143 species. The best-fit evolutionary models applied in Bayesian analyses were selected by MrModeltest v. 2.3 for each region of the four genes; the models for ITS, nLSU, nSSU, and RPB2 were GTR+I+G with equal frequency of nucleotides. Bayesian analysis resulted in a topology similar to that from ML analysis, with an average standard deviation of split frequencies = 0.009330. The ML topology was presented and annotated with ML bootstraps ≥50% and BI bootstraps ≥0.95.

The phylogenetic relationships of Thelephorales based on the combined datasets of ITS+nLSU and ITS+nLSU+nSSU+RPB2 sequences were contained in Figs. 1, 2, respectively. Six clades were formed in the phylogenetic tree of Thelephorales (Figs. 1, 2), including six families: Lenzitopsidaceae fam. nov. (100% ML, 1.00 BPP, Figs. 1, 2), Bankeraceae (69% ML, 1.00 BPP, Fig 1; 55% ML, 1.00 BPP, Fig 2), Polyozellaceae fam. nov. (1.00 BPP, Fig 1; 67% ML, 1.00 BPP, Fig 2), Sarcodonaceae fam. nov. (52% ML, 1.00 BPP, Fig 1; 78% ML, 1.00 BPP, Fig 2), Thelephoraceae (71% ML, 0.98 BPP, Fig 1; 68% ML, 1.00 BPP, Fig 2), Tomentellopsidaceae fam. nov. (79% ML, 0.95 BPP, Fig 1; 86% ML, 1.00 BPP, Fig 2). There are eleven genera involved in six families, viz., *Amaurodon*, *Boletopsis* (100% ML, 1.00 BPP, Figs. 1, 2), *Hydnellum* (98% ML, 1.00 BPP, Fig. 1; 99% ML, 1.00 BPP, Fig 2), *Lenzitopsis* (100% ML, 1.00 BPP, Figs. 1, 2), *Neosarcodon* (100% ML, 1.00 BPP, Figs. 1, 2), *Odontia* (74% ML, 0.99 BPP, Fig. 1; 73% ML, 1.00 BPP, Fig 2), *Sarcodon*, *Phellodon* (100% ML, 1.00 BPP, Figs. 1, 2), *Polyozellus* (1.00 BPP, Fig. 1; 67% ML, 1.00 BPP, Fig 2), *Thelephora* (100% ML, 1.00 BPP, Figs. 1, 2), *Tomentellopsis* (75% ML, 0.95 BPP, Fig. 1; 86% ML, 1.00 BPP, Fig 2).

Detailed studies for *Hydnellum*, *Phellodon*, and *Thelephora* were conducted on all available molecular sequences of these three genera, respectively (Figs. 3–5). There are 83 lineages formed in *Hydnellum*, of which eleven lineages were distant from other species and regarded as new species with high supports. There are 35 lineages formed in *Phellodon*, of which six lineages were distant from other species and regarded as new species with high supports. A total of 143 species were involved in *Thelephora*, and two new species formed a distinct well-supported branch distant from other species.

The phylogenetic analyses revealed that six clades at the family level were obtained in Thelephorales, and Thelephorales were confirmed to comprise six families, including four new families: Lenzitopsidaceae, Polyozellaceae, Sarcodonaceae, Tomentellopsidaceae, and two existing families: Bankeraceae and Thelephoraceae. There are twelve identified genera viz. *Amaurodon*, *Boletopsis*, *Corneroporus*, *Hydnellum*, *Lenzitopsis*, *Neosarcodon*, *Odontia*, *Sarcodon*, *Phellodon*, *Polyozellus*, *Thelephora* and *Tomentellopsis*.

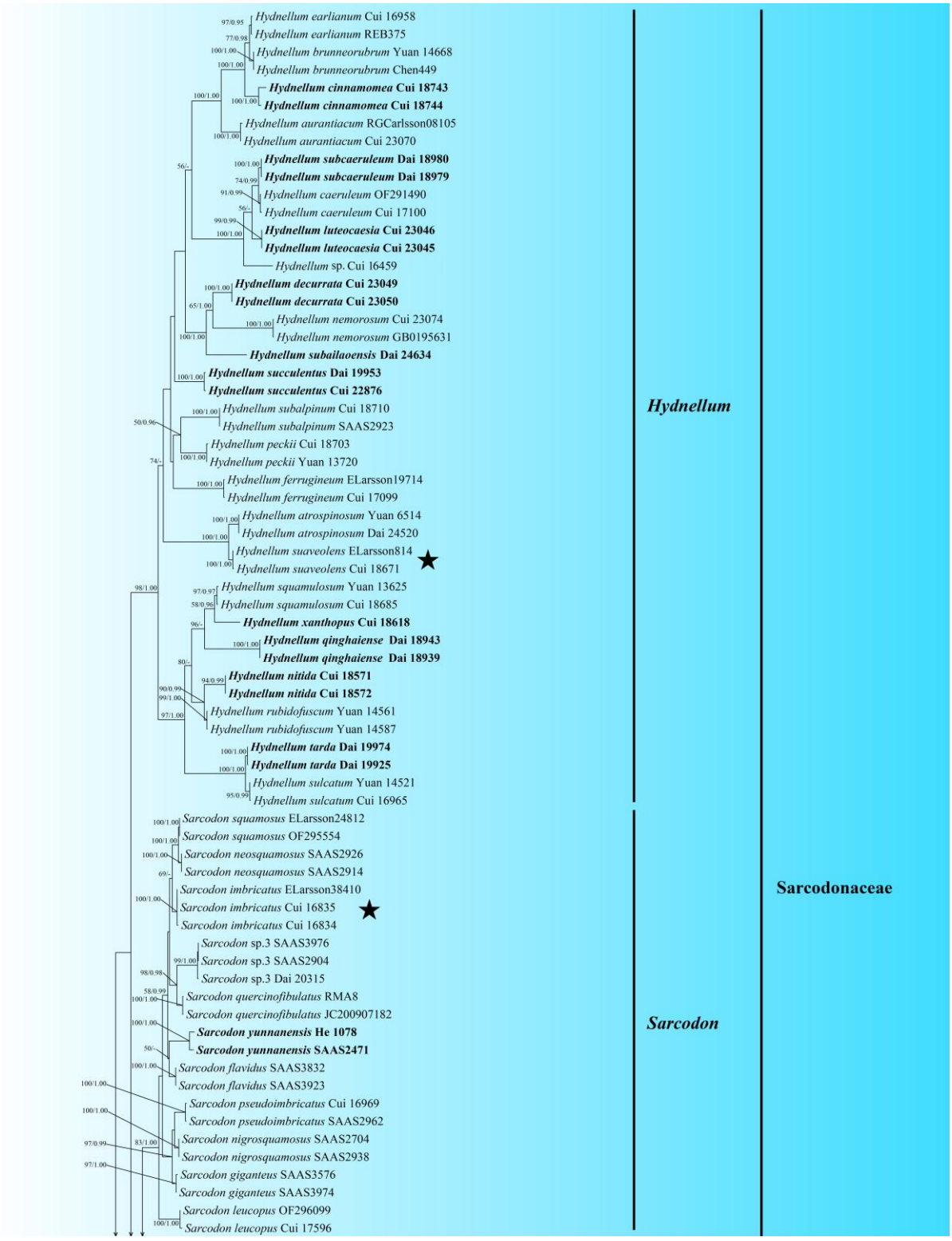

Fig. 1 – Maximum likelihood tree illustrating the phylogeny of Thelephorales based on the combined sequence dataset of ITS+nLSU. Branches are labeled with maximum likelihood bootstrap higher than 50% and Bayesian posterior probabilities more than 0.95 respectively. Bold names = New species. Black stars (★) represent generic type.

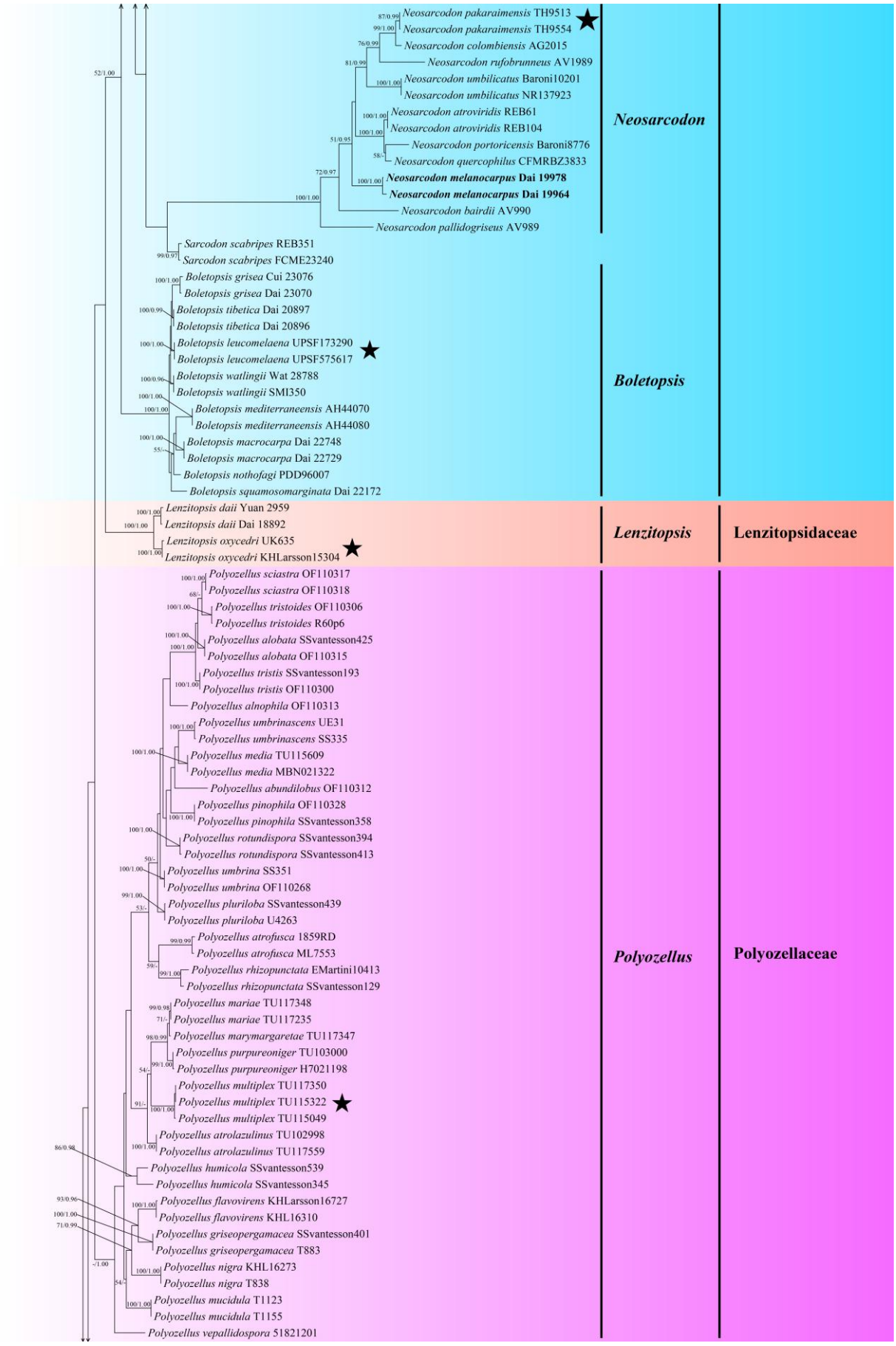

Figure 1 – Continued.

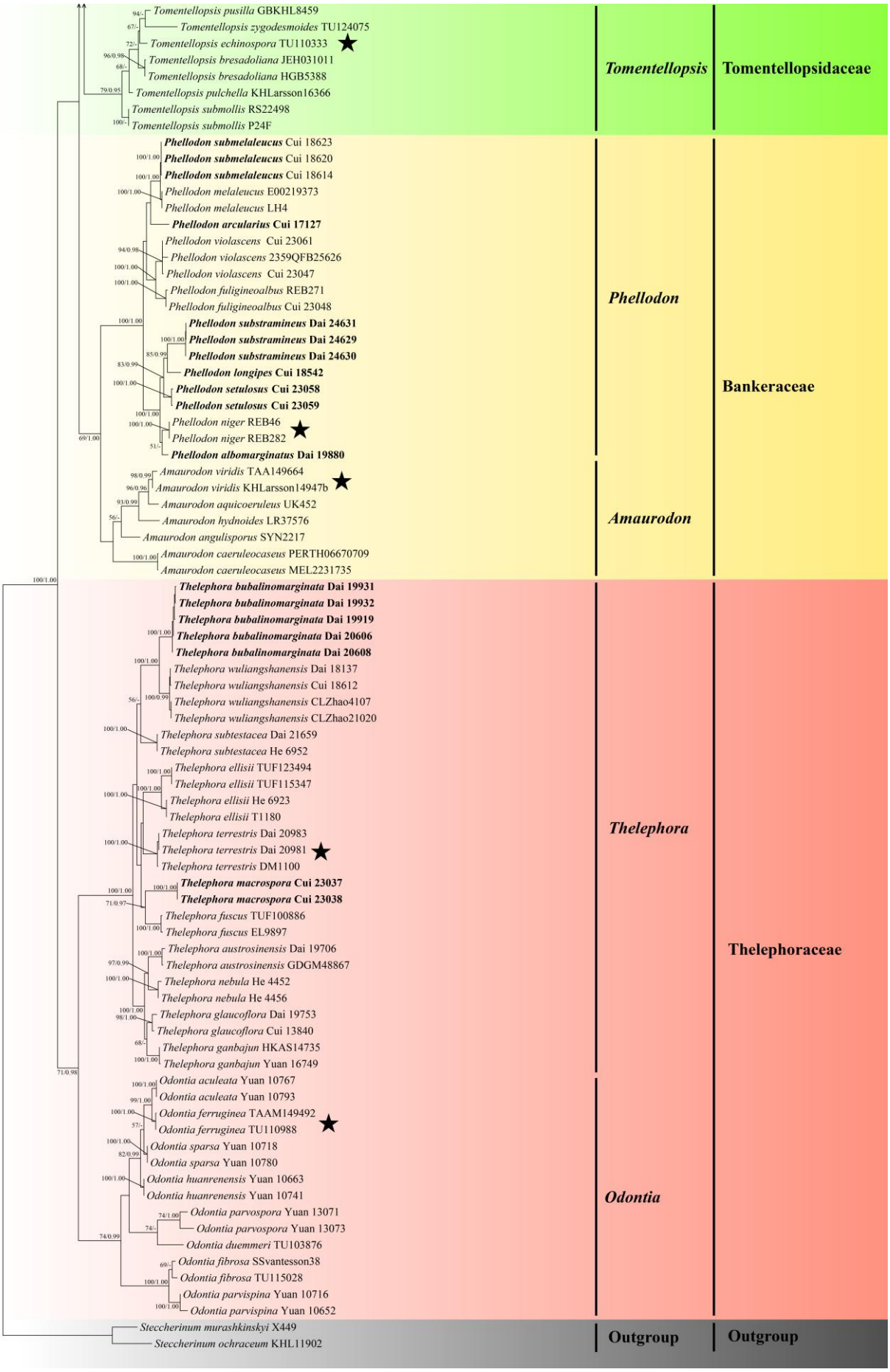

Figure 1 – Continued.

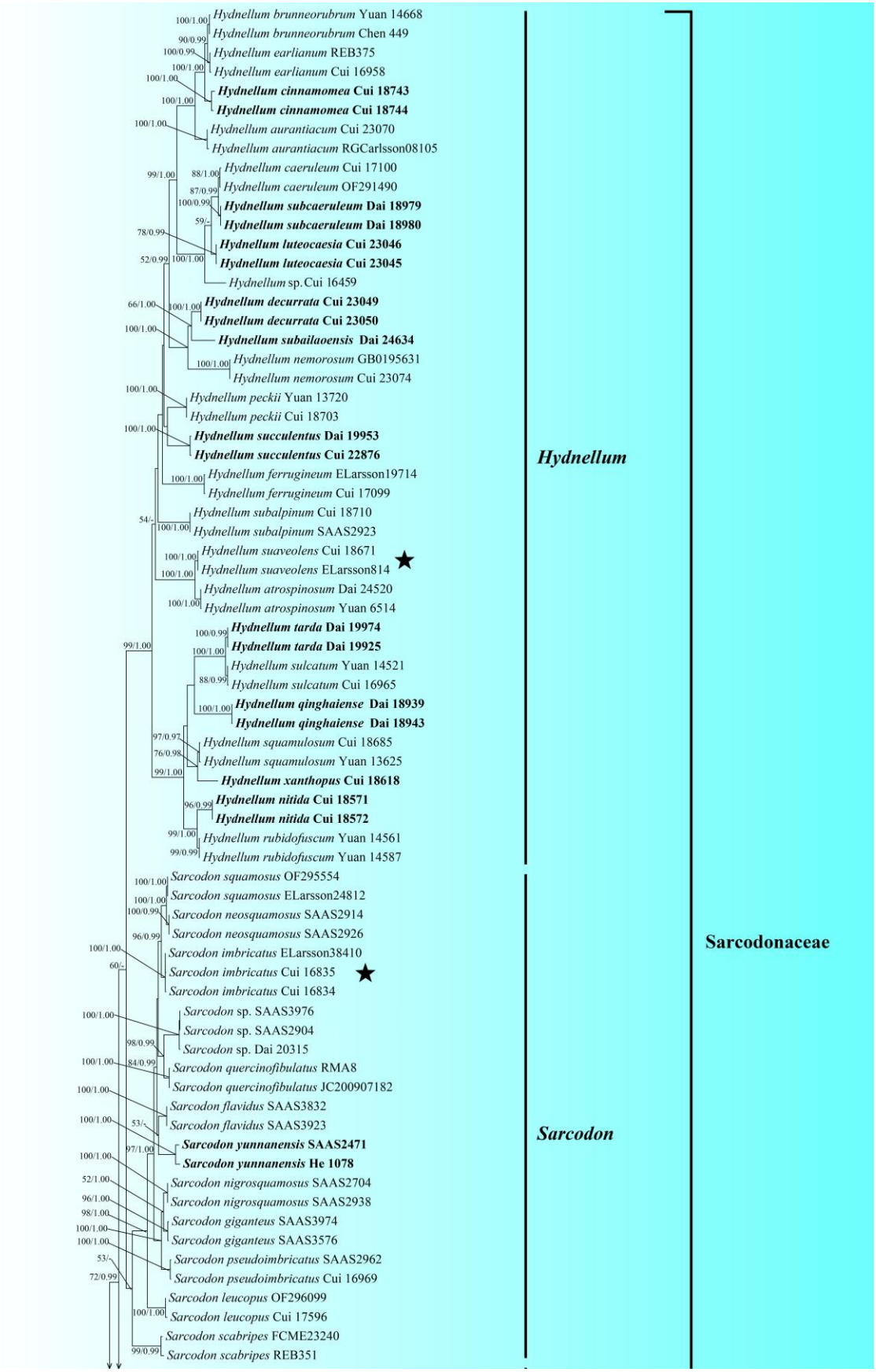

Fig. 2 Maximum likelihood tree illustrating the phylogeny of Thelephorales based on the combined sequence dataset of ITS+nLSU+nSSU+RPB2. Branches are labeled with maximum likelihood bootstrap higher than 50% and Bayesian posterior probabilities more than 0.95 respectively. Bold names = New species. Black stars (★) represent generic type.

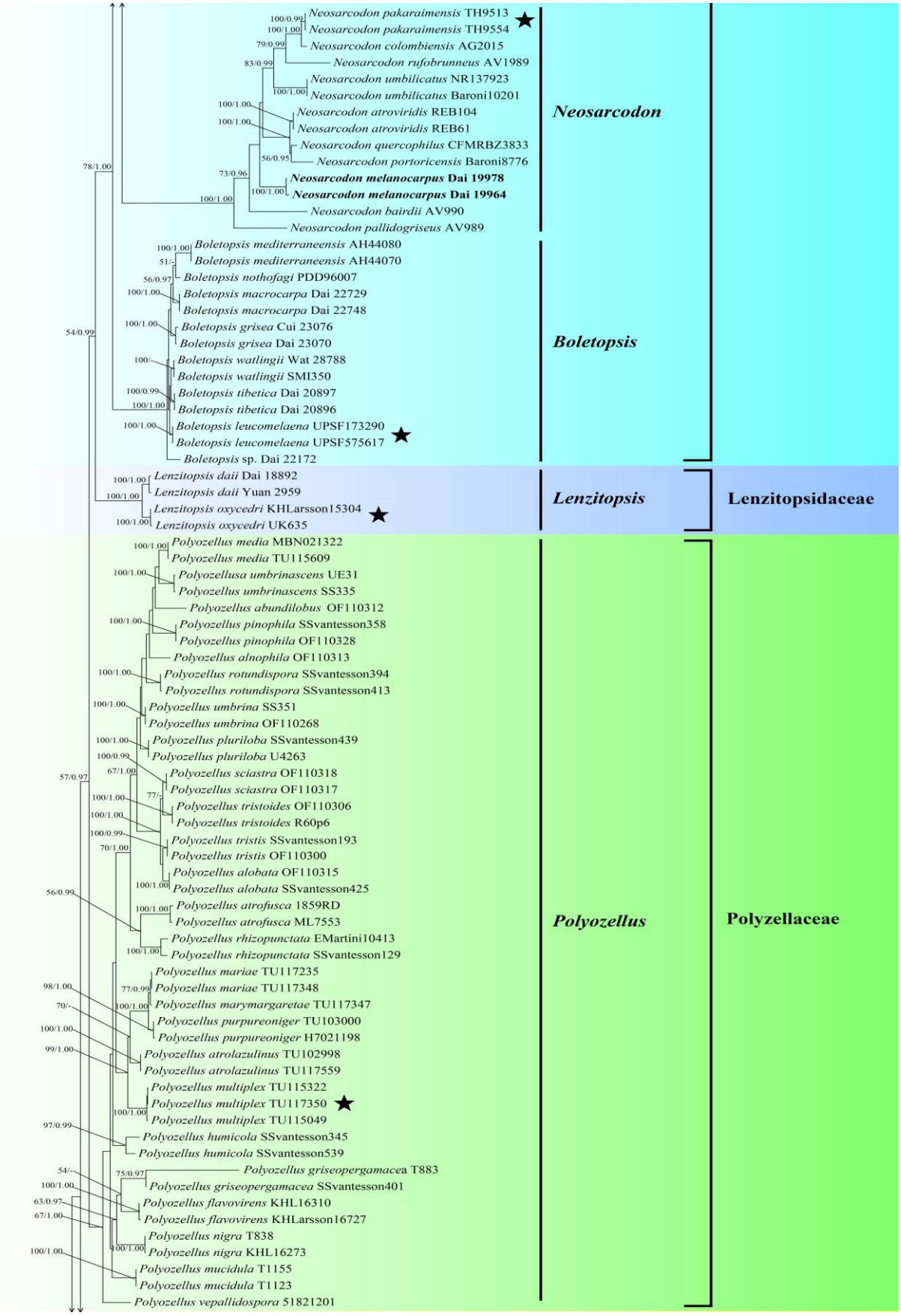

Figure 2 – Continued.

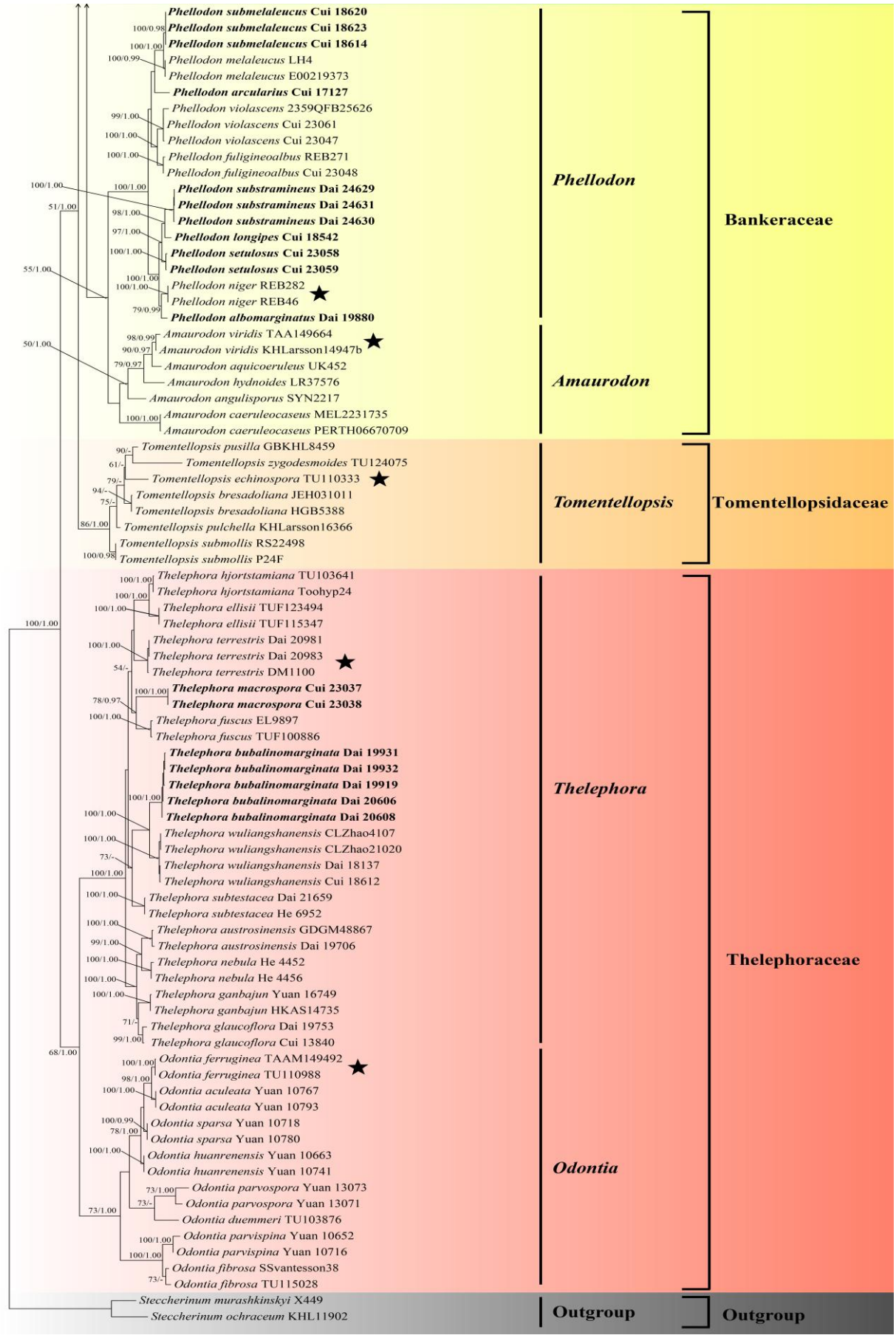

Figure 2 – Continued.

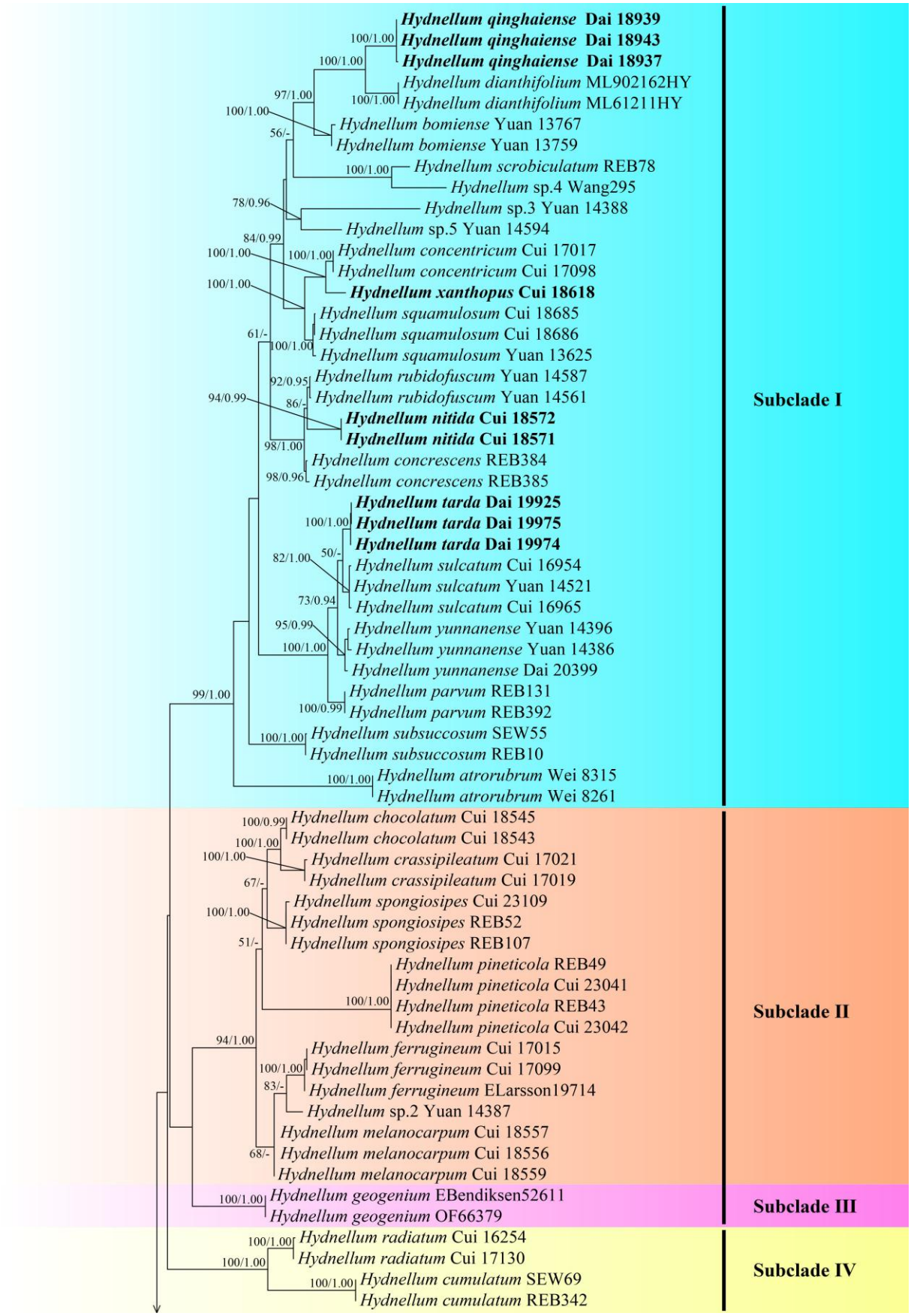

Fig. 3 Maximum likelihood tree illustrating the phylogeny of *Hydnellum* based on the combined sequence dataset of ITS+nLSU+nSSU+RPB2. Branches are labeled with maximum likelihood bootstrap higher than 50% and Bayesian posterior probabilities more than 0.95 respectively. Bold names = New species.

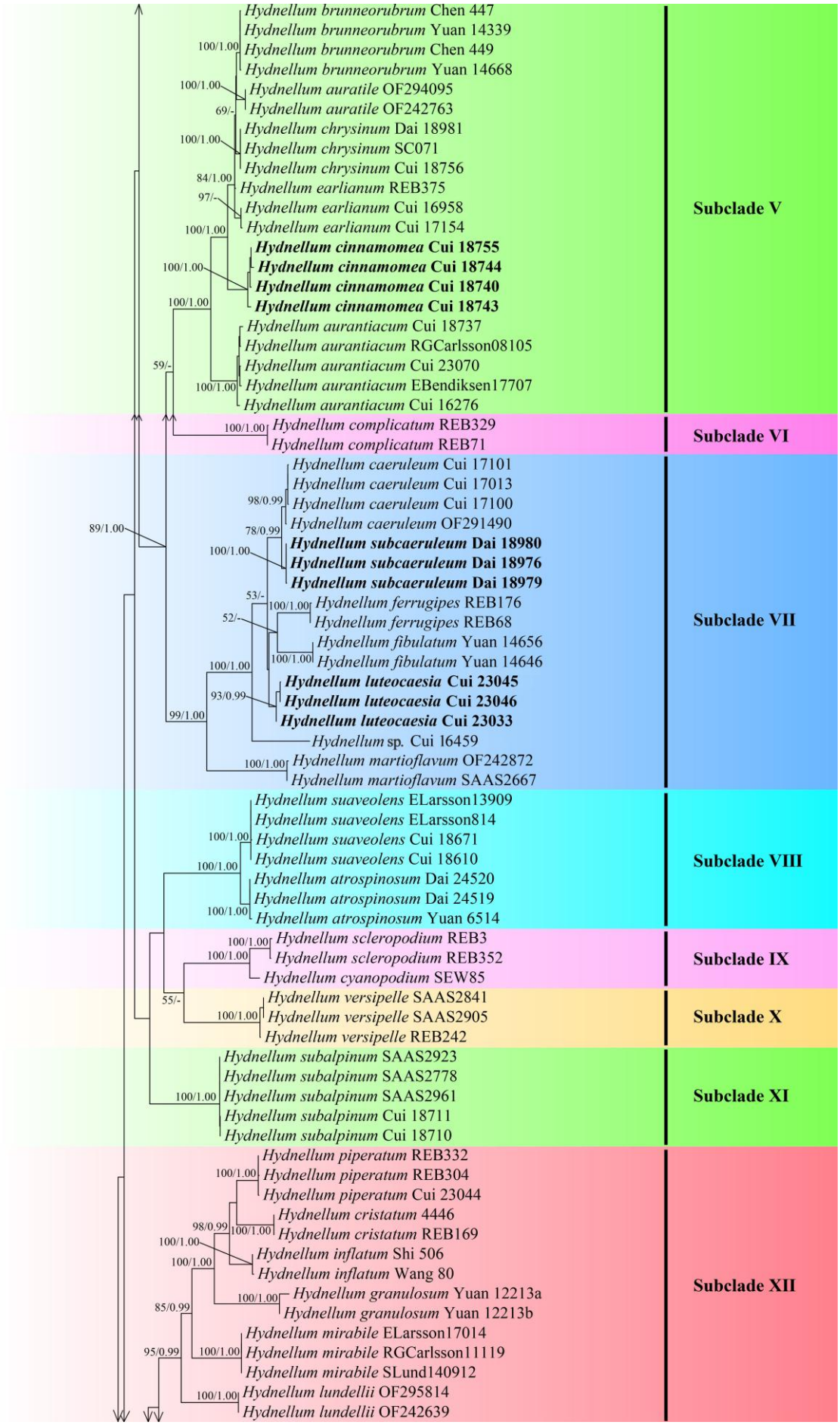

Figure 3 – Continued.

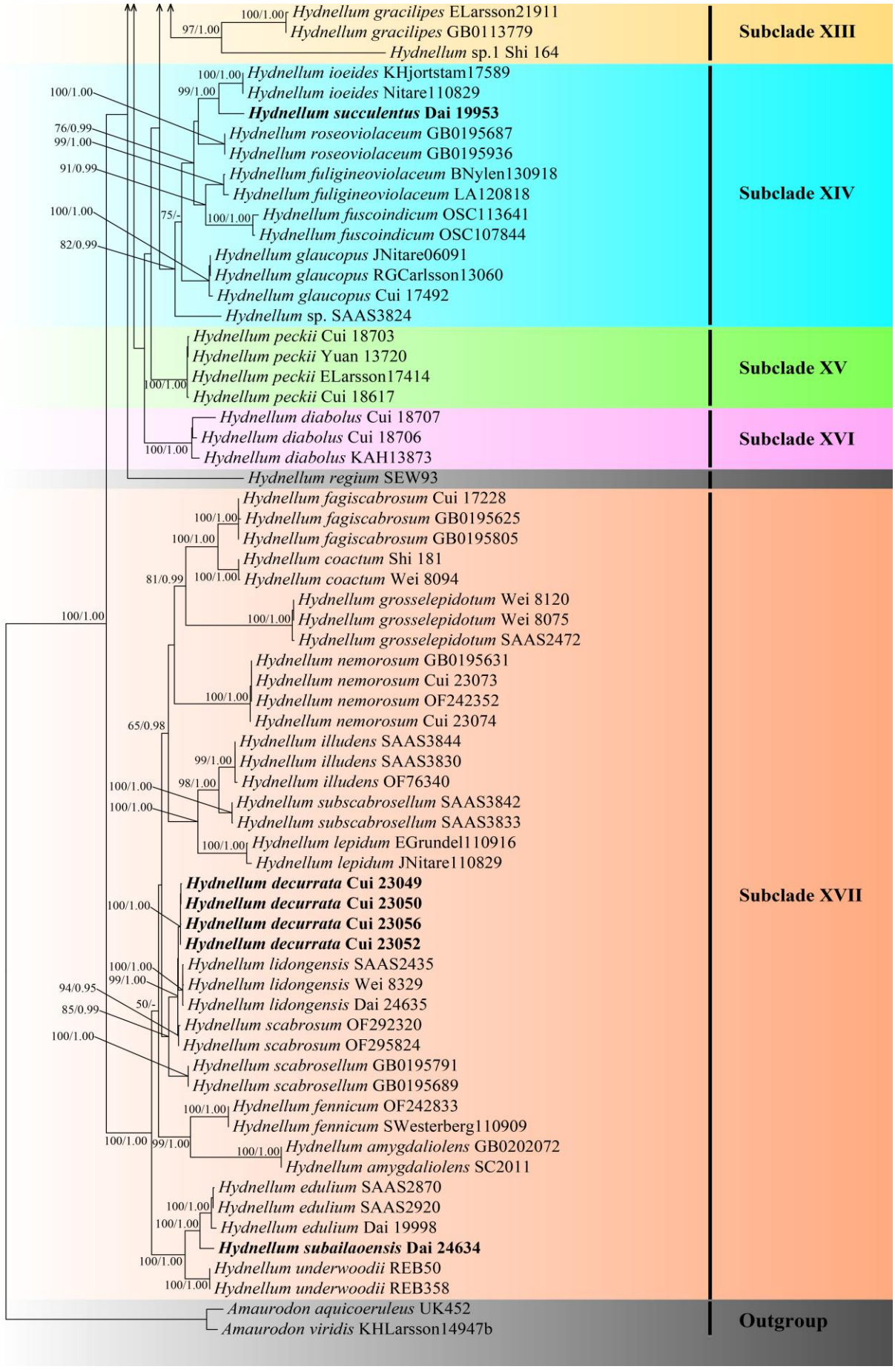

Figure 3 – Continued.

Fig. 4 Maximum likelihood tree illustrating the phylogeny of *Phellodon* based on the combined sequence dataset of ITS+nLSU+nSSU+RPB2. Branches are labeled with maximum likelihood bootstrap higher than 50% and Bayesian posterior probabilities more than 0.95 respectively. Bold names = New species.

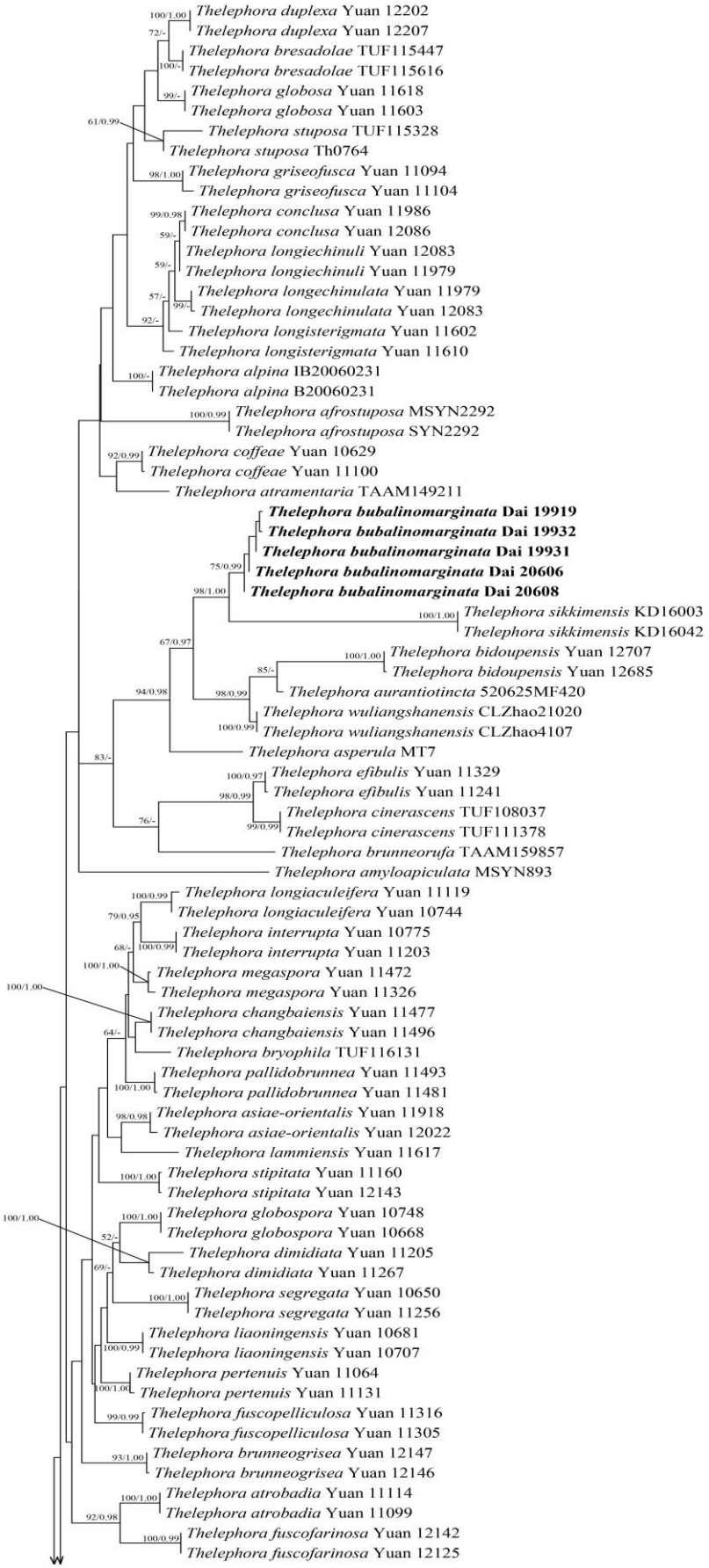

Fig. 5 Maximum likelihood tree illustrating the phylogeny of *Thelephora* based on the combined sequence dataset of ITS+nLSU. Branches are labeled with maximum likelihood bootstrap higher than 50% and Bayesian posterior probabilities more than 0.95 respectively. Bold names = New species.

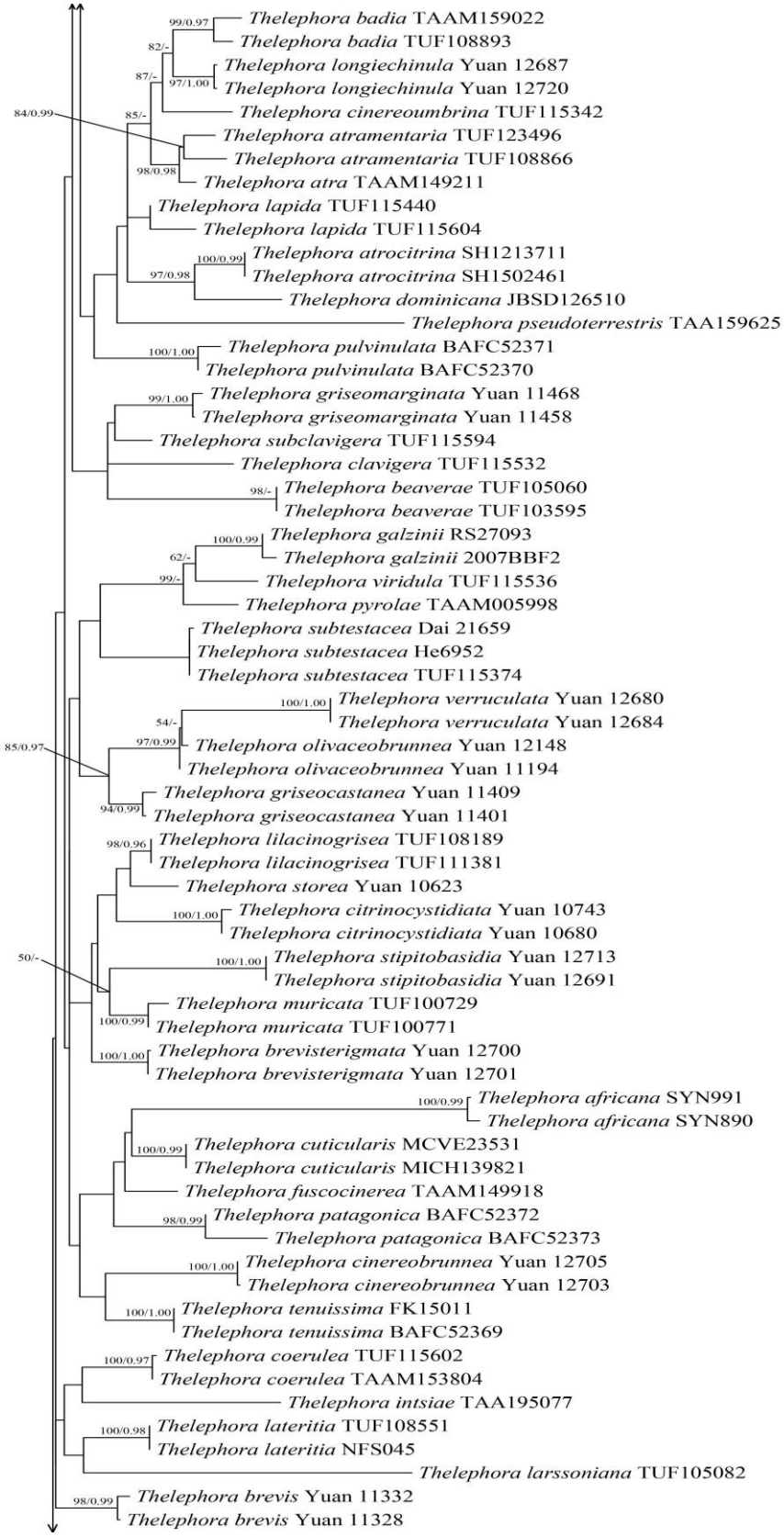

Figure 5 – Continued.

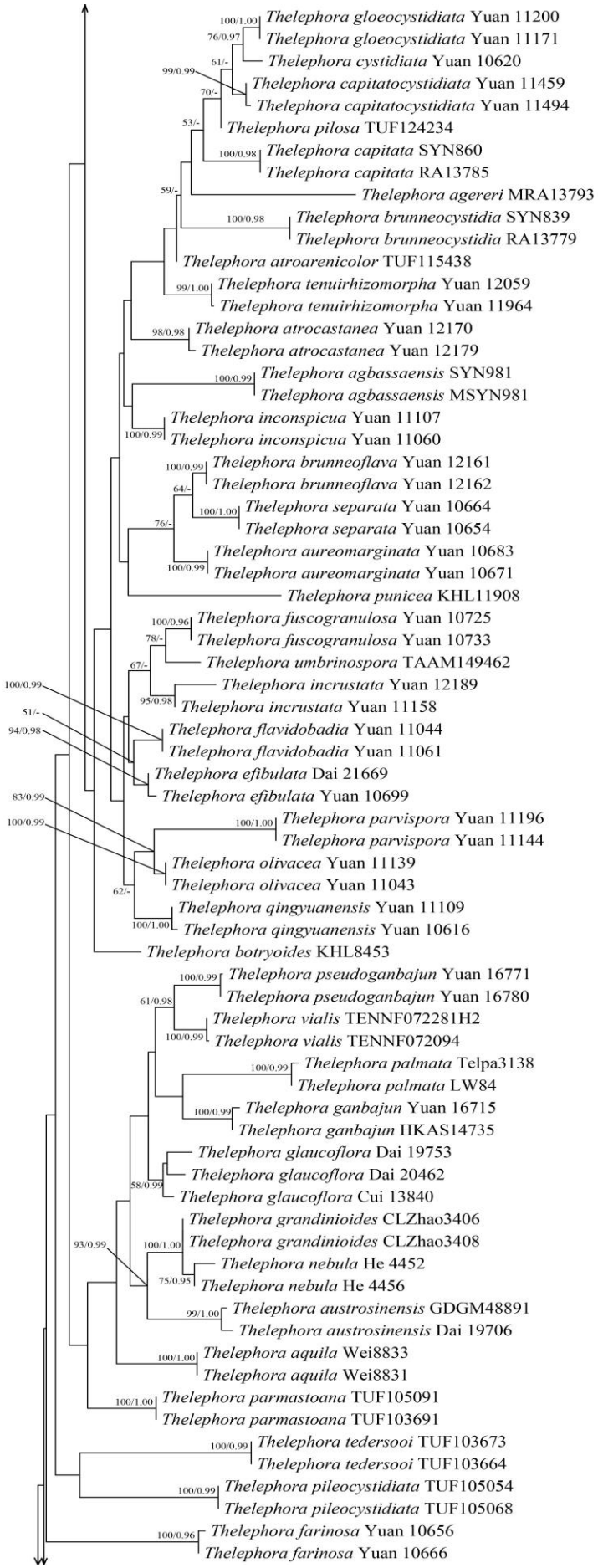

Figure 5 – Continued.

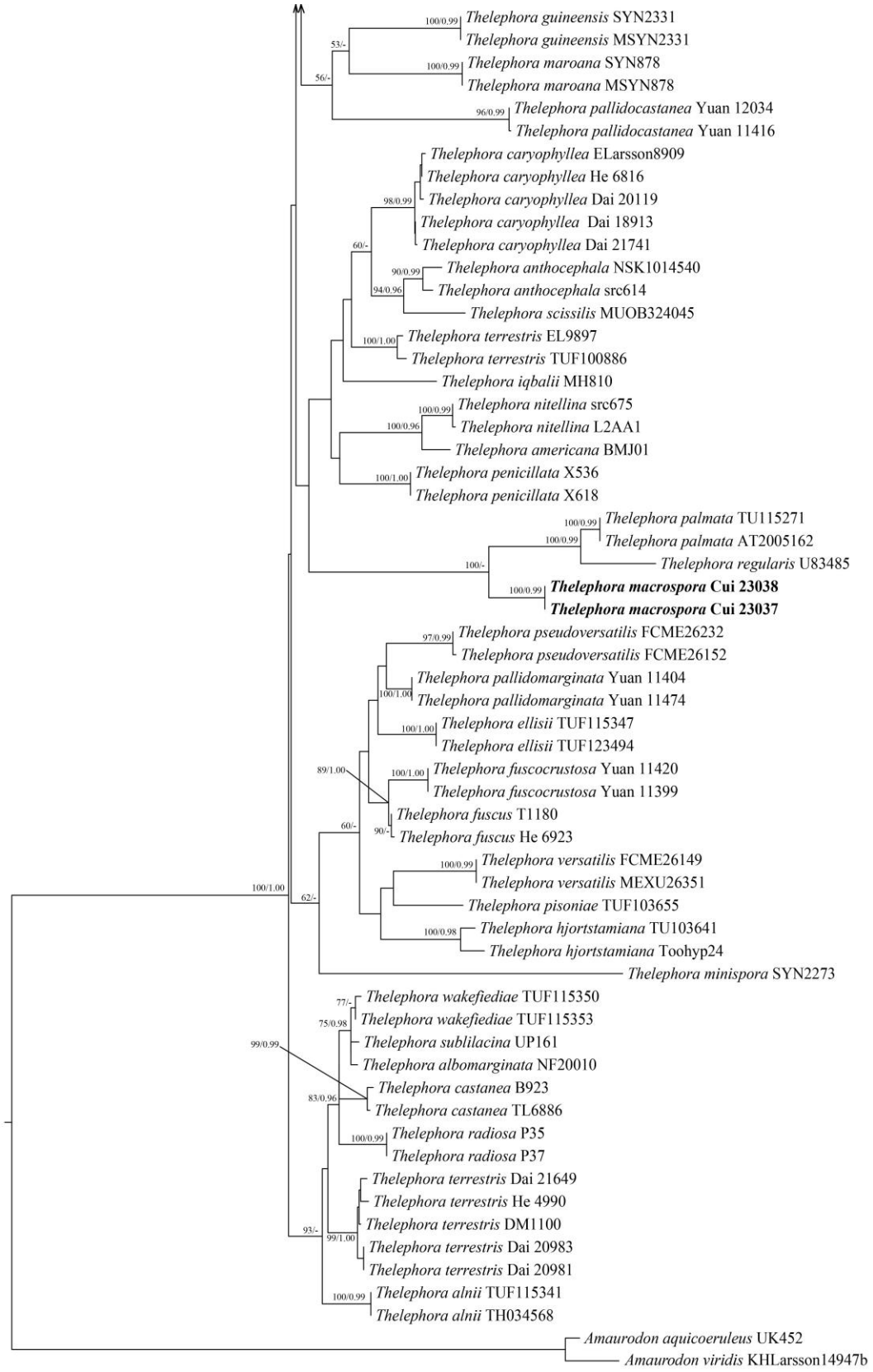

Figure 5 – Continued.

Divergence time estimation

The combined datasets of ITS, nLSU, nSSU, and RPB2 sequences from 92 fungal samples were used to infer the divergence times of Thelephorales (Fig. 6). It indicated that the ancestor of Thelephorales evolved during the late Jurassic Period, approximately 269.07 Mya, with a 95%

highest posterior density (HPD) of 126.7–349.43 Mya. Six families of Thelephorales were centralized differentiation in the Mesozoic (about 145.95–269.07 Mya). Among them, the first to appear was Thelephoraceae (269.07 Mya), and the latest were Lenzitopsidaceae and Polyozellaceae (145.95 Mya). Eleven other orders viz. Agaricales, Amylocorticiales, Atheliales, Boletales, Geastrales, Gloeophyllales, Hymenochaetales, Jaapiales, Polyporales, Russulales and Stereopsidales were also contained in the divergence time estimation, split at about 81.32–165.65 Mya, which generally consistent with the previous studies (Ji et al. 2022, Liu et al. 2023b). The estimated divergence times of the families and genera in Thelephorales were summarized in Table 2.

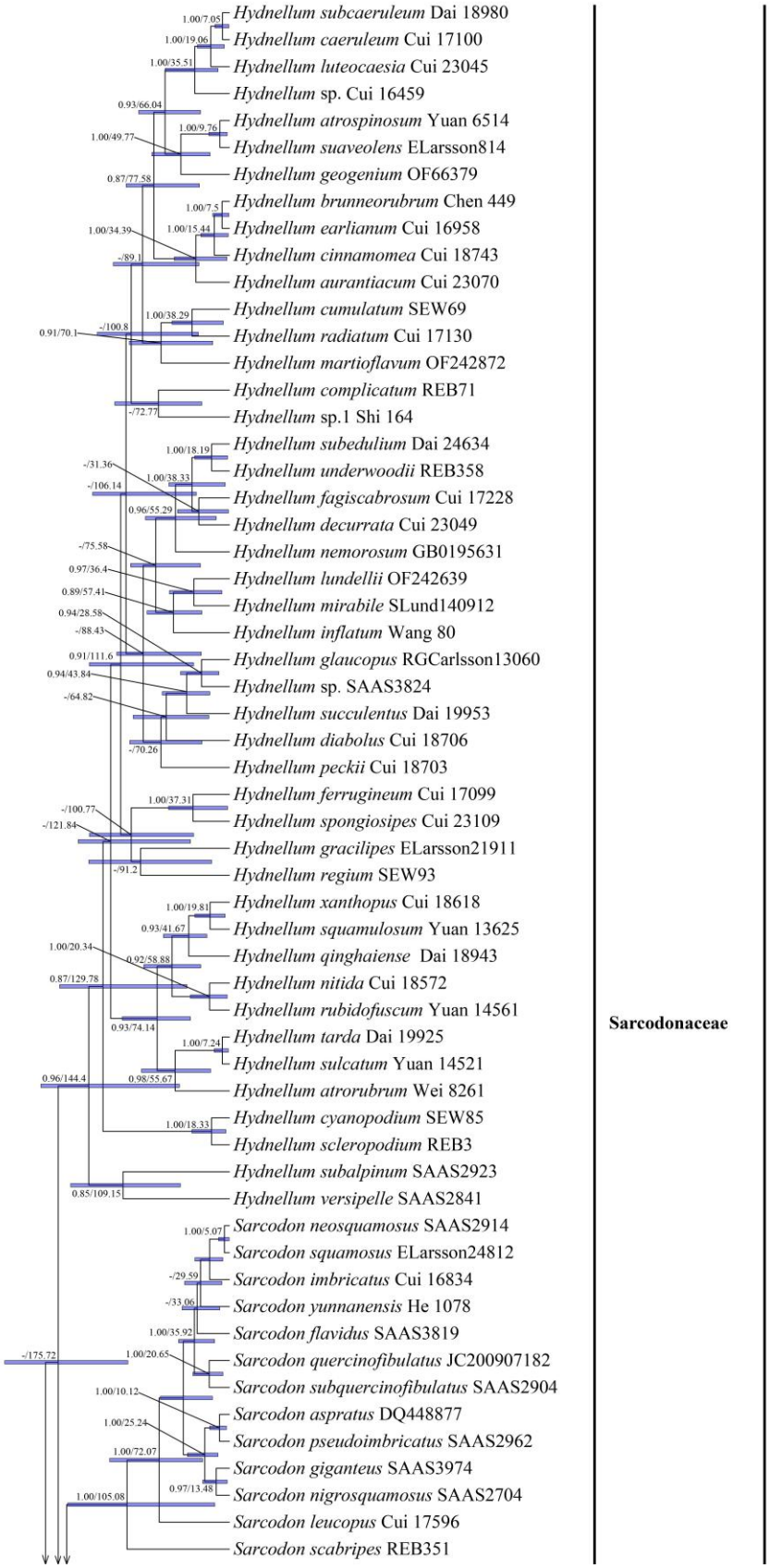

Fig. 6 Divergence time estimation of Thelephorales from Bayesian evolutionary analysis sampling tree based on ITS, nLSU, nSSU, and RPB2 multiple datasets. Posterior probabilities not less than 0.80 and the mean ages of each node are annotated. The 95% highest posterior densities of divergence time estimation are marked by horizontal bars.

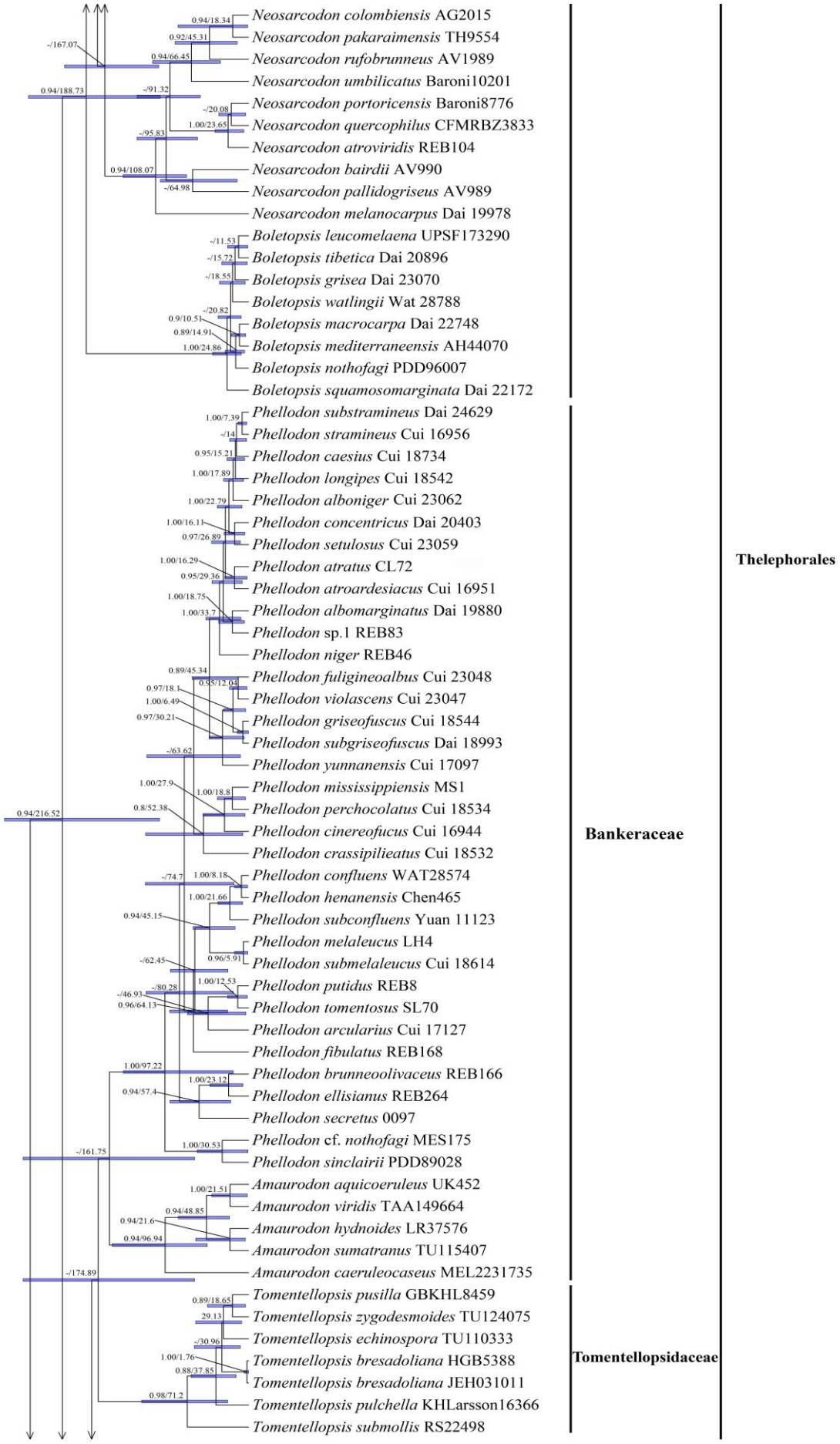

Figure 6 – Continued.

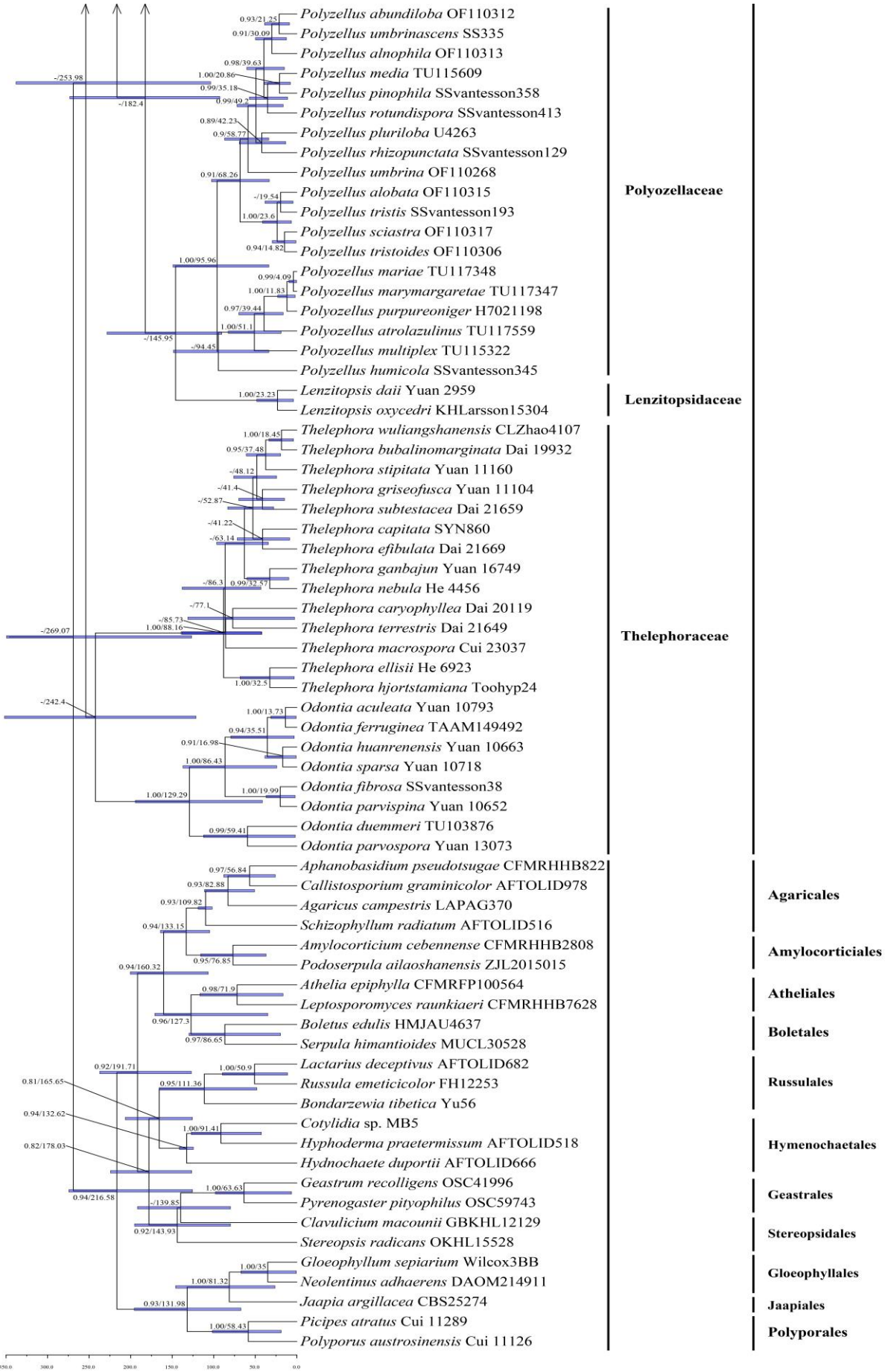

Figure 6 – Continued.

Table 2 The divergence times of the families and genera in Thelephorales

Families recognized in this study	Gengera recognized in this study	Mean of stem age (Mya)	95% HPD (Mya)
Lenzitopsidaceae		145.95	90.4–228.38
	Lenzitopsis	145.95	90.4–228.38
Bankeraceae		174.89	62.74–262.17
	Amaurodon	161.75	62.74–262.17
	Phellodon	161.75	62.74–262.17
Polyozellaceae		145.95	90.4–228.38
	Polyozellus	145.95	90.4–228.38
Sarcodonaceae		216.52	103.5–283.79
	Boletopsis	188.73	102.71–256.02
	Hydnellum	175.72	104.24–230.69
	Neosarcodon	167.07	104.48–214.04
	Sarcodon	167.07	104.48–214.04
Thelephoraceae		253.98	103.7–337.98
	Odontia	242.4	121.4–351.79
	Thelephora	242.4	121.4–351.79
Tomentellopsidaceae		174.89	62.74–262.17
	Tomentellopsis	174.89	62.74–262.17

Note: Mya: million years ago, HPD: highest posterior density.

Taxonomy

Thelephorales Corner ex Oberw.

Type family – Thelephoraceae Chevall.

Description – Basidiomata annual, pileate or resupinate, sessile to stipitate, colored in a wide variety of tints. Hymenophores white, blue to brown or darker, smooth, aculeate or poroid. Hyphal system monomitic or dimitic, generative hyphae with simple-septate or clamp connections. Cystidia absent or present, clavate, obclavate or acuminate. Basidia clavate to utriform, sometimes sinuous, 2(–4)–spored. Basidiospores hyaline or colored with pale buff to brown or blue, irregular, ellipsoid, subglobose to globose, smooth, echinulate or warted.

Notes – Thelephorales were established by Oberwinkler to describe fungi with colorless to strongly pigmented, non-amyloid, warted to typically echinulate basidiospores (Stalpers 1993). Previously, species in Thelephorales were usually divided into two families, Bankeraceae and Thelephoraceae, based on morphological characteristics (Stalpers 1993). However, due to the scarcity of molecular data and techniques, no systematic phylogenetic studies of Thelephorales were conducted. In this study, the DNA sequences of multiple loci (ITS+nLSU+nSSU+RPB2) were used to construct phylogenetic relationships and infer the divergence time of Thelephorales. The phylogenetic analyses revealed that the original two families, Bankeraceae and Thelephoraceae, did not form monophyletic clades respectively, and the entire Thelephorales formed six separate clades (Figs. 1, 2, 6). We confirmed that species of these clades can represent six families by combining with morphological studies. Therefore, the order Thelephorales was divided into six families.

Key to family of Thelephorales

1. Hymenophores sinuous to lenzitoid.....Lenzitopsidaceae
1. Hymenophores not sinuous to lenzitoid 2
2. Clamp connections absent .....Tomentellopsidaceae
2. Clamp connections present.....3
3. Cystidia present ..... Thelephoraceae
3. Cystidia absent.....4
4. Hymenophores reticulate or almost poroid to corticioid .....Polyozellaceae

4. Hymenophores not reticulate or almost poroid to corticioid 5
5. Basidiospores hyaline to pale yellow or blue ..... Bankeraceae
5. Basidiospores hyaline or brown..... Sarcodonaceae

Bankeraceae Donk, Persoonia 1 (4): 405. 1961.

Type genus – *Phellodon* P. Karst.

Description – Basidiomata annual, pileate or resupinate, often initially tomentose, glabrous with age, colored in a wide variety of tints. Hymenophores white, blue to brown or darker, smooth, aculeate or poroid. Hyphal system monomitic; generative hyphae with simple-septate or clamp connections. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores hyaline to pale yellow or blue, broadly subglobose to globose, smooth, echinulate or warted.

Notes – Donk (1961) established Bankeraceae with two genera: *Bankera* and *Phellodon*. However, Baird et al. (2013) recombined the type species of *Bankera* to *Phellodon* due to the consistent morphological characteristics with *Phellodon* and the included phylogenetic relationships of the *Phellodon* clade. It suggested that *Bankera* should be regarded as the synonym of *Phellodon*, and recent studies recognized this revision (Song et al. 2021, 2022a, 2023). In this study, *Phellodon* and *Amaurodon* formed an independent clade in Thelephorales with moderate support (69% ML, 1.00 BPP, Fig 1; 55% ML, 1.00 BPP, Fig. 2). Morphologically, the species in this clade can be identified by pileate or resupinate basidiomata, smooth, aculeate or poroid hymenophores, and hyaline to pale yellow or blue basidiospores. It is different from other families in Thelephorales. Besides, the divergence time estimation results showed that *Phellodon* and *Amaurodon* clustered together, and the ancestor of both evolved at 161.75 Mya, which was in line with the time range for the differentiation of other families in Thelephorales (Fig. 6). The family name Bankeraceae was in honor of the mycologist H. J. Banker (Donk 1961), and the original type genus *Bankera* has been grouped into *Phellodon*. Thus, the family Bankeraceae consist of *Phellodon* and *Amaurodon*, with *Phellodon* as the type genus.

Key to genera of Bankeraceae

1. Basidiospores smooth or warted ..... *Amaurodon*
1. Basidiospores echinulate ..... *Phellodon*

Amaurodon J. Schröt., Kryptogamen-Flora von Schlesien 3–1(4): 461, 1888.

Type species – *Amaurodon viridis* (Alb. & Schwein.: Fr.) J. Schröt.

Description – Basidiomata annual, resupinate, blue to yellow-green. Hymenophores blue, smooth, aculeate, or poroid. Hyphal system monomitic; generative hyphae with simple-septate or clamp connections. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores hyaline to pale yellow or blue, ellipsoid or subglobose, smooth to warted. For a detailed description of *Amaurodon*, see Kõljalg (1996) and Svantesson et al. (2022).

Notes – *Amaurodon*, established by J. Schröt. in 1888, has grown on standing angiosperm wood in the middle stages of decay (Schröter 1888, Miettinen & Kõljalg 2007, Gardt et al. 2011). *Amaurodon* species have been reported from Europe and Asia (Bourdot & Galzin 1924, 1928, Wakefield 1952, Burdsall & Larsen 1974, Kõljalg 1996; Agerer & Bougher 2001, Číñek et al. 2007, Melo et al. 2006), Australia (Agerer & Bougher 2001), America (Gilbertson 1974, Ginns 1989), and tropical areas of Africa (Miettinen & Kõljalg 2007, Gardt et al. 2011). *Amaurodon* species were characterized by resupinate, lignicolous, and corticioid basidiomata, with smooth or aculeate hymenophores, blue to green, which turns green after drying, and hyaline to pale yellow or blue basidiospores that turn purple in KOH (Kõljalg 1996, Svantesson et al. 2022). Currently, eleven species are contained in *Amaurodon* (He et al. 2019, Svantesson et al. 2022), which were considered saprotrophic (Kõljalg 1996, Kõljalg & Ryvarden 1997, Agerer & Bougher 2001, Miettinen & Kõljalg 2007, Gardt et al. 2011, Svantesson et al. 2022). *Amaurodon*, together with *Tomentella* Pers. ex-Pat., *Pseudotomentella* Svrèek, and *Tomentellopsis* Hjortstam, were commonly termed tomentelloid genera, because of the resupinate basidiomata (Kõljalg 1996, Larsson et al.

2004). Kõljalg (1996) and Larsson et al. (2004) confirmed that *Amaurodon* can be classified among Thelephorales Corner ex Oberw. as a distinct monophyletic genus. However, *Tomentella*, *Pseudotomentella*, and *Tomentellopsis* all belong to ectomycorrhizal fungi (Lu & Yuan 2021, Svantesson et al. 2022, Kõljalg et al. 2009). Our phylogenetic analysis contains seven fungal samples representing five species (Figs. 1, 2). In this study, *Amaurodon* was divided into two parts, of which four species clustered together with proper support (56% ML, Fig. 1; 50% ML, 1.00 BPP, Fig. 2), and *Amaurodon caeruleocaseus* formed an independent branch in Thelephorales with high support (100% ML, 1.00 BPP, Figs. 1, 2). Morphologically, *A. caeruleocaseus* differs from other *Amaurodon* species by stipitate basidiomata and smooth basidiospores. Due to the inadequate specimens of *Amaurodon*, the phylogenetic relationships of the genus cannot be fully resolved for the time being. More specimens and credible sequences are needed to clarify the taxonomic status of *Amaurodon*.

Phellodon P. Karst., Revue Mycologique Toulouse 3 (9): 19, 1881.

Type species – *Phellodon niger* (Fr.) P. Karst.

Description – Basidiomata annual, pileate, centrally or laterally stipitate, single to concrescent. Pileus depressed to infundibuliform or irregular, brown, greyish brown, straw buff, to almost black, glabrous, fibrillose, spongy to tomentose, often strigose hairy becoming matted or pitted. Hymenophores white, blue, brown or darker, aculeate. Hymenophores white, grey or tinged violaceous, aculeate, sometimes decurrent. Hyphal system monomitic; generative hyphae with simple-septate or clamp connections. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores hyaline, ellipsoid, subglobose to globose, echinulate. For a detailed description of *Phellodon*, see Karsten (1881) and Song et al. (2021, 2022a, 2023).

Notes – *Phellodon* was established by Karsten (Karsten 1881). *Phellodon* species were often found under pine needles or oak leaves in coniferous or oak forests or mixed forests (Song et al. 2023). The wet woodlands where they grow are often covered with dense moss to prevent water loss. According to previous studies, *Phellodon* species often grow at high altitudes (from 870 to 3320 m, Song et al. 2023). However, the specimens collected in the United States in this study grew in forests at more than 400 m altitudes. The genus *Phellodon* may be widely distributed in the Northern Hemisphere. It has been reported in North America (Harrison 1961, 1964, 1968, 1972, 1984, Harrison & Grund 1987a, 1987b, Maas Geeseranus 1971, 1975, Baird 1986a, 1986b, Baird et al. 1987, 2013), the UK (Parfitt et al. 2007), and Asian (Li 2017). In addition, *Phellodon* species have a significant presence in China and were found in northeast, southwest, northwest, and central China (Song et al. 2021, 2022a, 2023). According to previous studies, about 37 species have been described and transferred to *Phellodon* (Song et al. 2021, 2022a, 2023). *Phellodon* species can be characterized by pileate and stipitate basidiomata, pileus colored in a wide variety of tints, hyaline, and echinulate basidiospores. *Phellodon* presents macro- and micro-morphology similar to *Hydnellum*. However, it can be distinguished by its woody pileus and hyaline basidiospores (Maas Geesteranus 1971). In this study, *Phellodon* was shown to be an independent genus with solid support (100% ML, 1.00 BPP, Figs. 1, 2). With the addition of morphological evidence, six new species were described proposed, and redescribed.

Phellodon albomarginatus B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 7 a, b; 10 a; 13).

Index Fungorum number: IF 902652; Facesoffungi number: FoF 16238

Diagnosis – Differs from other *Phellodon* species by its black basidiomata and white pileal margin.

Type – **CHINA**. Yunnan Province, Pingbian County, Daweishan National Forest Park, on the ground of mixed forest, approx. 103° 42' 30" E22° 58' 13" N, alt. 1500 m, 27 June 2019, Dai 19880 (holotype in BJFC, isotype in IFP).

Etymology – *albomarginatus* (Lat.), refers to the white pileal margin of the basidiomata.

Fruiting body – Basidiomata annual, pileate, centrally stipitate, single to concrescent, with light fenugreek when fresh. Pileus circular, up to 3 cm in diam, and 0.2 cm thick at the center.

Pileal surface black when fresh at the center, brown near the margin, and becoming deep olive to mouse grey upon drying, zonate, tomentose at the center, fibrillose near margin; margin white when fresh and becoming mouse grey upon drying, and up to 0.2 cm wide. Spines soft, white when fresh, pale mouse grey upon drying, fragile, and up to 1 mm long. Context dark grey upon drying, fragile, and up to 0.2 cm thick. Stipes cylindrical, tomentose, black, and up to 2.5 cm long, 1 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green to black in KOH.

Pileus – Generative hyphae dark olive green, thick-walled, rarely branched, regularly arranged, and 2–6 µm in diam.

Spines – Generative hyphae clay-buff, slightly thick-walled, occasionally branched, regularly arranged, and 2–5 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 23–40 × 5–6.5 µm; sterigmata 2–4 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae fuscous to black, thick-walled, occasionally branched, regularly arranged, 2–6 µm in diam.

Spores – Basidiospores, hyaline, subglobose to globose, thin-walled, echinulate, IKI–, CB–, 5–6 × (4.5–) 5–5.5 µm, L = 5.53 µm, W = 5.15 µm, Q = 1.07 (n = 30/1, without the ornamentation).

Notes – *Phellodon albomarginatus* was collected from southwest China under a subtropical humid mountain monsoon climate. In this study, *P. albomarginatus* was closely related to *P. niger* (Fr.) P. Karst (Fig. 4). Morphologically, *P. albomarginatus* might be confused with *P. niger* by having black pileal surface and black stipe. However, it can be distinct by its zonate pileal surface, white pileal margin, and larger basidiospores (5–6 × 4–5 µm, Baird et al. 2013).

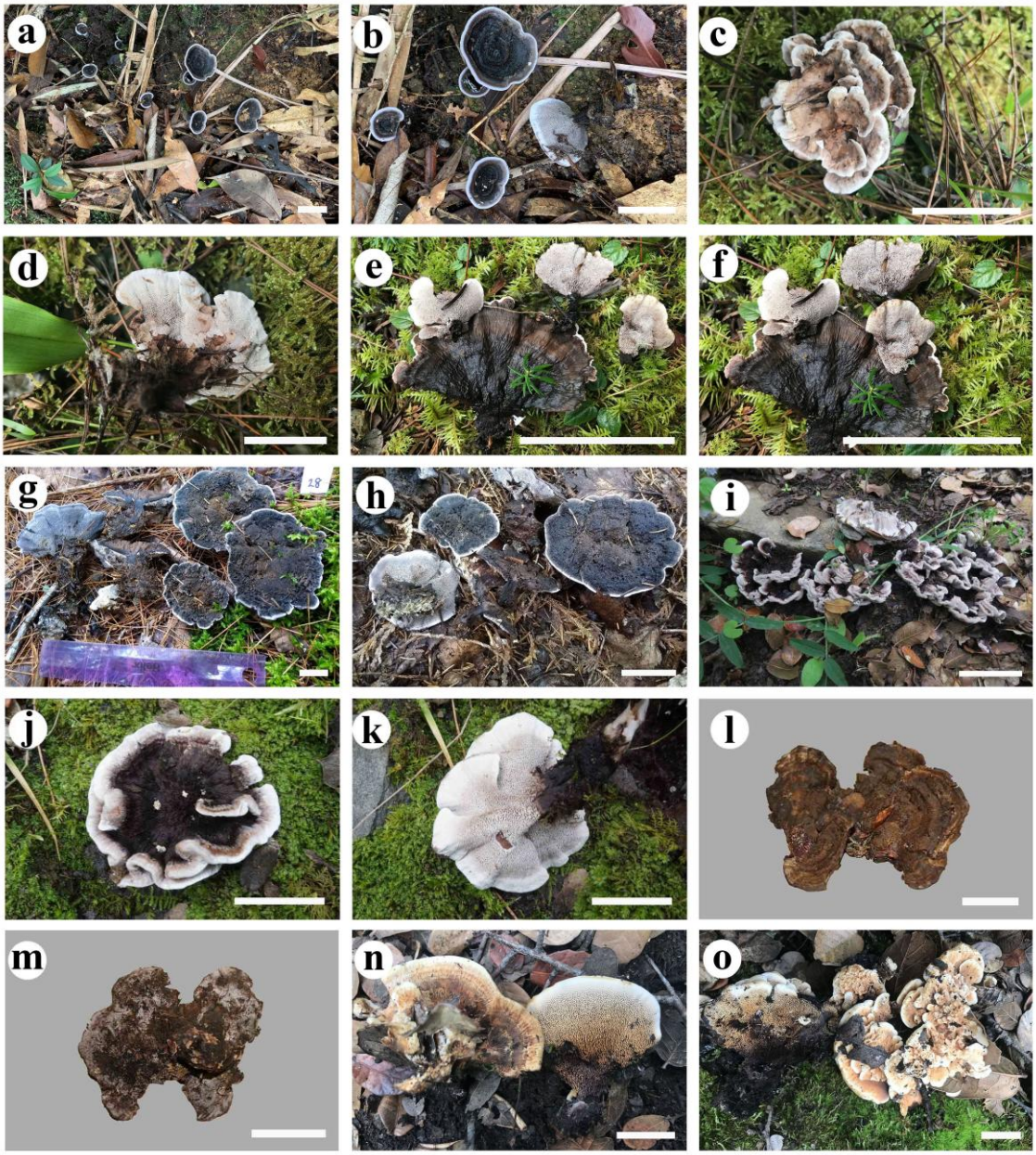

Fig. 7 Basidiocarps of new species. **a, b** *Phellodon albomarginatus* (Dai 19880); **c, d** *Phellodon arcularius* (Cui 17127); **e, f** *Phellodon longipes* (Cui 18542); **g, h** *Phellodon setulosus* (Cui 23031); **i, j, k** *Phellodon submelaleucus* (i from Cui 18620, j-k Cui 18614); **l, m** *Phellodon substramineus* (Dai 24629); **n, o** *Hydnellum cinnamomea* (Cui 18744, Cui 18757).

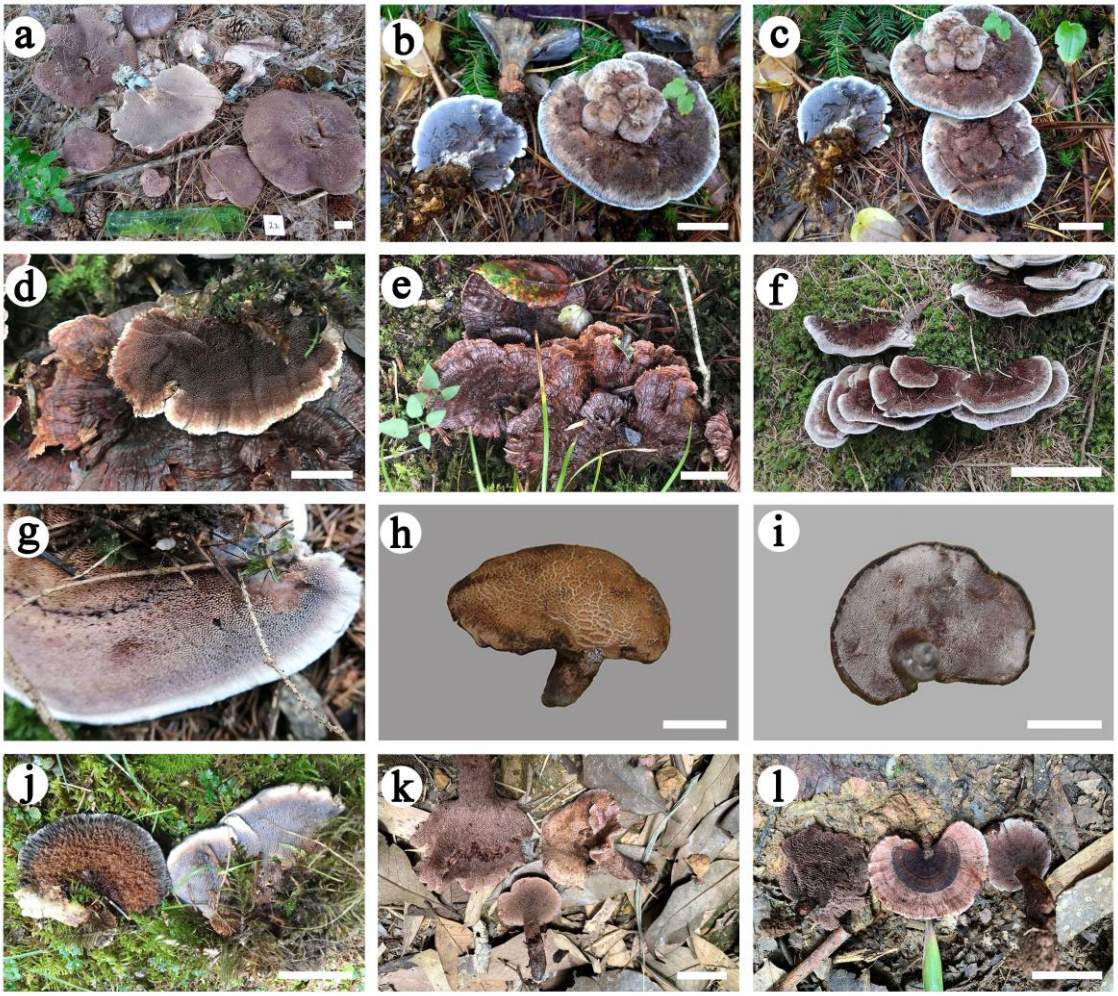

Fig. 8 Basidiocarps of new species. **a** *Hydnellum decurrata* (Cui 23049); **b, c** *Hydnellum luteocaesia* (Cui 23045, Cui 23046); **d, e** *Hydnellum nitida* (Cui 18571, Cui 18572); **f, g** *Hydnellum qinghaiense* (Dai 18939); **h, i** *Hydnellum subailaoensis* (Dai 24634); **j** *Hydnellum subcaeruleum* (Dai 18976); **k,** *Hydnellum succulentus* (Dai 19953); **l** *Hydnellum tarda* (Dai 19925).

Fig. 9 Basidiocarps of new species. **a** *Hydnellum tarda* (Dai 19974); **b**, **c** *Hydnellum xanthopus* (Cui 18618)**; d, e** *Neosarcodon melanocarpus* (Dai 19964); **f, g** *Sarcodon yunnanensis* (He 1078); **h, i, j** *Thelephora bubalinomarginata* (h from Dai 19919, i-j from Dai 19931); **k, l** *Thelephora macrospora* (k from Cui 23037, l from Cui 23038).

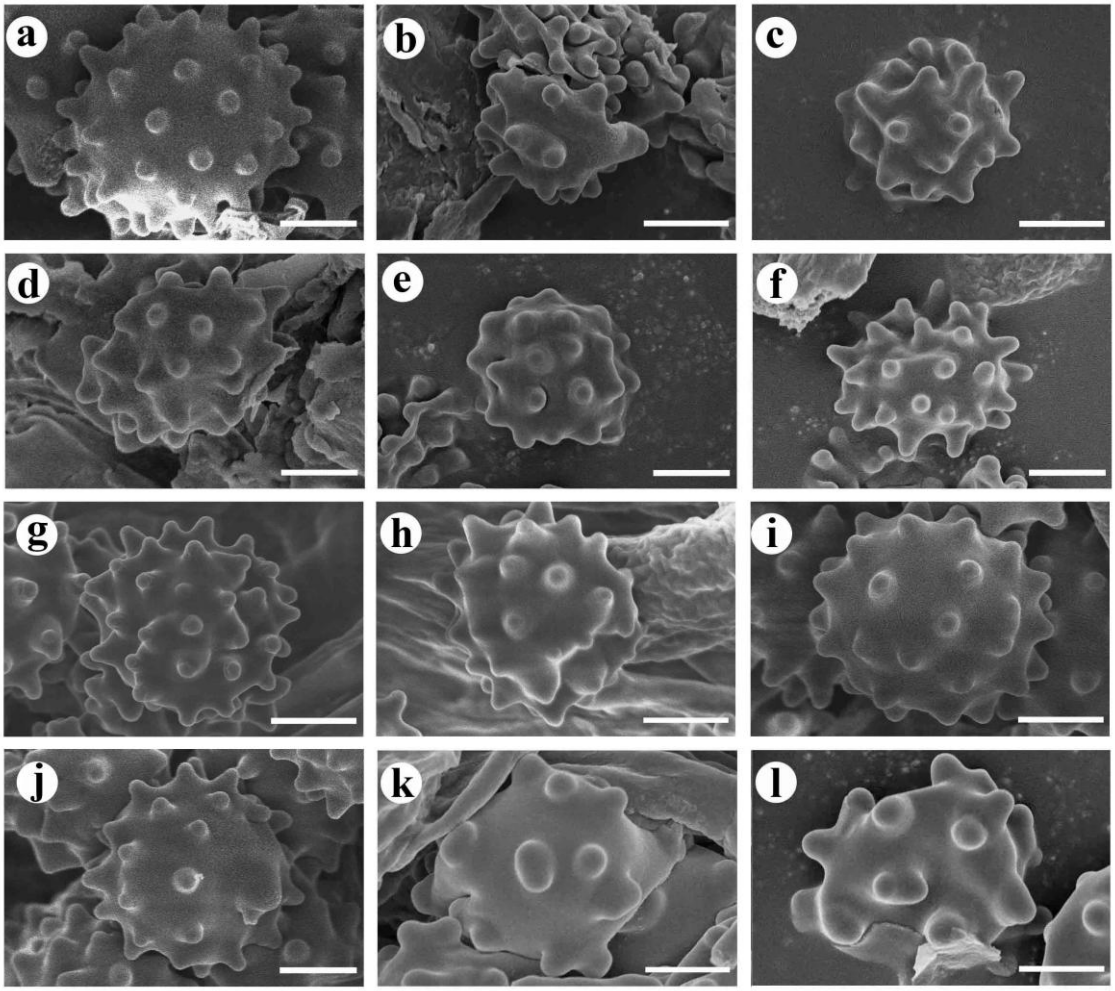

Fig. 10 Scanning Electron Microscope (SEM) of basidiospores of new species. **a** *Phellodon albomarginatus*; **b**, **c** *Phellodon arcularius*; d *Phellodon longipes*; **e, f** *Phellodon setulosus*; **g, h** *Phellodon submelaleucus*; **i, j** *Phellodon substramineus*; **k** *Hydnellum cinnamomea*; **l** *Hydnellum decurrata*. Bars: 2 µm.

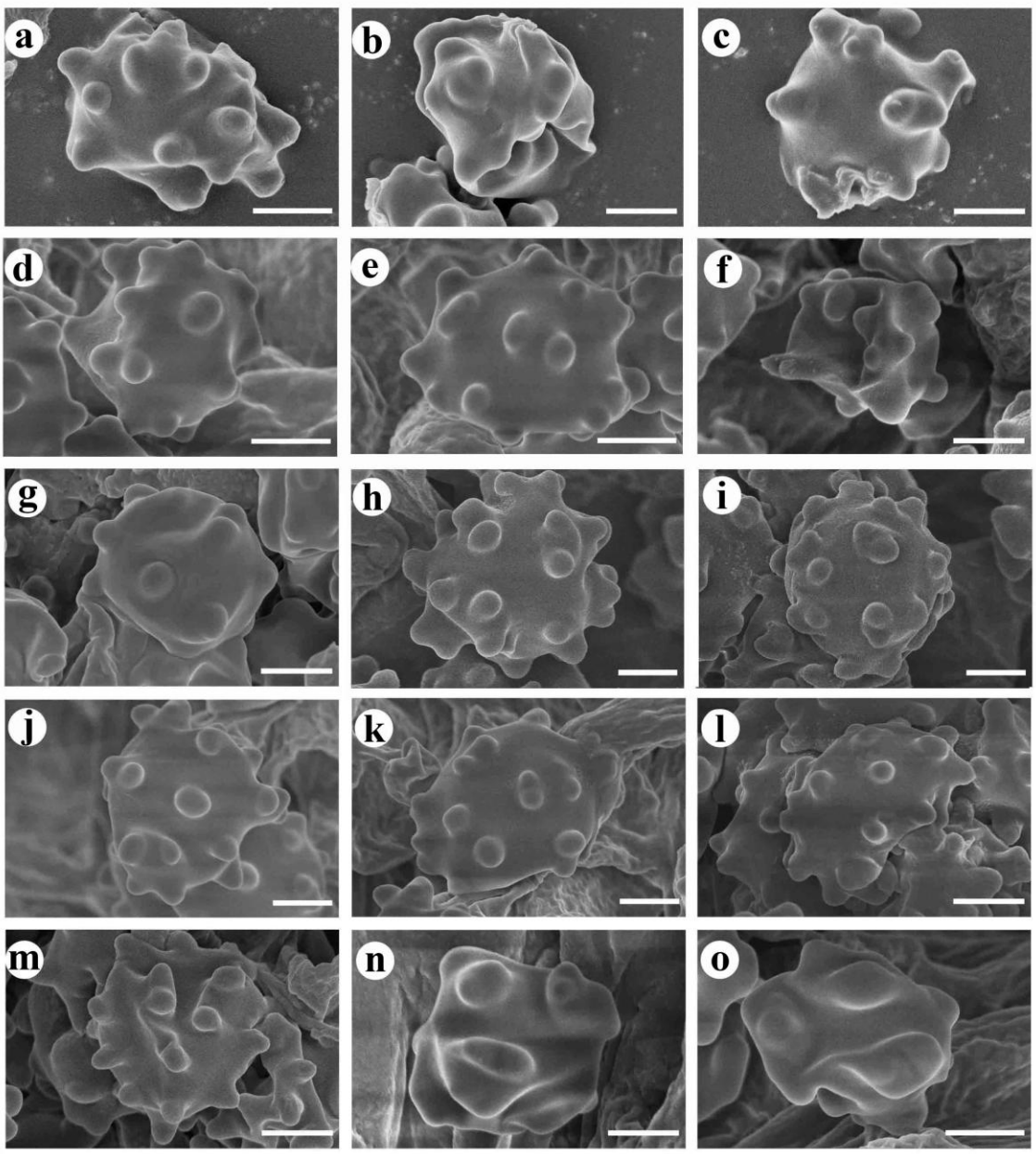

Fig. 11 Scanning Electron Microscope (SEM) of basidiospores of new species. **a** *Hydnellum decurrata* **b, c** *Hydnellum luteocaesia*; **d, e** *Hydnellum nitida*; **f, g** *Hydnellum qinghaiense*; **h, i** *Hydnellum subailaoensis*; **j, k** *Hydnellum subcaeruleum*; **l, m** *Hydnellum succulentus*; **n, o** *Hydnellum tarda*. Bars: 2 µm.

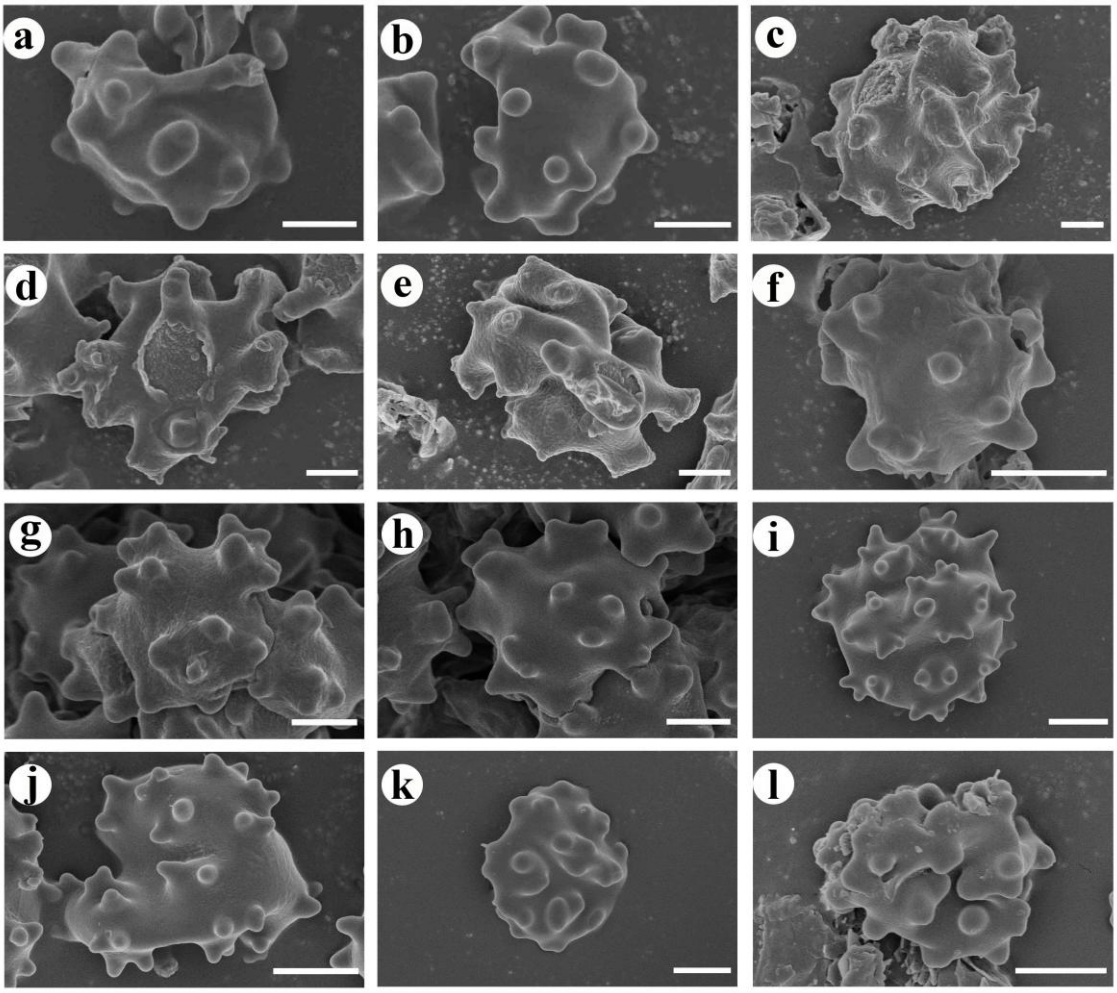

Fig. 12 Scanning Electron Microscope (SEM) of basidiospores of new species. **a**, **b** *Hydnellum xanthopus*; **c, d, e** *Neosarcodon melanocarpus*; **g, h** *Sarcodon yunnanensis*; **i, j** *Thelephora bubalinomarginata*; **k, l** *Thelephora macrospora*. Bars: 2 µm.

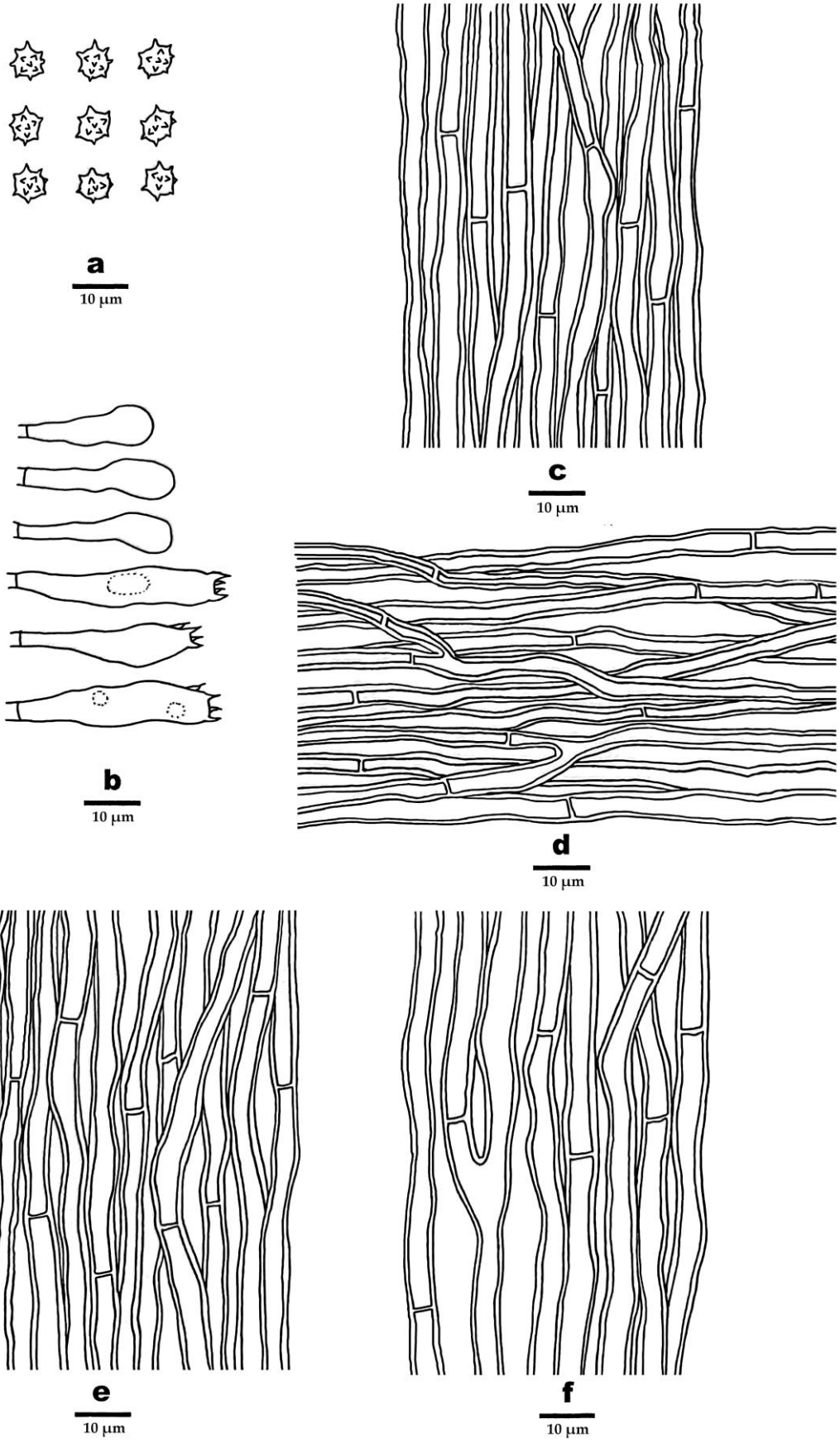

Fig. 13 Microscopic structures of *Phellodon albomarginatus* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Phellodon arcularius B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 7 c, d; 10 b, c; 14).

Index Fungorum number: IF 902653; Facesoffungi number: FoF 16239

Diagnosis – Differs from other *Phellodon* species by its overlapped and zonate pileus, generally thin context, and small basidiospores.

Type – **CHINA.** Yunnan Province, Lanping County, Tongdian, Jianganchang, on the ground of forest dominated by *Pinus armandii* and *Rhododendron*, approx. 99° 29' 51" E 26° 46' 44" N, alt. 2600 m, 18 September 2018, Cui 17127 (holotype in BJFC, isotype in IFP).

Etymology – *arcularius* (Lat.), refers to the infundibuliform pileus.

Fruiting body – Basidiomata annual, pileate, centrally stipitate, concrescent, with a light fenugreek odor when dry. Pileus depressed or infundibuliform, irregular, always overlapped, up to 4.2 cm in diam, and 0.6 cm thick at the center. Pileal surface light brown to greyish brown when fresh and becoming cinnamon buff, light brown to brown upon drying, zonate, fribrillose to tomentose; margin white when fresh and becoming pinkish buff upon drying, and up to 0.5 cm wide. Spines soft, white to light brown when fresh, cream to buff-yellow upon drying, fragile, and up to 2 mm long. Context light brown to pinkish buff upon drying, fragile, and up to 0.15 cm thick. Stipes cylindrical, glabrous, surface layer greyish brown to dark brown, inner layer fuscous, and up to 3.5 cm long, 1.2 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff, thick-walled, rarely branched, regularly arranged, and 2–6 µm in diam.

Spines – Generative hyphae clay-buff, thick-walled, occasionally branched, regularly arranged, and 2–5 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 26–38 × 4.5–6 µm; sterigmata 2–5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, thick-walled, occasionally branched, regularly arranged, and 2–6 µm in diam.

Spores – Basidiospores, hyaline, subglobose, thin-walled, echinulate, IKI–, CB–, 3.5–4.5 × 3–4 µm, L = 3.95 µm, W = 3.54 µm, Q = 1.11 (n = 30/1, without the ornamentation).

Notes – *Phellodon arcularius* was collected from southwest China under a low-latitude mountain monsoon climate. In this study, *P. arcularius* was grouped with *P. tomentosus* (L.) Banker and *P. putidus* (G.F. Atk.) Banker (Fig. 4). *Phellodon arcularius* is similar to *P. tomentosus* and *P. putidus* in having tomentose and zonate pileal surface. However, *P. arcularius* can be distinct by its irregular pileus and greyish-brown to dark brown stipe (Baird et al. 2013).

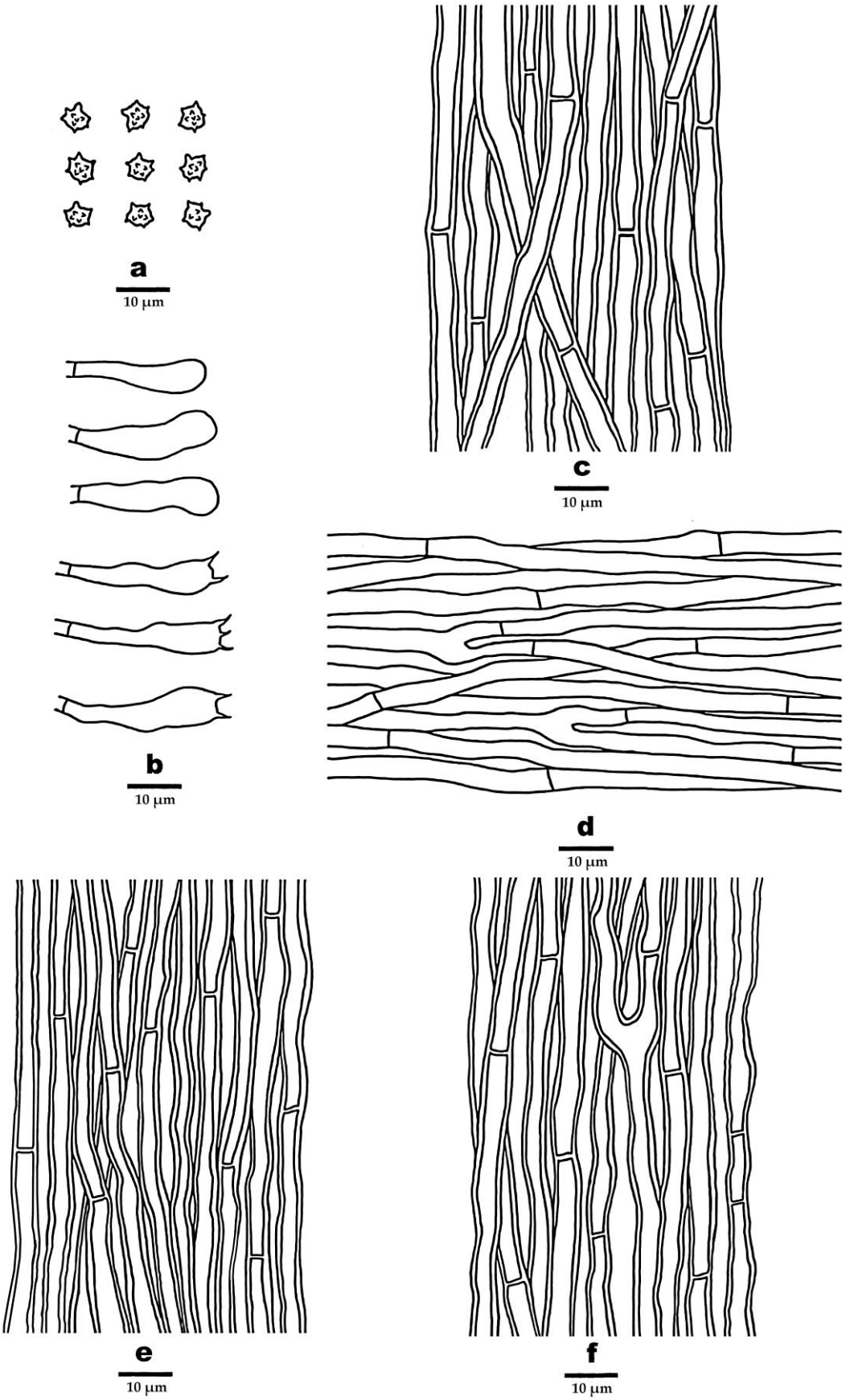

Fig. 14 Microscopic structures of *Phellodon arcularius* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Phellodon longipes B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 7 e, f; 10 d; 15).

Index Fungorum number: IF 902656; Facesoffungi number: FoF 16240

Diagnosis – Differs from other *Phellodon* species by its imbricate and zonate pileus, dark brown to fuscous pileal surface, and long stipe.

Type – **CHINA.** Sichuan Province, Jiuzhaigou County, on the ground of mixed forest, approx. 104° 14' 57" E 33° 15' 38" N, alt. 2400 m, 19 September 2020, Cui 18542 (holotype in BJFC, isotype in IFP).

Etymology – *longipes* (Lat.), refers to the long stipe.

Fruiting body – Basidiomata annual, pileate, centrally stipitate, concrescent, and with a light fenugreek odor when dry. Pileus imbricate, up to 2.5 cm in diam, and 0.8 cm thick at the center. Pileal surface dark brown to fuscous when fresh and becoming mouse grey upon drying, zonate, glabrous; margin white to light brown when fresh and becoming mouse grey upon drying, and up to 0.4 cm wide. Spines soft, white to light brown when fresh, pale mouse grey upon drying, fragile, and up to 2 mm long. Context dark grey upon drying, fragile, and up to 0.5 cm thick. Stipes cylindrical, glabrous, fuscous to black, and up to 7.5 cm long, 1 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa in hyphal of pileus, spines, and the inner layer of stipe, mostly with simple-septa, occasionally with clamp connections in hyphal of the outer layer in stipe; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff to brown, thick-walled, rarely branched, regularly arranged, and 2–5 µm in diam.

Spines – Generative hyphae clay-buff, thick-walled, occasionally branched, regularly arranged, and 2–3 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 40–75 × 5–7 µm; sterigmata 2–3.5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, thick-walled, occasionally branched, interwoven in the surface layer, regularly arranged in the inner layer and 2–5.5 µm in diam.

Spores – Basidiospores, hyaline, subglobose, thin-walled, echinulate, IKI–, CB–, 4–5.5 × 4–5 µm, L = 4.66 µm, W = 4.28 µm, Q = 1.08 (n = 30/1, without the ornamentation).

Notes – *Phellodon longipes* was collected from southwest China, under a plateau humid climate. In this study, *P. longipes* was shown to be a distinct lineage in *Phellodon* (Fig. 4). It is a distinct species due to its dark brown to fuscous pileal surface and long stipe.

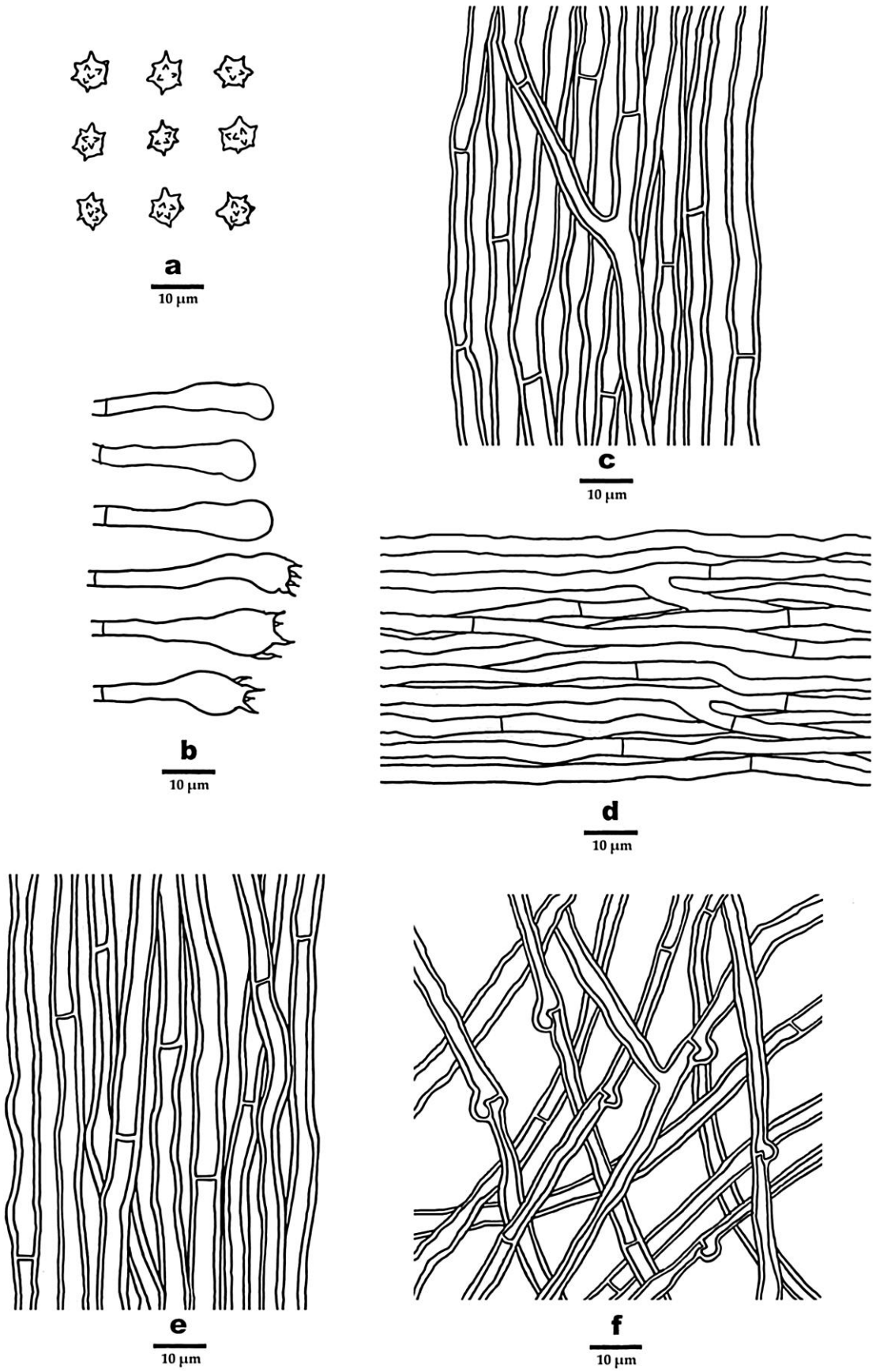

Fig. 15 Microscopic structures of *Phellodon longipes* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Phellodon setulosus B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 7 j, h; 10 e, f; 16).

Index Fungorum number: IF 902657; Facesoffungi number: FoF 16241

Diagnosis – Differs from other *Phellodon* species by its circular and tomentose pileus, blueish grey spines, and spongy stipe.

Type – **USA.** New York, Franklin County, on the ground of forest dominated by *Pinus* sp., approx. 79° 50' 17" W 41° 23' 32" N, alt. 459 m, 23 August 2019, Cui 23031 (holotype in BJFC, isotype in IFP).

Etymology – *setulosus* (Lat.), refers to the spongy tomentose pileus.

Fruiting body – Basidiomata annual, pileate, centrically stipitate, single to concrescent, with light fenugreek odor when dry. Pileus circular, up to 5 cm in diam, 0.4 cm thick at center. Pileal surface white to blueish grey when fresh, and becoming dark grey upon drying, azonate, tomentose; margin white when fresh and becoming dark grey upon drying, up to 0.4 cm wide. Spines soft, blueish grey when fresh, becoming fragile, pale mouse grey upon drying, up to 3 mm long. Context dark blueish grey upon drying, fragile, up to 0.2 cm thick. Stipes cylindrical, spongy, inflated at the lower end, surface layer greyish brown to fuscous, inner layer black, and up to 3.8 cm long, 1.2 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; all tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff to light olive green, thick-walled, occasionally branched, with simple-septa, interwoven in the surface layer, regular in the inner layer, 2–5 µm in diam.

Spines – Generative hyphae clay-buff to light olive green, slightly thick-walled, occasionally branched, with simple-septa, regularly arranged, 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 28–38 × 5–7 µm; sterigmata 1.5–4 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae black, thick-walled, occasionally branched, with simple-septa, regularly arranged, 2–5 µm in diam.

Spores – Basidiospores, hyaline, globose, thin-walled, echinulate, IKI–, CB–, 4–5 × 3.5–4.5 µm, L = 4.35 µm, W = 3.96 µm, Q = 1.08–1.13 (n = 60/2, without the ornamentation).

Additional specimen (paratype) examined – **USA.** Windham County, on the ground of forest dominated by *Albas* sp., approx. 73° 58' 21" W 40° 45' 10" N, alt. 470 m, 23 August 2019, Cui 23040 (BJFC, duplicate in IFP).

Notes – *Phellodon setulosus* was collected from the east-central United States under a temperate humid continental climate. It grows on the ground of a mossy forest dominated by *Albas* sp. In this study, *P. setulosus* was close to *P. concentricus* B.K. Cui & C.G. Song (Fig. 4). Morphologically, *P. setulosus* can be distinguished by its tomentose and blueish grey pileal surface, blueish grey spines, and dark blueish grey context (Song et al. 2023).

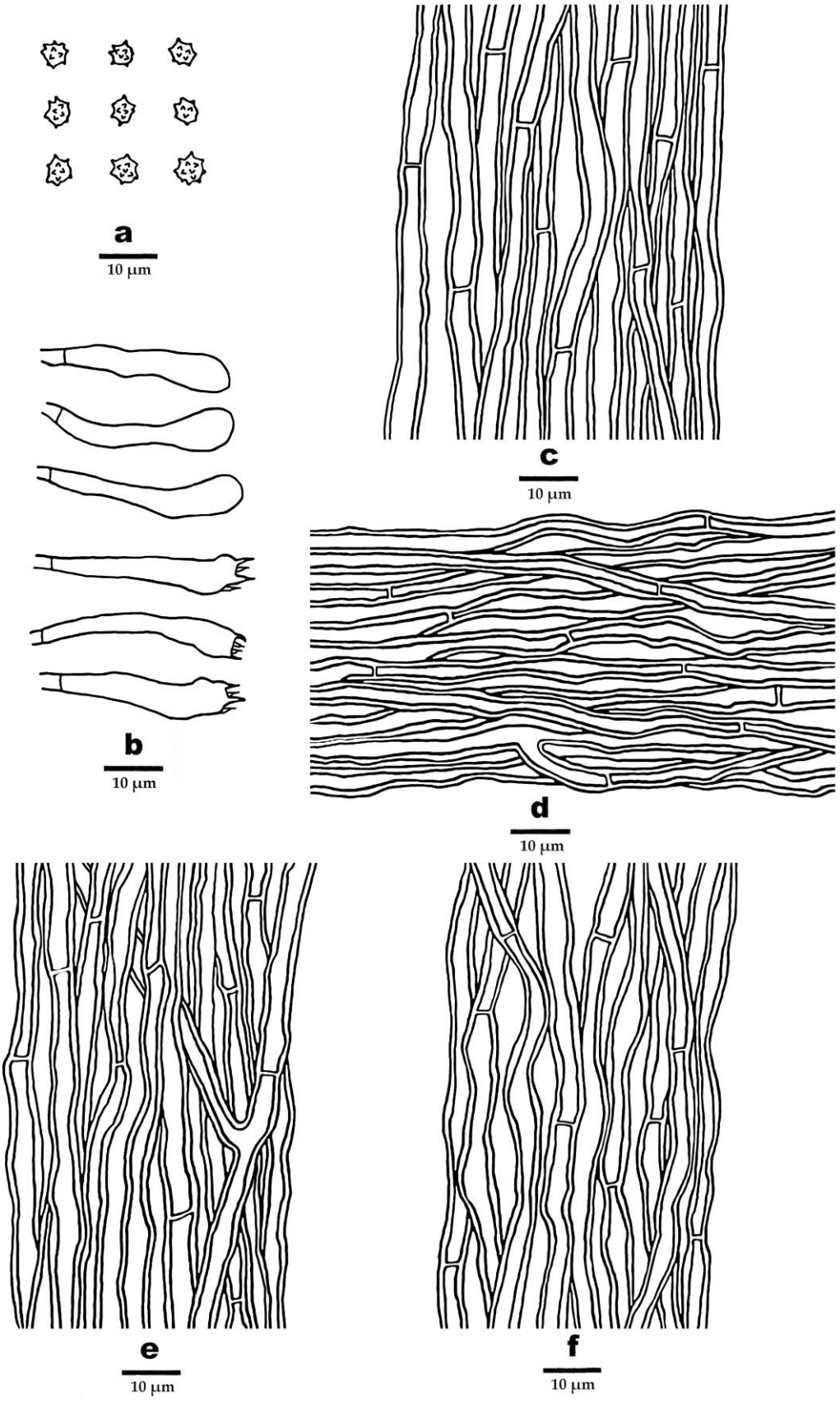

Fig. 16 Microscopic structures of *Phellodon setulosus* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; f Hyphae from the surface layer of stipe. Bars: 10 μm.

Phellodon submelaleucus B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov**. (Figs. 7 i, j, k; 10 g, h; 17).

Index Fungorum number: IF 902658; Facesoffungi number: FoF 16242

Diagnosis – Differs from other *Phellodon* species by solitary or strong gregarious basidiomata, upward curled pileal margin, short spines, and the presence of both simple-septa and clamp connections in generative hyphae of spines.

Type – **CHINA**. Sichuan Province, Xiaojin County, Meiwo, on the ground of forest dominated by trees of *Quercus* sp., approx. 102° 29' 24" E 30° 52' 2" N, alt. 3200 m, 1 August 2020, Cui 18614 (holotype in BJFC, isotype in IFP).

Etymology – *submelaleucus* (Lat.), refers to the species that resembles *P. melaleucus* in morphology.

Fruiting body – Basidiomata annual, pileate, centrally or eccentrically stipitate, solitary or strong concrescent, with a strong fenugreek odor when dry. Pileus depressed or infundibuliform, and margin curls upward, up to 4.3 cm in diam, 0.6 cm thick at the center. Pileal surface fuscous to black when fresh and becoming vinaceous grey upon drying, azonate, glabrous, wrinkled at the center; margin blunt or irregular, white when fresh, becoming greyish brown upon drying, up to 0.5 cm wide. Spines soft, white when fresh, becoming fragile, grey to pale mouse-grey upon drying, up to 2.5 mm long. Context light vinaceous grey, tough, up to 0.3 cm thick. Stipes cylindrical, glabrous, surface layer dark brown to fuscous, inner layer black, and up to 2.3 cm long, 1.7 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae mostly with simple-septa, occasionally with clamp connections; all the hyphae IKI–, CB–; tissues of pileus and stipe turned olive green to black, while tissues of spines turned to black in KOH.

Pileus – Generative hyphae clay-buff to greyish brown, thick-walled, rarely branched, with simple-septa, regularly arranged, 2–7 µm in diam.

Spines – Generative hyphae clay-buff, thin-walled, branched, mostly with simple-septa, occasionally with clamp connections, regularly arranged, 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 16–36 × 5–7 µm; sterigmata 1.5–4.5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae vinaceous grey, thick-walled, rarely branched, with simple-septa, regularly arranged, 3–6 µm in diam.

Spores – Basidiospores, hyaline, subglobose to globose, thin-walled, echinulate, IKI–, CB–, 4–5 × 3.5–4.5µm, L = 4.2 µm, W = 3.8 µm, Q = 1.03–1.1 (n = 90/3, without the ornamentation).

Additional specimens (paratypes) examined – **CHINA**. Sichuan Province, Xiaojin County, Meiwo, on the ground of forest dominated by trees of *Quercus* sp., approx. 102° 29' 24" E 30° 52' 2" N, alt. 3200 m, 1 August 2020, Cui 18620 (BJFC, duplicate in IFP) & Cui 18623 (BJFC, duplicate in IFP).

Notes – *Phellodon submelaleucus* was collected from southwest China under a temperate alpine climate. In this study, it is closely related to *P. melaleucus* (Sw. ex Fr.) P. Karst. (Fig. 4). *Phellodon melaleucus* might be confused with *P. submelaleucus* in having solitary or gregarious basidiomata and white pileal margin. However, *P. melaleucus* is distinguished by its lighter color pileal surface and smaller basidiospores (3.5–4.5 × 3–4 µm, Baird et al. 2013).

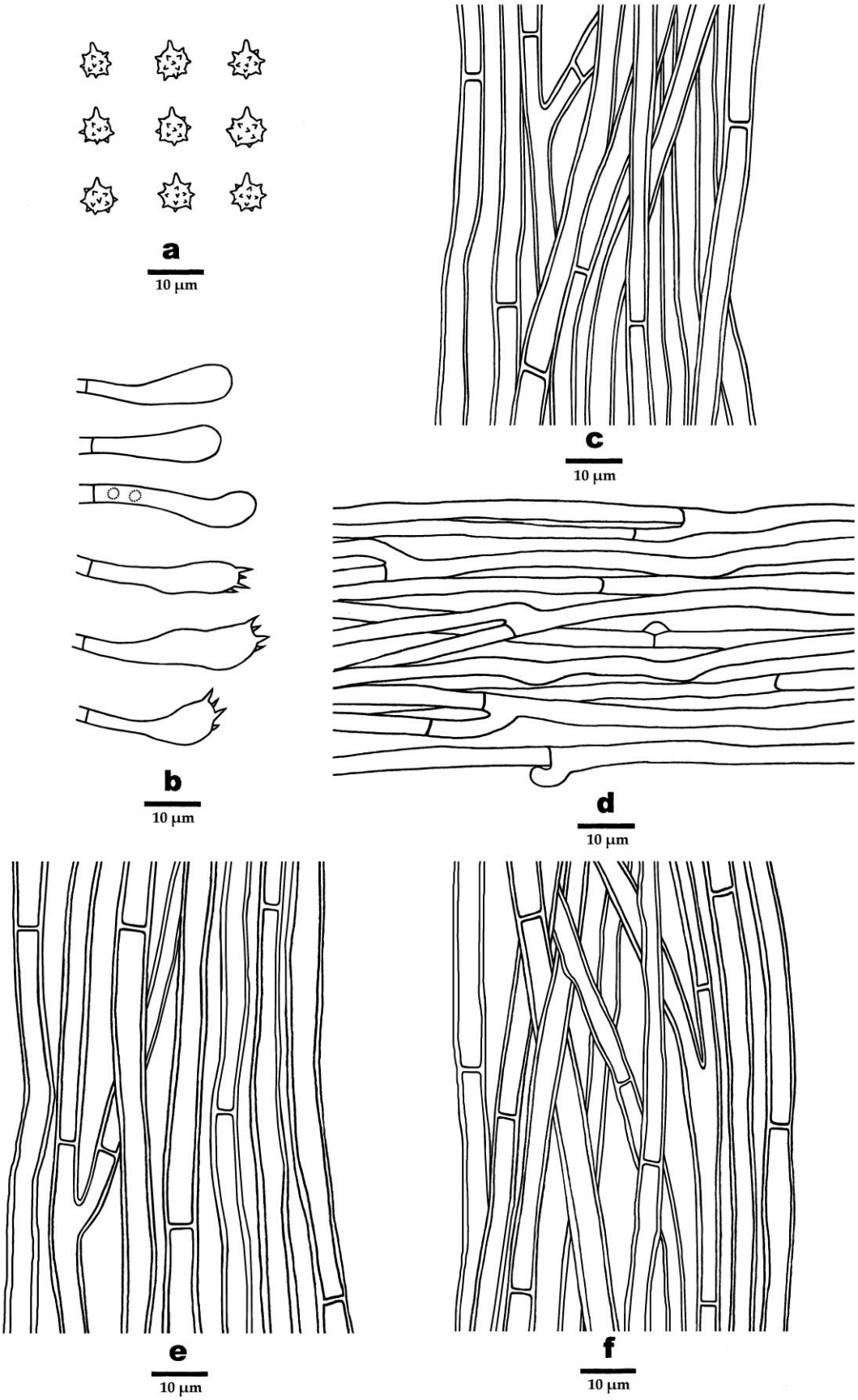

Fig. 17 Microscopic structures of *Phellodon submelaleucus* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Phellodon substramineus B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 7 l, m; 10 i, j; 18).

Index Fungorum number: IF 902659; Facesoffungi number: FoF 16243

Diagnosis – Differs from other *Phellodon* species by its zonate pileal surface and light vinaceous grey spines.

Type – **CHINA**. Yunnan Province, Dayao County, on the ground of forest, approx. 101° 19' 45" E 25° 43' 36" N, alt. 2000 m, 6 October 2022, Dai 24629 (holotype in BJFC, isotype in IFP).

Etymology – *substramineus* (Lat.), refers to the new species resembling *P. stramineus* in morphology.

Fruiting body – Basidiomata annual, pileate, centrally or eccentrically stipitate, concrescent, and odor of fenugreek when dry. Pileus circular to irregular, up to 5.8 cm in diam, and 0.4 cm thick at the center. Pileal surface fawn, brown to greyish brown when fresh and becoming honey yellow, brown, to greyish brown upon drying, zonate, fibrillose to tomentose; margin dark brown to black when fresh and becoming brown to black upon drying, and up to 0.4 cm wide. Spines soft, light vinaceous grey to ash grey when fresh, dark grey upon drying, fragile, and up to 3 mm long. Context dark grey upon drying, tough, and up to 0.3 cm thick. Stipes cylindrical, fibrillose to tomentose, surface layer brown to greyish brown, inner layer fuscous to black, and up to 3.3 cm long, 1.4 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff, thick-walled, rarely branched, regularly arranged, and 2–5 µm in diam.

Spines – Generative hyphae clay-buff, thick-walled, branched, regularly arranged, and 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 28–48 × 5–6.5 µm; sterigmata 2–4 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff to black, thick-walled, rarely branched, regularly arranged in the outter layer, interwoven in the inner layer and 2–5 µm in diam.

Spores – Basidiospores, hyaline, subglobose, thin-walled, echinulate, IKI–, CB–, 4–6 × 4–5.5 µm, L = 5.09 µm, W = 4.65 µm, Q = 1.09 (n = 60/2, without the ornamentation).

Additional specimens (paratypes) examined – **CHINA**. Yunnan Province, Dayao County, on the ground of forest, approx. 101° 19' 45" E 25° 43' 36" N, alt. 2000 m, 6 October 2022, Dai 24630 (BJFC, duplicate in IFP) & Dai 24631 (BJFC, duplicate in IFP).

Notes – *Phellodon substramineus* was collected from southwest China under a north subtropical monsoon climate. In this study, it is closely related to *P. stramineus* B.K. Cui & C.G. Song (Fig. 4). Morphologically, *P. substramineus* is similar to *P. stramineus* in the zonate pileal surface and the ash grey spines. However, *P. substramineus* differs by its fawn to greyish brown pileal surface and fibrillose to tomentose stipe (Song et al. 2021).

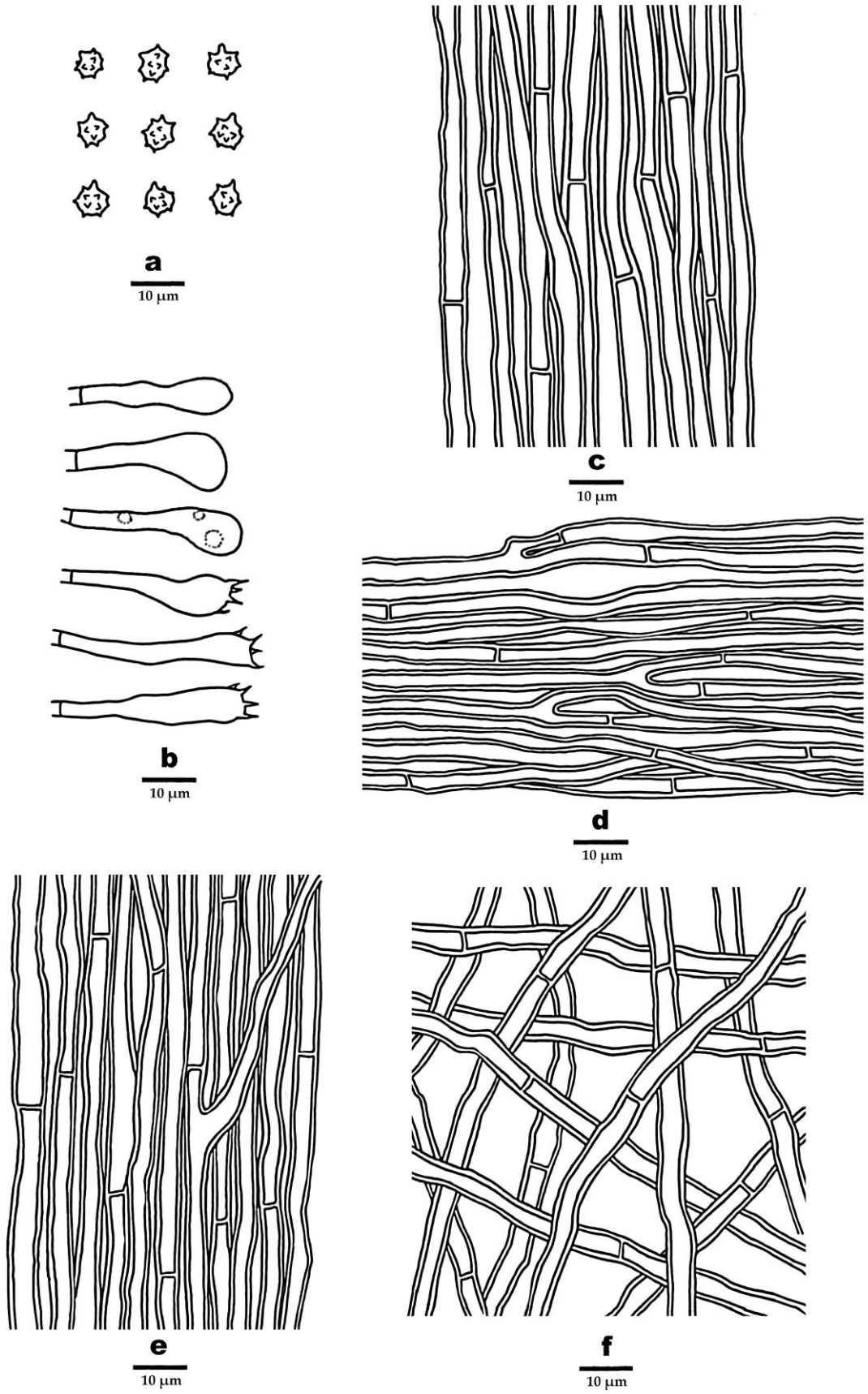

Fig. 18 Microscopic structures of *Phellodon substramineus* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; f Hyphae from the surface layer of stipe. Bars: 10 μm.

Lenzitopsidaceae B.K. Cui, Y.F. Sun and C.G. Song, **fam. nov.**

Index Fungorum number: IF 902846; Facesoffungi number: FoF 16772

Type genus – *Lenzitopsis* Malençon & Bertault

Description – Basidiomata annual, resupinate, dark. Hymenophores white to brown, irregular, sinuous to lenzitoid. Hyphal system monomitic; generative hyphae with clamp connections. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores pale brown, globose to subglobose, warted.

Notes – In this study, two species of *Lenzitopsis* were grouped together and formed a single clade with high support in Thelephorales (100% ML, 1.00 BPP, Figs. 1, 2). Previously, *Lenzitopsis* was placed in Thelephoraceae because of its brownish and echinulate spores (Malençon & Bertault 1963, Ryvarden & Gilbertson 1993). However, *L. oxycedri* Malençon & Bertault and *L. daii* L.W. Zhou & Kõljalg possessed lenzitoid hymenophores as well as brown hyphae (Malençon and Bertault 1963, Zhou & Kõljalg 2013), which was significantly different from other taxa of Thelephorales. In addition, the divergence time estimation showed that the ancestor of *Lenzitopsis* evolved at about 145.95 Mya, which was in line with the time range for the differentiation of other families in Thelephorales (Fig. 6). Thus, based on comprehensive analyses, a new family Lenzitopsidaceae was proposed to accommodate *Lenzitopsis*.

Lenzitopsis Malençon & Bertault, Bulletin de la Société Mycologique de France 79 (1): 82, 1963.

Type species – *Lenzitopsis oxycedri* Malençon & Bertault

Description – Basidiomata annual, resupinate or pileate, sessile to stipitate, dark colored. Hymenophores white to brown, irregular, sinuous to lenzitoid. Hyphal system monomitic; generative hyphae with clamp connections. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores pale brown, globose to subglobose, warted. For a detailed description of *Lenzitopsis*, see Malençon & Bertault (1963), Zhou & Kõljalg (2013).

Notes – *Lenzitopsis*, established by Malençon & Bertault (Malençon & Bertault 1963), has been found growing in forests dominated by *Juniperus* sp. (Zhou & Kõljalg 2013). *Lenzitopsis* species have been reported in Morocco (Malençon & Bertault 1963), Europe (García-Manjón & Moreno 1981, Ryvarden 1991, Bernicchia 2000, Karadelev et al. 2013), China (Dai et al. 2007, Zhou & Kõljalg 2013), and Turkey (Doğan et al. 2007). Currently, *Lenzitopsis* comprises two species: *L. oxycedri* and *L. daii* (Zhou & Kõljalg 2013). The original morphological description of *L. oxycedri* was based on a specimen collected from Morocco (Malençon & Bertault 1963). It can be characterized by perennial, resupinate to effuse reflexed basidiomata, pale brownish, finely warted, and nonamyloid basidiospores. *Lenzitopsis oxycedri* was growing on living *Juniperus*, which occurred in arid and semi-arid regions of the Northern Hemisphere and only reached the Southern Hemisphere in eastern Africa (Zhou & Kõljalg 2013). *Lenzitopsis daii* was described from China as growing on *Juniperus chinensis*, and it was characterized by annual, pileate, sessile to stipitate and imbricate basidiomata, pale brownish, warted, and amyloid basidiospores (Zhou & Kõljalg 2013). In this study, we collected the basidiomata of *L. daii* growing on the living tree of *Sabina* sp. Morphologically, *L. daii* differs from *L. oxycedri* by annual basidiomata and amyloid basidiospores. In this study, the two species grouped together within Thelephorales and formed a single clade with high support (100% ML, 1.00 BPP, Figs. 1, 2).

Polyozellaceae B.K. Cui, Y.F. Sun and C.G. Song, **fam. nov.**

Index Fungorum number: IF 902847; Facesoffungi number: FoF 16753

Type genus – *Polyozellus* Murrill

Description – Basidiomata annual to perennial, resupinate or pileate, sessile or stipitate colored in a wide variety of tints. Hymenophores white, pale yellow, blue, purple, brown to dark, reticulate or almost poroid to corticioid. Hyphal system monomitic or dimitic; generative hyphae with simple-septate or clamp connections. Cystidia and cystidioles absent. Basidia clavate or narrowly clavate, 2(–4)–spored. Basidiospores white to brown, subcircular to slightly ellipsoid, angular, lobed, or warted.

Notes – In this study, species of *Polyozellus* grouped within Thelephorales and formed a single clade with high support (1.00 BPP, Fig. 1; 55% ML, 1.00 BPP, Fig. 2), but could not be placed in any recognized family. Morphologically, *Polyozellus* can be characterized by pileate or resupinate basidiomata, reticulate or almost poroid to corticioid hymenophores, monomitic or dimitic hyphal system, and lobed or warted basidiospores. *Polyozellus* spp. have different morphology from any of the presently known families of the Thelephorales. Besides, the divergence time estimation results showed that the ancestor of *Polyozellus* evolved at 145.95 Mya, which was in line with the time range for the differentiation of other families in Thelephorales (Fig. 6). Thus, a new family Polyozellaceae, was proposed to accommodate *Polyozellus*, and only one genus was accepted in Polyozellaceae.

Polyozellus Murrill, North American Flora 9 (3): 171, 1910.

Type species – *Polyozellus multiplex* (Underw.) Murrill

Description – For a detailed description of *Polyozellus*, see Svantesson et al. (2021).

Notes – *Polyozellus* was described by Murrill (1910) with *Polyozellus multiplex* as the type. Many *Polyozellus* species have been reported to occur in old-growth forests, in the Northern Hemisphere (Kõljalg 1996, Kõljalg & Larsson 1998, Kõljalg & Dunstan 2001, Martini & Hentic 2002, 2003, Svantesson et al. 2019, 2021). Morphologically, *Polyozellus* can be distinct by its pileate or resupinate, fleshy to woody basidiomata, and poroid to corticioid hymenophores. So far, *Polyozellus* comprises 26 species (Svantesson et al. 2021). In this study, *Polyozellus* species formed a separate clade with moderate support (1.00 BPP, Fig. 1; 55% ML, 1.00 BPP, Fig. 2) within Thelephorales.

Sarcodonaceae B.K. Cui, Y.F. Sun and C.G. Song, **fam. nov.**

Index Fungorum number: IF 902848; Facesoffungi number: FoF 16754

Type genus – *Sarcodon* Quél. Ex P. Karst.

Describtion – Basidiomata annual, pileate, stipitate, colored in a wide variety of tints, often initially tomentose, glabrous with age, smooth or scaly. Hymenophores white, orange, brown, or darker, aculeate or poroid. Stipes concolorous with the pileus or darker. Hyphal system monomitic, generative hyphae with simple-septa or clamp connections. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores hyaline or brown, subglobose to globose or broadly ellipsoid, warted.

Notes – In this study, four genera, including *Boletopsis*, *Hydnellum*, *Neosarcodon*, and *Sarcodon*, grouped together within Thelephorales and formed a distinct clade with high support (52% ML, 1.00 BPP, Fig. 1; 78% ML, 1.00 BPP, Fig. 2). Morphologically, species in this clade can be characterized by pileate and basidiomata, aculeate or poroid hymenophores, and ellipsoid or subglobose to globose basidiospores with fine tubercles. Species in this clade, belonging to the EcM fungi, could not be placed in any recognized families. Besides, the divergence time estimation results showed that the ancestor of this clade evolved at 216.52 Mya, which was in line with the time range for the differentiation of other families in Thelephorales (Fig. 6). Thus, a new family Sarcodonaceae was proposed to accommodate this clade. In this study, *Corneroporus* was not included in the phylogenetic analyses since there were no available specimens to obtain sequences, and it was treated as an independent genus within Sarcodonaceae since it was separated from *Boletopsis* (Hattori 2001).

Key to genera of Sarcodonaceae

1. Hymenophores poroid 2
1. Hymenophores aculeate 3
2. Basidiospores angular-warted and usually colored in mass ..... *Boletopsis*
2. Basidiospores echinulate and hyaline ..... *Corneroporus*
3. Pileus colored in a wide variety of tints ..... *Hydnellum*
3. Pileus pale brown to dark brown 4

4. Pileus circular to irregular ..... *Sarcodon*
4. Pileus conic, broadly conic to planoconvex ..... *Neosarcodon*

Boletopsis Fayod, Malpighia 3: 72, 1889.

Type species – *Boletopsis leucomelaena* (Pers.) Fayod

Description – Basidiomata annual, pileate, centrally or laterally stipitate, single to imbricated, fleshy. Pileus grey, pale sordid brown to black, smooth to finely fibrillose or finely scaly. Hymenophores white to cream at first, soon attaining a pale lilac-grey or smoky grey-brown tint inside the tubes, poroid. Stipes often concolorous with pileal surface or paler. Hyphal system monomitic; generative hyphae with clamp connections, of highly variable diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores pale buff to pale brownish, irregular, warted. For a detailed description of *Boletopsis*, see Ryvarden & Gilbertson (1993).

Notes – *Boletopsis* Fayod was established by Fayod (Zhou et al. 2022). *Boletopsis* species have been collected in hardwood forests with scattered conifers, especially Pinaceae and Fagaceae (Vasas 2008, Zhou et al. 2022). Previously, all *Boletopsis* species were described from Europe (Vasas 2008, Ryvarden & Melo 2017), North America (Watling & Milne 2008), New Zealand (Hjortstam & Ryvarden 1982), Thailand and China (Cooper & Leonard 2012, Zhou et al. 2022). It can be characterized by stipitate and pileate basidiocarps with poroid hymenophores and pale buff to pale brownish, warted basidiospores. Based on morphological characteristics, nine species were accepted in *Boletopsis* (Zhou et al. 2022). In this study, eight species were included to construct the phylogenetic trees, and they form an independent clade with high support (100% ML, 1.00 BPP, Figs. 1, 2), which indicates the genus is monomitic.

Corneroporus T. Hatt., Mycoscience 42 (5): 426, 2001.

Type species – *Corneroporus subcitrinus* (Corner) T. Hatt.

Description – Basidiomata annual, pileate, stipitate, single to imbricated, fleshy. Pileus buff citron, sometimes with slightly dark zones, subtomentose. Hymenophores cream white to pale buff citron, subdecurrent, poroid. Stipes concolorous with pileal surface. Hyphal system monomitic; generative hyphae with clamp connections. Cystidia and cystidioles absent. Basidia clavate, slightly ventricose below the subcylindric distal half, 4–spored. Basidiospores hyaline, subangular to warted. For a detail description of *Corneroporus*, see Hattori (2001).

Notes – Hattori (2001) separated *Corneroporus subcitrinus* from *Boletopsis* due to its unique complete lack of dark coloration basidiomata and echinulate and hyaline basidiospores, and established *Corneroporus* as a new genus. So far, there is only one species in the genus. However, since the lack of sequences for *Corneroporus*, we treat it as an independent genus in this study. More specimens and credible sequences are needed to clarify the taxonomic status of *Corneroporus*.

Hydnellum P. Karst., Meddelanden af Societas pro Fauna et Flora Fennica 5: 41, 1879.

Type species – *Hydnellum suaveolens* (Scop.) P. Karst.

Description – Basidiomata annual, pileate, centrally or laterally stipitate, single to gregarious or concrescent. Pileus subcircular, circular, infundibuliform or irregular, aurantia, brown, reddish brown, to almost fuscous, glabrous, fibrillose, spongy to tomentose, often strigose hairy becoming matted or pitted, scrobiculate, scaly to smooth. Hymenophores white, grey to brown, aculeate. Stipes concolorous with pileal surface. Hyphal system monomitic; generative hyphae with simple-septate or clamp connections. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores brown, ellipsoid, subglobose to globose, warted. For a detailed description of *Hydnellum*, see Karsten (1879) and Baird et al. (2013).

Notes – *Hydnellum* was established by Petter Karsten (Karsten 1881). *Hydnellum* species tend to grow in moist woodlands with thick mosses, under pine needles or oak leaves, which help to reduce water loss (Song et al. 2022b). Similar with *Phellodon*, *Hydnellum* species tend to grow in coniferous forests, oak forests, or mixed forests, and often grow above at altitude of 400 m (Song et

al. 2022b). Species in *Hydnellum* have so far been found in North America (Baird 1986a, b, Baird et al. 2013), Europe (Maas Geesteranus 1975), Australia, New Guinea (Maas Geesteranus 1971) and Asia (Maas Geesteranus 1971, Mu et al. 2021, Song et al. 2022b). *Hydnellum* species can be characterized by stipitate basidiomata, aculeate hymenophores, spines various in color, brown, and warted basidiospores. So far, about 74 species have been described and transferred to *Hydnellum* according to the previous studies, of which 21 are described in China (Mu et al. 2021, Song et al. 2022b, Wang et al. 2024). In this study, 81 species of *Hydnellum* were included to construct the phylogenetic trees, and they formed an independent lineage within Sarcodonaceae with high support (98% ML, 1.00 BPP, Fig. 1; 99% ML, 1.00 BPP, Fig. 2). Based on morphological characters and phylogenetic evidence, ten new species were described and illustrated is provided.

Hydnellum cinnamomea B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 7 n, o; 10 k, l; 19).

Index Fungorum number: IF 902651; Facesoffungi number: FoF 16244

Diagnosis – Differs from other *Hydnellum* species by its eccentrically stipitate, strongly overlapped to fan-shaped to subcircular pileus, salmon, clay-buff, cinnamon to fawn pileal surface, and short stipe.

Type – **CHINA**. Sichuan Province, Aba Tibetan and Qiang Autonomous Prefecture, on the ground of forest dominated by trees of *Quercus* sp., approx. 102° 13' 5" E 31° 54' 37" N, alt.3320 m, 3 September 2021, Cui 18743 (holotype in BJFC, isotype in IFP).

Etymology – *cinnamomea* (Lat.), refers to the cinnamon pileal surface.

Fruiting body – Basidiomata annual, eccentrically stipitate, single to strong concrescent, odorless when dry. Pileus strongly overlapped in the middle when young, fan-shaped to subcircular with age, up to 6.2 cm in diam, 1.3 cm thick at the center. Pileal surface salmon, clay-buff, cinnamon to fawn when young, dark yellowish-brown with age when fresh and becoming greyish brown upon drying, azonate when young, zonate after mature, tomentose when young, fibrillose or glabrous with age, with white tomentum at the margin, with radially aligned stripes near the margin; margin white to light brown when fresh, becoming greyish brown upon drying, up to 1.2 cm wide. Spines soft, brown to greyish brown when fresh, greyish brown upon drying, up to 3 mm long. Context dark yellow-brown upon drying, tough, up to 0.5 cm thick. Stipes cylindrical, glabrous, surface layer dark brown to vinaceous grey, inner layer greyish brown, up to 1.2 cm long, 0.6 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae mostly with simple-septa, rarely with clamp connections; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff, thick-walled on the surface, occasionally branched, with simple-septa, regularly arranged, 2–6 µm in diam.

Spines – Generative hyphae clay-buff, thick-walled, occasionally branched, mostly with simple-septa, rarely with clamp connections, regularly arranged, 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 25–47 × 6–7 µm; sterigmata 2.5–5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, thick-walled in the surface layer, rarely branched, with simple-septa, interwoven in the surface layer, regularly arranged in the inner layer, 2–5 µm in diam.

Spores – Basidiospores, brown, subglobose to globose, thin-walled, warted, IKI–, CB–, (4–)4.5–6 × 4–5 µm, L = 5.2 µm, W = 4.5 µm, Q =1.14–1.16 (n = 90/3, without the ornamentation).

Additional specimens (paratypes) examined – **CHINA**. Sichuan Province, Aba Tibetan and Qiang Autonomous Prefecture, on the ground of forest dominated by trees of *Quercus* sp., approx. 102° 13' 5" E 31° 54' 38" N, alt. 3310 m, 3 September 2021, Cui 18740 (BJFC, duplicate in IFP) & Cui 18755 (BJFC, duplicate in IFP) & Cui 18757 (BJFC, duplicate in IFP).

Notes – *Hydnellum cinnamomea* was collected from southwest China under a subtropical monsoon humid climate. In this study, *H. cinnamomea* was related to *H. brunneorubrum* Y.H. Mu & H.S. Yuan, *H. earlianum* Banker, *H. chrysinum* K.A. Harrison and *H. auratile* (Britzelm.) Maas Geest (Fig. 3). However, *Hydnellum cinnamomea* can be distracted by its salmon, clay-buff,

cinnamon to fawn pileal surface, and short stipe (Harrison 1964, Maas Geesteranus 1971, Mu et al. 2021).

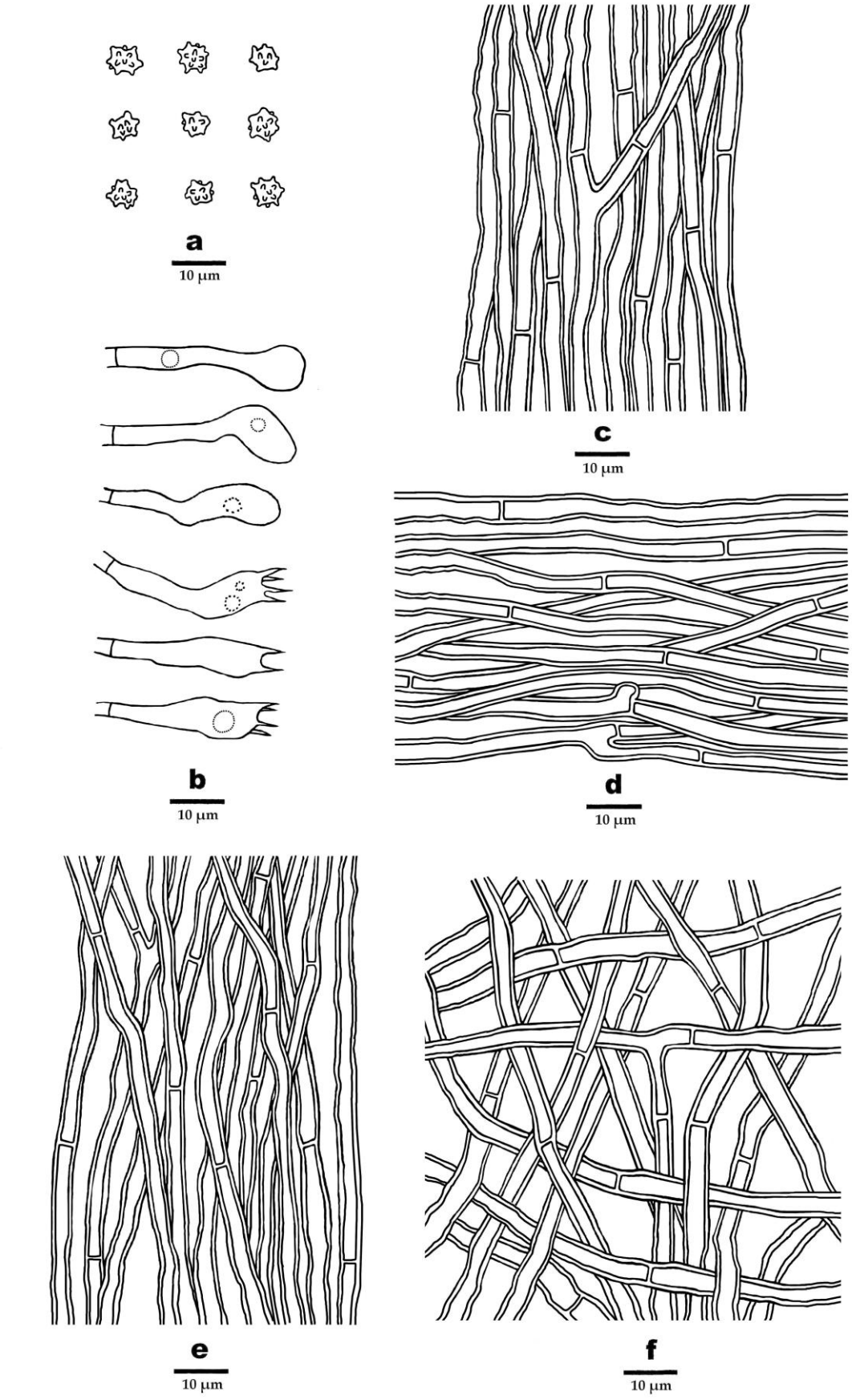

Fig. 19 Microscopic structures of *Hydnellum cinnamomea* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 µm.

Hydnellum decurrata B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 a; 10 l; 11 a; 20).

Index Fungorum number: IF 902661; Facesoffungi number: FoF 16246

Diagnosis – Differs from other *Hydnellum* species by its fleshy basidiomata, scaly pileal surface, and decurrent spines.

Type – **USA.** New York, on the ground of conifer forest, approx. 73° 52' 34" W 40° 50' 32" N, alt. 470 m, 7 September 2019, Cui 23050 (holotype in BJFC, isotype in IFP).

Etymology – *decurrata* (Lat.), refers to the decurrent spines.

Fruiting body – Basidiomata annual, centrally stipitate, single to concrescent, with a fenugreek odor when dry. Pileus circular and depressed, fleshy, up to 12 cm in diam, 2 cm thick at center. Pileal surface brown when fresh and becoming greyish brown to dark brown upon drying, azonate, glabrous, scaly; margin light brown near margin when fresh and becoming brown upon drying, up to 0.6 cm wide. Spines soft, decurrent, cream to light brown when fresh, becoming fragile, greyish brown to brown upon drying, up to 4 mm long. Context greyish cream upon drying, fragile, up to 1.6 cm thick. Stipes cylindrical, glabrous, light brown, up to 5 cm long, 2 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; all tissues turned olive green in KOH.

Pileus – Generative hyphae clay buff, thick-walled, branched, with simple-septa, interwoven, inflated, 4–23 µm in diam.

Spines – Generative hyphae clay buff, slightly thick-walled, occasionally branched, with simple-septa, regularly arranged, 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 15–29 × 5–6 µm; sterigmata 2–4 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay buff, thick-walled, occasionally branched, with simple-septa, regularly arranged, 3–12 µm in diam.

Spores – Basidiospores, hyaline, subglobose to globose, thin-walled, warted, IKI–, CB–, 5–6.5(–7) × (4.5–)5–5.5 µm, L = 5.75 µm, W = 5.08 µm, Q = 1.09–1.16 (n = 90/3, without the ornamentation).

Additional specimens (paratypes) examined – **USA.** New York, on the ground of conifer forest, approx. 73° 52' 34" W 40° 50' 32" N, alt. 490 m, 4 September 2019, Cui 23049 (BJFC); on the ground of conifer forest, alt. 210 m, 7 September 2019, Cui 23052 (BJFC, duplicate in IFP); Franklin County, Saranac Lake, on the ground of conifer forest, approx. 79° 50' 15" W 41° 23' 46" N, alt. 475 m, 9 September 2019, Cui 23056 (BJFC, duplicate in IFP).

Notes – *Hydnellum decurrata* was collected from the east-central United States under a temperate continental humid climate. In this study, *H. decurrata* clustered with *H. lidongensis* (Fig. 3). Morphologically, *H. decurrata* resembles *H. lidongensis* in having circular pileus scaly and fleshy pileal surface. However, *H. decurrata* can be distinguished by its decurrent and light brown stipe and larger basidiospores (4.1–6 × 4–5 µm, Mu et al. 2020).

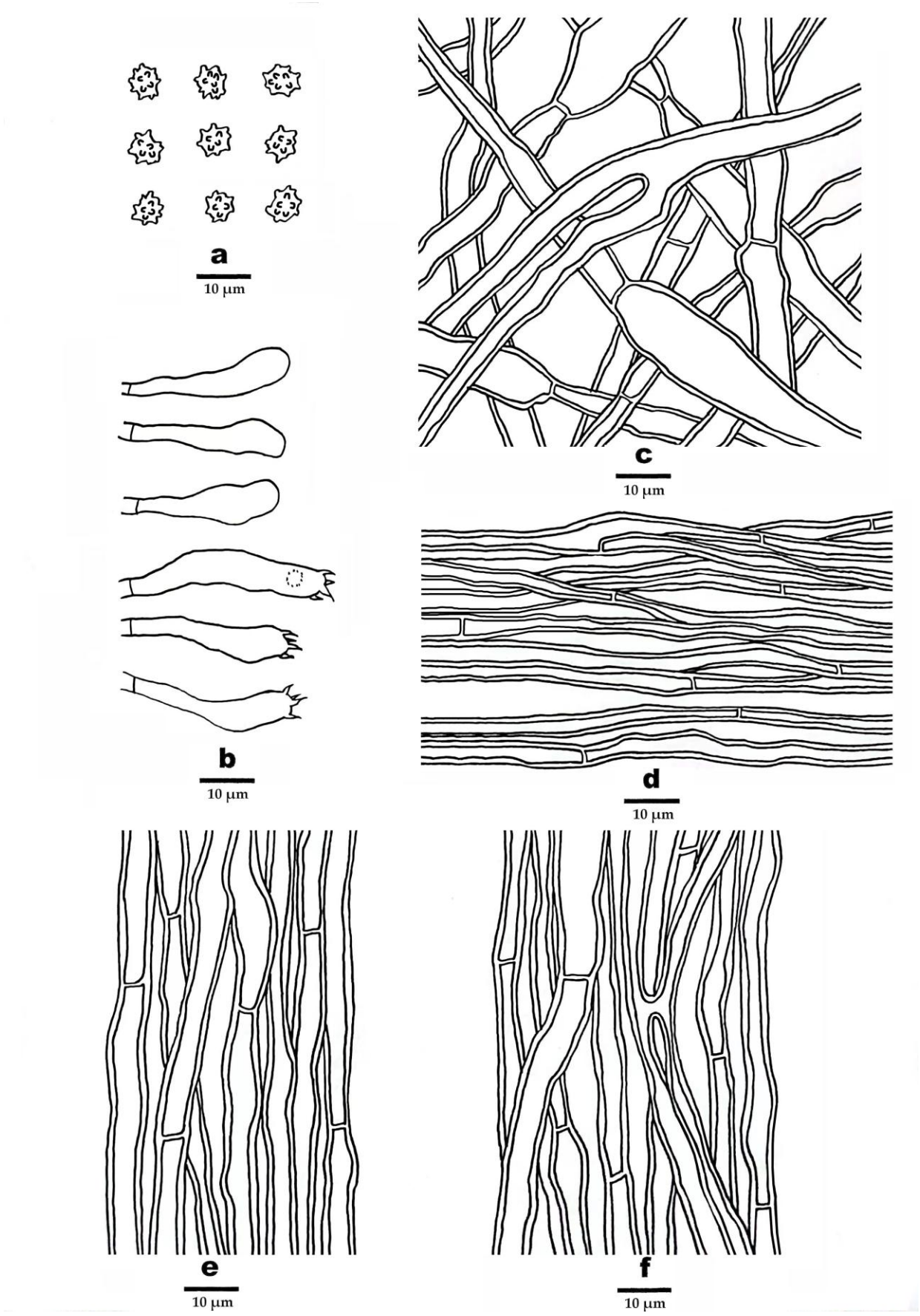

Fig. 20 Microscopic structures of *Hydnellum decurrata* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum luteocaesia B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 b, c; 11 b, c; 21).

Index Fungorum number: IF 902686; Facesoffungi number: FoF 16247

Diagnosis – Differs from other *Hydnellum* species by its tomentose pileus, blueish grey to olivaceous buff pileal surface.

Type – **USA.** New York, Franklin County, on the ground of conifer forest, approx. 79° 50' 15" W 41° 23' 46" N, alt. 430 m, 23 August 2019, Cui 23033 (holotype in BJFC, isotype in IFP).

Etymology – *luteocaesia* (Lat.), refers to the blueish to yellowish pileal surface.

Fruiting body – Basidiomata annual, eccentrically stipitate, single to concrescent, odorless when dry. Pileus circular, up to 7 cm in diam, 1.5 cm thick at center. Pileal surface white to blueish grey when young, olivaceous buff near the margin with age when fresh, and becoming brown to yellowish brown upon drying, azonate, tomentose when young, glabrous with age; margin blueish grey when fresh and becoming cream upon drying, up to 0.7 cm wide. Spines soft, slightly decurrent, blueish grey when fresh, becoming fragile, greyish brown to brown upon drying, up to 4 mm long. Context dark blueish grey upon drying, tough, up to 1 cm thick. Stipes cylindrical, glabrous, light brown, up to 6.2 cm long, 1.3 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; all tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff to brown, thick-walled, occasionally branched, with simple-septa, regular in the outter layer, interwoven in the inner layer, inflated, 3–6 µm in diam.

Spines – Generative hyphae clay-buff to brown, slightly thick-walled, branched, with simple-septa, regularly arranged, 2–5 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 28–67 × 5–7 µm; sterigmata 3–5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff to brown, thick-walled, occasionally branched, with simple-septa, regularly arranged, 2.5–6 µm in diam.

Spores – Basidiospores, hyaline, subglobose to globose, thin-walled, warted, IKI–, CB–, 5–6.5 × (3.5–)4–5 µm, L = 5.25 µm, W = 4.39 µm, Q = 1.18–1.2 (n = 90/3, without the ornamentation).

Additional specimens (paratypes) examined – **USA.** New York, Franklin County, on the ground of conifer forest, approx. 79° 50' 15" W 41° 23' 46" N, alt. 468 m, 4 September 2019, Cui 23045 (BJFC, duplicate in IFP); 24 September 2019, Cui 23046 (BJFC, duplicate in IFP).

Notes – *Hydnellum luteocaesia* was collected from the east-central United States under a temperate continental humid climate. In this study, *H. luteocaesia* was grouped with *H. caeruleum* (Hornem.) P. Karst. and *H. subcaeruleum* (Fig. 3). Morphologically, *H. luteocaesia* can be distinguished by its tomentose and blueish grey to olivaceous buff pileal surface, blueish grey spines, and dark blueish grey context (Hrouda 1999).

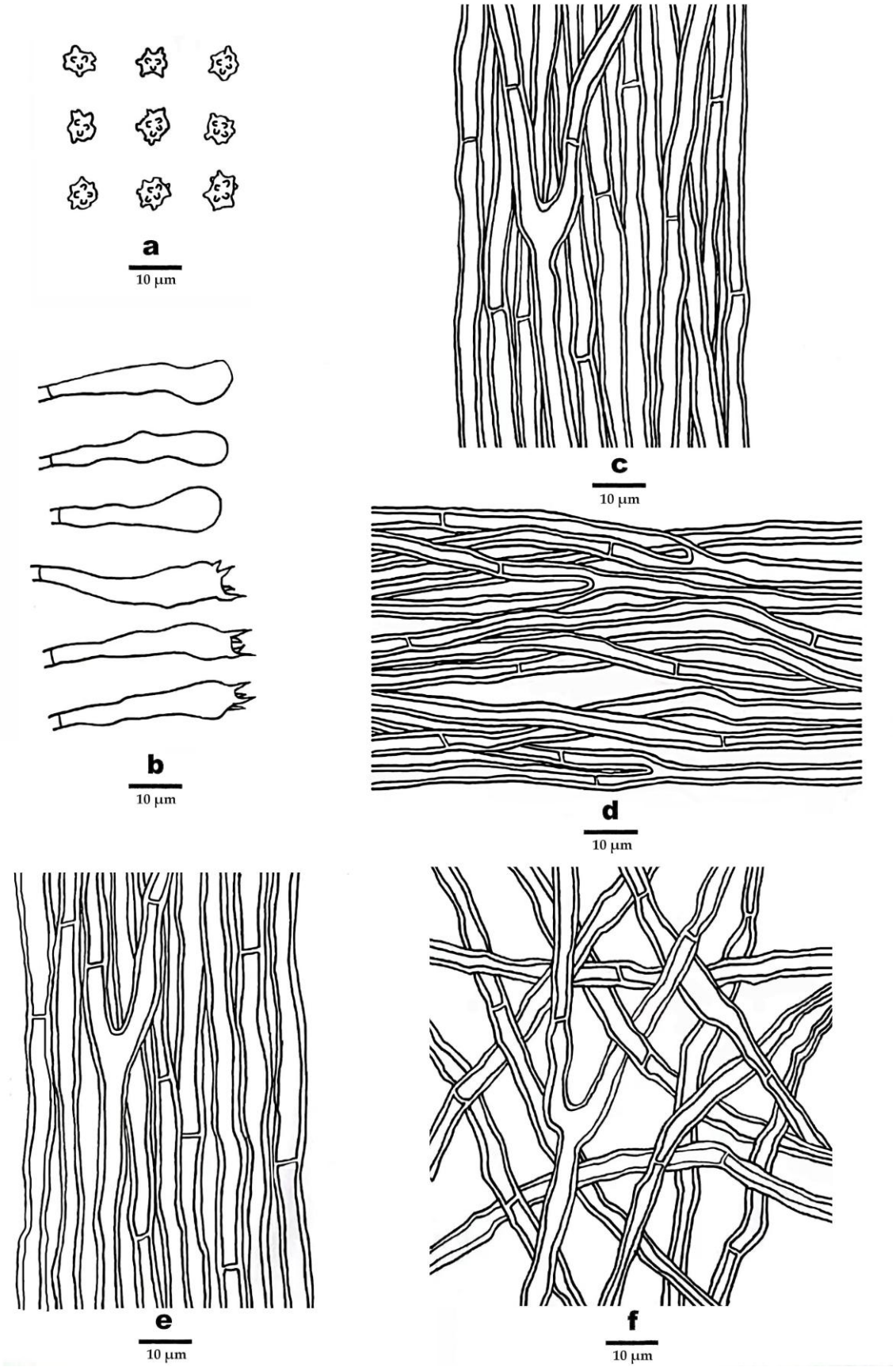

Fig. 21 Microscopic structures of *Hydnellum luteocaesia* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum nitida B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 d, e; 11 d, e; 22).

Index Fungorum number: IF 902687; Facesoffungi number: FoF 16248

Diagnosis – Differs from other *Hydnellum* species by its short stipe, reddish brown, greyish-brown to dark brown pileal surface with lacquer-like sheen.

Type – **CHINA**. Sichuan Province, Jiuzhaigou County, Ganmeizi Belay Station, on the ground of mixed forest, approx. 104° 15' 47" E 33° 10' 38" N, alt. 2458 m, 21 September 2020, Cui 18571 (holotype in BJFC, isotype in IFP).

Etymology – *nitida* (Lat.), refers to the pileal surface with a lacquer-like sheen.

Fruiting body – Basidiomata annual, centrally or eccentrically stipitate, single to concrescent, odorless when dry. Pileus circular to irregular, with lacquer-like sheen on pileal surface, up to 11 cm in diam, 1.1 cm thick at the center. Pileal surface reddish brown, greyish-brown to dark brown when fresh and becoming greyish brown to fuscous upon drying, zonate, glabrous, with radially aligned stripes; margin white when fresh, becoming greyish brown upon drying, up to 1.5 cm wide. Spines soft, reddish brown to greyish brown when fresh, becoming fragile, fuscous upon drying, up to 4 mm long. Context greyish brown upon drying, tough, up to 0.3 cm thick. Stipes cylindrical, glabrous, surface layer greyish brown, inner layer fuscous, up to 1.7 cm long, 1.1 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; all tissues turned olive green to black in KOH.

Pileus – Generative hyphae greyish brown, slightly thick-walled on the surface, branched, with simple-septa, regularly arranged, 2–5 µm in diam.

Spines – Generative hyphae clay-buff, thick-walled, occasionally branched, with simple-septa, regularly arranged, 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 18–35 × 5.5–8 µm; sterigmata 1.5–5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, slightly thick-walled in the surface layer, rarely branched, with simple-septa, interwoven in the surface layer, regularly arranged in the inner layer, 2–7 µm in diam.

Spores – Basidiospores, brown, subglobose to globose, thin-walled, warted, IKI–, CB–, (4.5–)4.8–6 × 4–5(–5.2) µm, L = 5.2 µm, W = 4.7 µm, Q = 1.08–1.2 (n = 60/2, without the ornamentation).

Additional specimen (paratype) examined – **CHINA**. Sichuan Province, Jiuzhaigou County, Jiuzhaigou Reverse, Ganmeizi Belay Station, On the ground of the mixed forest, approx. 104° 15' 47" E 33° 10' 38" N, alt. 2458 m, 21 September 2020, Cui 18572 (BJFC, duplicate in IFP).

Notes – *Hydnellum nitida* was collected from southwest China under a plateau humid climate. In this study, *H. nitida* was closely related to *H. concrescens* (Pers.) Banker and *H. rubidofuscum* Y.H. Mu & H.S. Yuan in the phylogenetic tree (Fig. 3). Morphologically, *H. concrescens* might be confused with *H. nitida* by having single to concrescent basidiomata. However, *H. concrescens* can be distinguished by its longer stipe (up to 3.3 cm), shorter spines (up to 2 mm), and bigger basidiospores (5.5–6.5 × 4–4.8 µm, Baird & Khan 1986). Morphologically, *H. rubidofuscum* might be confused with *H. nitida* by having reddish brown, zonate, glabrous pileal surface and reddish brown to greyish-brown spines. However, *H. rubidofuscum* can be distinguished by its lacquer-like sheen pileal surface, wider basidia (14–37 × 4–6 µm), and smaller basidiospores (4.1–5 × 3.9–4.6 µm, Mu et al. 2021).

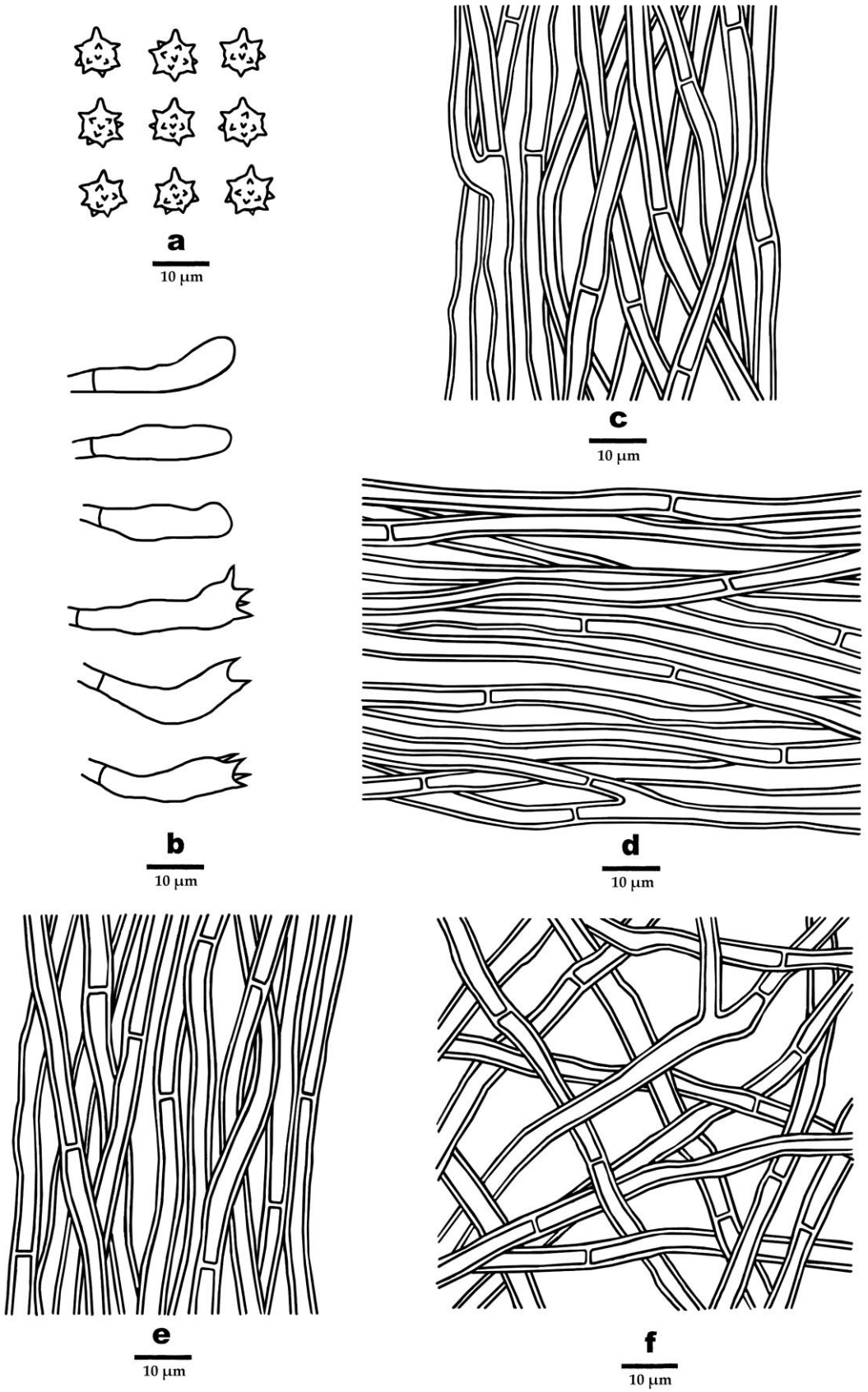

Fig. 22 Microscopic structures of *Hydnellum nitida* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum qinghaiense B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 f, g; 11 f, g; 23).

Index Fungorum number: IF 902688; Facesoffungi number: FoF 16249

Diagnosis – Differs from other *Hydnellum* species by its azonate pileal surface, glabrous pileus, and smaller basidiospores.

Type – **CHINA**. Qinghai Province, Jianza County, Kanbula Forest Park, on the ground of forest dominated by *Picea crassifolia*, approx. 101° 44' 34" E 36° 7' 52 " N, alt. 2700 m, 4 September 2018, Dai 18939 (holotype in BJFC, isotype in IFP).

Etymology – *qinghaiense* (Lat.), refers to the specimens collected from Qinghai Province.

Fruiting body – Basidiomata annual, centrally or eccentrically stipitate, single or concrescent, odorless when dry. Pileus circular to depressed, often imbricated, up to 4 cm in diam, 0.3 cm thick at the center. Pileal surface reddish brown when fresh, and becoming greyish-brown upon drying, azonate, tomentose; margin white to light grey when fresh, and becoming pale mouse-grey to light brown upon drying, up to 3 cm wide. Spines soft, greyish blue to brown when fresh, and becoming greyish brown to black upon drying, up to 4 mm long. Context light greyish-brown upon drying, tough, up to 0.2 cm thick. Stipes cylindrical, glabrous, surface layer brown, greyish-brown to dark brown, inner layer dark brown to fuscous, up to 2 cm long, 0.4 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff to light brown, slightly thick-walled, branched, with simple-septa, regularly arranged, 2.5–5 µm in diam.

Spines – Generative hyphae bright clay-buff, slightly thick-walled, occasionally branched, with simple-septa, regularly arranged, 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 21–34 × 5–6.5 µm; sterigmata 2–3.5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae bright clay-buff, slightly thick-walled, rarely branched, with simple-septa, regularly arranged, 2–5 µm in diam.

Spores – Basidiospores, brown, irregularly subglobose to irregularly elliptical, thin-walled, warted, IKI–, CB–, 4–5 × 3–4(–4.5) µm, L = 4.35 µm, W = 3.75 µm, Q =1.1–1.24 (n = 60/2, without the ornamentation).

Additional specimen (paratype) examined – **CHINA**. Qinghai Province, Huangnan Prefecture, Jianza County, Kanbula Forest Park, on the ground of forest dominated by *Picea crassifolia*, approx. 101° 44' 34" E 36° 7' 52" N, alt. 2700 m, 4 September 2018, Dai 18943 (BJFC, duplicate in IFP).

Notes – *Hydnellum qinghaiense* was collected from northwest China under a plateau continental climate. In this study, *H. qinghaiense* was closely related to *H. dianthifolium* Loizides, Arnolds & P.-A. Moreau (Fig. 3). Morphologically, *H. qinghaiense* resembles *H. dianthifolium* in having single to concrescent basidiomata and irregularly subglobose to elliptical basidiospores (Loizides et al. 2016). However, *H. qinghaiense* can be distracted from *H. dianthifolium* by its reddish-brown pileal surface, greyish-blue spines, and smaller basidiospores (4.5–5.5 × 3.5–4.5 µm, Loizides et al. 2016).

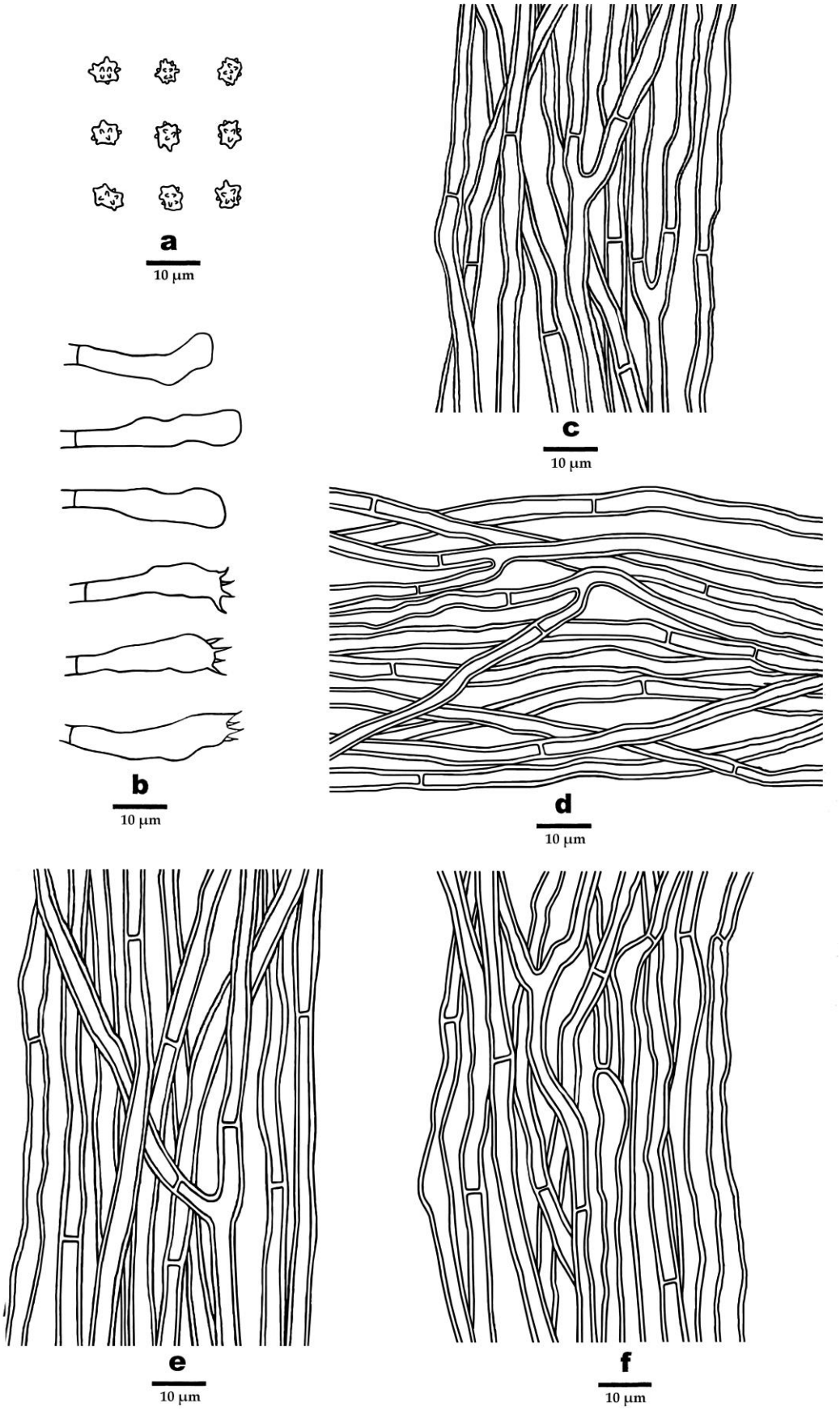

Fig. 23 Microscopic structures of *Hydnellum qinghaiense* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum subailaoensis B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 h, i; 11 h, i; 24).

Index Fungorum number: IF 902689; Facesoffungi number: FoF 16250

Diagnosis – Differs from other *Hydnellum* species by its scaly pileus, fawn to greyish brown pileal surface, white context, and light vinaceous grey spines.

Type – **CHINA.** Yunnan Province, Wuding County, on the ground of forest, approx. 102° 24' 55" E 25° 31' 49" N, alt. 1700 m, 8 October 2022, Dai 24634 (holotype in BJFC, isotype in IFP).

Etymology – *subailaoensis* (Lat.), refers to the new species resembling *H. ailaoensis* in morphology.

Fruiting body – Basidiomata annual, eccentrically stipitate, single, and odorless when fresh. Pileus circular, up to 6.2 cm in diam, and 1.5 cm thick at the center. Pileal surface fawn, brown to greyish brown when fresh and becoming honey yellow upon drying, scaly, azonate, glabrous; margin brown to dark brown when fresh and becoming dark brown upon drying, and up to 0.6 cm wide. Spines soft, light vinaceous grey when fresh, brown to greyish brown upon drying, fragile, and up to 3 mm long. Context white when fresh, brownish-white to cream upon drying, and up to 1 cm thick. Stipes cylindrical, glabrous, brown to dark brown in the outer layer, white in the inner layer, and up to 3 cm long and 1 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green to black in KOH.

Pileus – Generative hyphae light clay-buff, thick-walled, occasionally branched, regularly arranged, and 3.5–13 µm in diam.

Spines – Generative hyphae light brown, thick-walled, occasionally branched, regularly arranged, and 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 21–40 × 5–8 µm; sterigmata 2–4 µm long; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, thick-walled, rarely branched, regularly arranged, and 2–8 µm in diam.

Spores – Basidiospores, brown, subglobose, thin-walled, warted, IKI–, CB–, 6–7.5 × 5–6.5 µm, L = 6.35 µm, W = 5.62 µm, Q = 1.12 (n = 30/1, without the ornamentation).

Notes – *Hydnellum subailaoensis* was collected from southwest China under a north subtropical monsoon climate. It can be mainly characterized by its scaly pileus, fawn to greyish brown pileal surface, light vinaceous grey spines, and white context. In this study, *H. subailaoensis* was sister to *H. ailaoensis* (Fig. 3). However, it can be distinct by its larger basidiospores (4.5–5.5 × 5.5–7 µm, Lei et al. 2023).

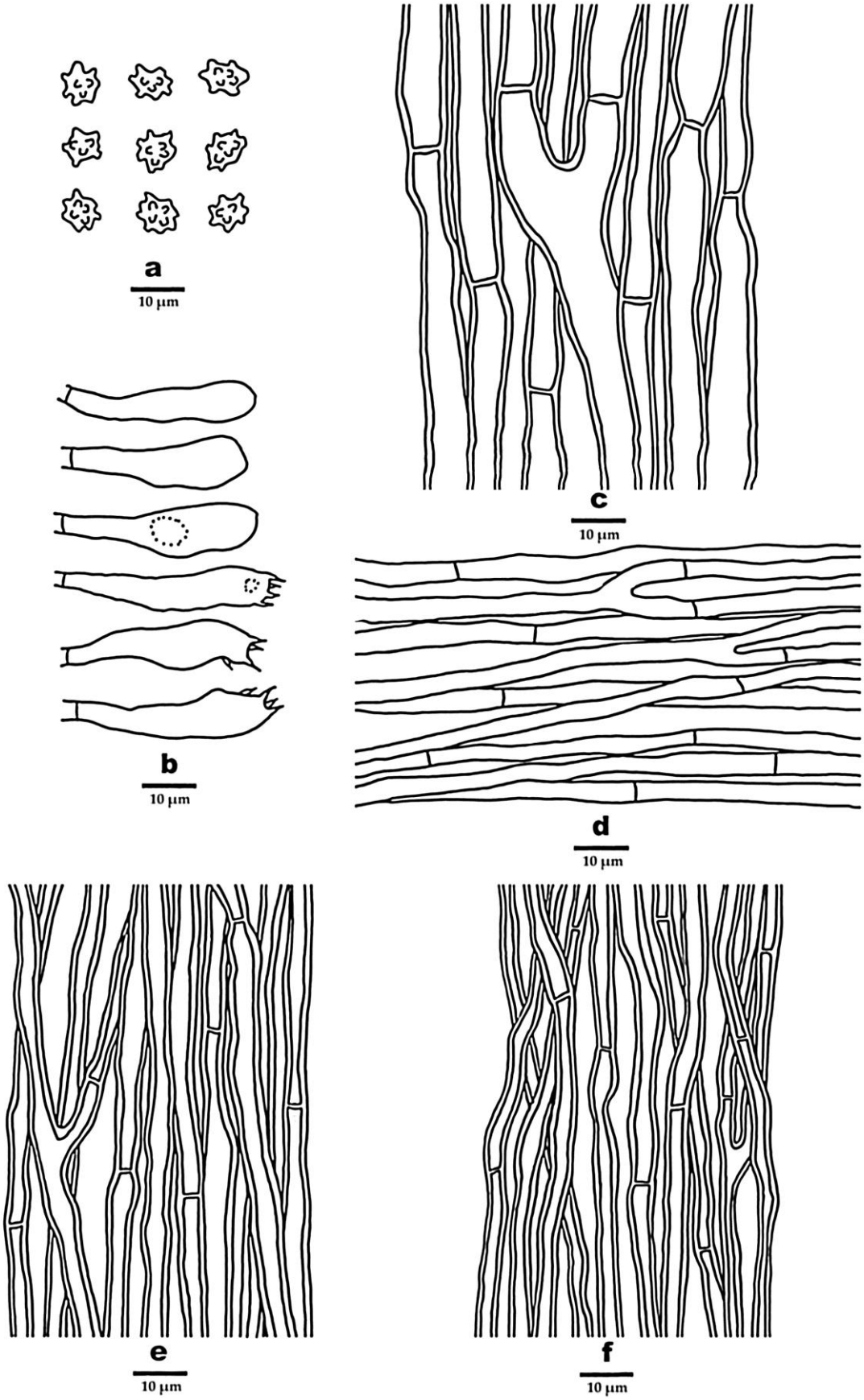

Fig. 24 Microscopic structures of *Hydnellum subailaoensis* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum subcaeruleum B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 j; 11 j, k; 25).

Index Fungorum number: IF 902690; Facesoffungi number: FoF 16251

Diagnosis – Differs from other *Hydnellum* species by its eccentrically stipitate, spongy to tomentose pileus, and the bluish grey to dark bluish grey pileal margin.

Type – **CHINA**. Gansu Province, Zhangye, Qilianshan Nature Reserve, Xishui Bely Station, on the ground of forest dominated by trees of *Picea* sp., approx. 100° 20' 14" E 38° 36' 27" N, alt. 2860 m, 3 September 2018, Dai 18976 (holotype in BJFC, isotype in IFP).

Etymology – *subcaeruleum* (Lat.), refers to the new species resembling *H. caeruleum* in morphology.

Fruiting body – Basidiomata annual, eccentrically stipitate, single to concrescent, odorless when dry. Pileus ellipsoid to irregular, up to 5 cm in diam, 1.5 cm thick at the center. Pileal surface clay-buff, reddish brown to dark brown when fresh and becoming greyish brown to fuscous upon drying, zonate, spongy to tomentose; margin bluish grey to dark bluish grey when fresh, becoming fuscous upon drying, up to 0.7 cm wide. Spines soft, olivaceous-buff to clay-buff near the stipe, white to bluish grey near margin when fresh, fuscous upon drying, up to 4 mm long. Context brown upon drying, tough, up to 0.8 cm thick. Stipes cylindrical, glabrous, surface layer dark brown to fuscous upon drying, inner layer greyish brown upon drying, up to 3.2 cm long, 2.3 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae greyish brown, thick-walled, branched, with simple-septa, regularly arranged, 2.5–6 µm in diam.

Spines – Generative hyphae clay-buff to greyish brown, slightly thick-walled, branched, with simple-septa, regularly arranged, 2.5–5 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 25–40 × 6–6.5 µm; sterigmata 2–3 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae dark brown, thick-walled, rarely branched, with simple-septa, interwoven in the surface layer, regularly arranged in the inner layer, 2–6 µm in diam.

Spores – Basidiospores, brown, subglobose to ellipsoidal, thin-walled, warted, IKI–, CB–, 4.5–6 × 4–5 µm, L = 5.2 µm, W = 4.5 µm, Q = 1.13–1.19 (n = 90/3, without the ornamentation).

Additional specimens (paratypes) examined – **CHINA**. Gansu Province, Zhangye, Qilianshan Nature Reserve, Xishui Bely Station, on the ground of forest dominated by trees of *Picea* sp., approx. 100° 20' 14" E 38° 36' 27" N, alt. 2860 m, 3 September 2018, Dai 18979 (BJFC, duplicate in IFP) & Dai 18980 (BJFC, duplicate in IFP).

Notes – *Hydnellum subcaeruleum* was collected in northwest China under a continental alpine subhumid mountain climate. In this study, *H. subcaeruleum* was closely related to *H. caeruleum* K. Harrison (Fig. 3). Morphologically, *H. caeruleum* is similar to *H. subcaeruleum* in having single to concrescent basidiomata, cottony to tomentose pileal surface, and the same reaction in KOH. However, *H. caeruleum* differs from *H. subcaeruleum* in having longer sterigmata (4–6 µm) and longer basidia (29–60 × 6.5–9 µm, Baird & Khan 1986).

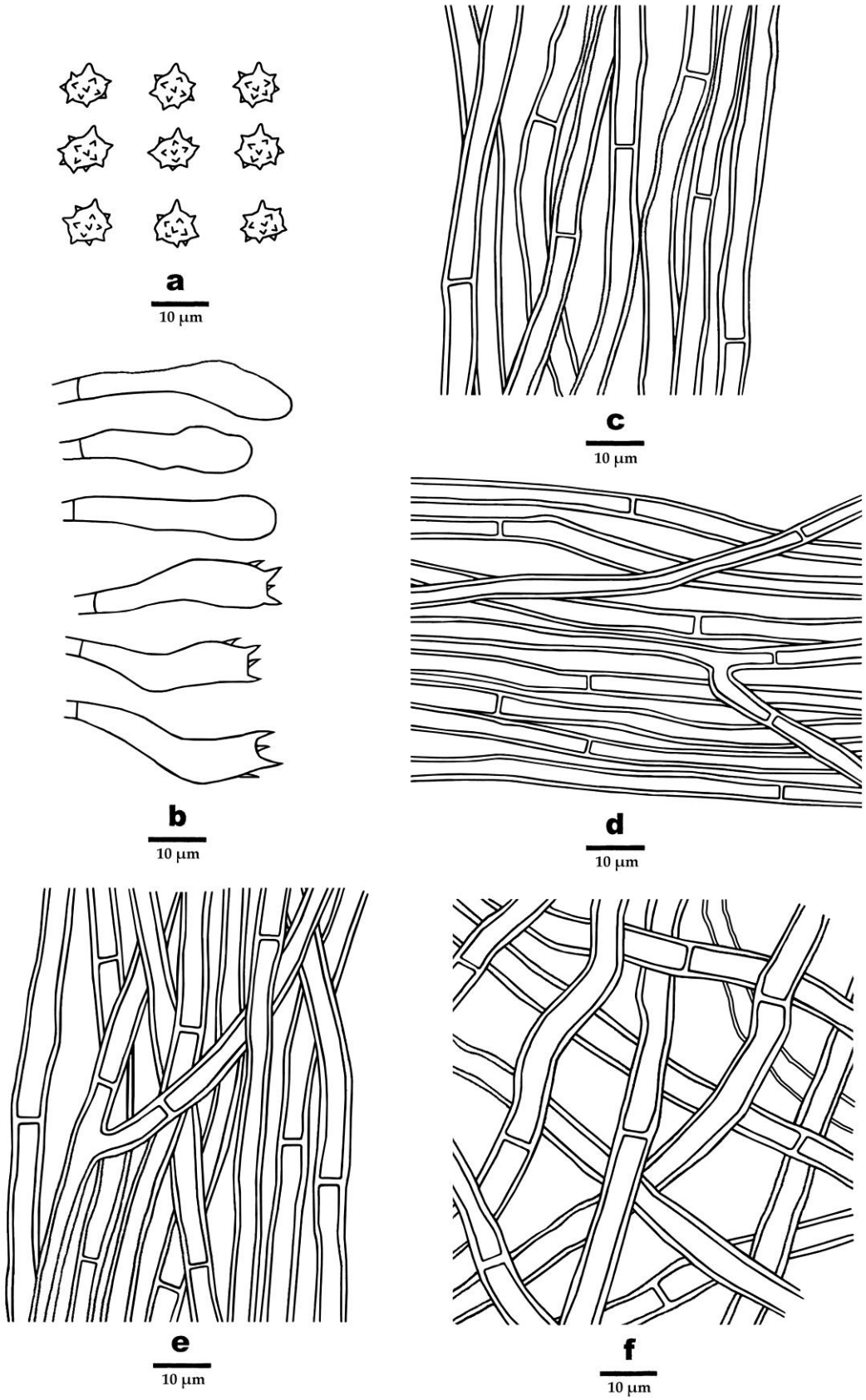

Fig. 25 Microscopic structures of *Hydnellum subcaeruleum* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum succulentus B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 k; 11 l, m; 26).

Index Fungorum number: IF 902691; Facesoffungi number: FoF 16252

Diagnosis – Differs from other *Hydnellum* species by its depressed or infundibuliform pileus succulent context.

Type – **CHINA**. Yunnan Province, Xichou County, Xiaoqiaogou, on the ground of angiosperm forest, approx. 104° 41' 33" E 23° 21' 52" N, alt. 1500 m, 29 June 2019, Dai 19953 (holotype in BJFC, isotype in IFP).

Etymology – *succulentus* (Lat.), refers to the succulent context.

Fruiting body – Basidiomata annual, centrally stipitate, single, and odorless when dry. Pileus depressed or infundibuliform, up to 5 cm in diam, and 0.9 cm thick at the center. Pileal surface light brown to brown when fresh and becoming light brown to greyish brown upon drying, azonate, glabrous; margin greyish brown when fresh and becoming brown to dark brown upon drying, and up to 0.3 cm wide. Spines soft, pale reddish brown when fresh, brown to dark brown drying, fragile, and up to 4 mm long. Context succulent, brownish vinaceous to light reddish brown when fresh, brownish vinaceous upon drying, fragile, and up to 0.4 cm thick. Stipes cylindrical, spongy, brown in the outer layer, reddish brown in the inner layer, up to 4.5 cm long, 0.8 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff, slightly thick-walled, occasionally branched, regularly arranged, and 4–13 µm in diam.

Spines – Generative hyphae clay-buff, thick-walled, occasionally branched, regularly arranged, and 2–5 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 25–37 × 5.5–8 µm; sterigmata 1.5–3.5 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, thick-walled, rarely branched, interwoven in the surface layer, regularly arranged in the inner layer, and 2–12 µm in diam.

Spores – Basidiospores, brown, subglobose to globose, thin-walled, warted, IKI–, CB–, 4–5 × 4–5.5 µm, L = 4.96 µm, W = 4.38 µm, Q = 1.1–1.19 (n = 60/2, without the ornamentation).

Additional specimen (paratype) examined – **CHINA**. Yunnan Province, Lijiang, Yulong County, Laojun Mountain, Jiushijiulongtan, on the ground of forest, approx. 99° 46' 59" E 26° 39' 14" N, alt. 2800 m, 12 August 2023, Cui 22876 (BJFC, duplicate in IFP).

Notes – *Hydnellum succulentus* was collected from southwest China under a north subtropical monsoon climate. In this study, *H. succulentus* was sister to *H. joeides* (Pass.) E. Larss., K.H. Larss. & Kõljalg (Fig. 3). However, *H. succulentus* can be distinct by its succulent context and pale reddish-brown spines (Maas Geesteranus 1971).

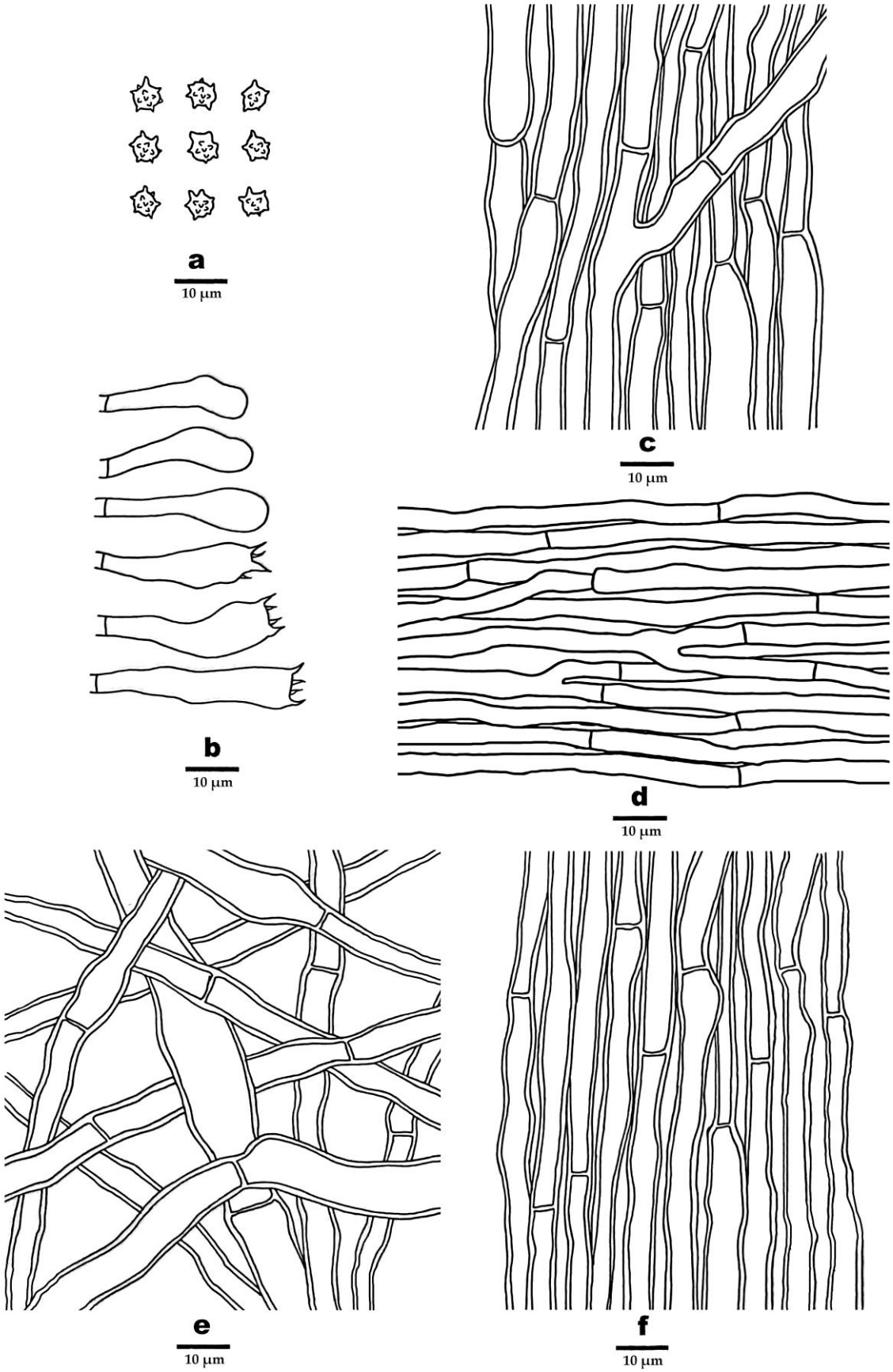

Fig. 26 Microscopic structures of *Hydnellum succulentus* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum tarda B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 8 l; 9 a; 11 n, o; 27).

Index Fungorum number: IF 902692; Facesoffungi number: FoF 16253

Diagnosis – Differs from other *Hydnellum* species by its reddish brown pileal surface.

Type – **CHINA**. Yunnan Province, Xichou County, Xiaoqiaogou, on the ground of forest, approx. 104° 41' 33" E 23° 21' 52" N, alt. 1500 m, 29 June 2019, Dai 19925 (holotype in BJFC, isotype in IFP).

Etymology – *tarda* (Lat.), refers to the reddish brown pileal surface.

Fruiting body – Basidiomata annual, centrally stipitate, single to concrescent, odorless when dry. Pileus circular, up to 3.5 cm in diam, 0.3 cm thick at the center. Pileal surface dark reddish brown when fresh at the center, becoming fawn, dark brown, greyish brown to fuscous upon drying, zonate, glabrous to fibrillose, with radially aligned stripes; margin white to pale reddish brown when fresh, becoming fawn, greyish brown to dark brown upon drying, up to 0.3 cm wide. Spines soft, reddish brown to dark reddish brown near stipe, pale reddish brown near margin when fresh, becoming greyish brown upon drying, up to 3 mm long. Context reddish brown when fresh, becoming brown to dark brown upon drying, brittle, up to 0.15 cm thick. Stipes cylindrical, glabrous, outer layer brown to reddish brown when fresh, becoming greyish brown to fuscous upon drying, inner layer dark reddish brown to dark brown when fresh, becoming greyish brown to dark brown upon drying, up to 2.8 cm long, 0.4 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; tissues turned olive green to black in KOH.

Pileus – Generative hyphae clay-buff, slightly thick-walled, branched, with simple-septa, regularly arranged, 2–5.5 µm in diam.

Spines – Generative hyphae clay-buff, thin-walled, occasionally branched, with simple-septa, regularly arranged, 2–4 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 21–35 × 6–8 µm; sterigmata 1.5–4 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, slightly thick-walled, rarely branched, with simple-septa, interwoven in the surface layer, regularly arranged in the inner layer, 2–5 µm in diam.

Spores – Basidiospores, brown, irregularly ellipsoid to subglobose, thin-walled, warted, IKI–, CB–, 4.5–6 × 4–5 µm, L = 5.18 µm, W = 4.36 µm, Q = 1.17–1.2 (n = 60/2, without the ornamentation).

Additional specimens (paratypes) examined – **CHINA**. Yunnan Province, Xichou County, Xiaoqiaogou, on the ground of forest, approx. 104° 41' 33" E 23° 21' 52" N, alt. 1800 m, 29 June 2019, Dai 19974 (BJFC, duplicate in IFP) & Dai 19975 (BJFC, duplicate in IFP).

Notes – *Hydnellum tarda* was collected from southwest China under a north subtropical monsoon climate. In this study, *H. tarda* was sister to *H. sulcatum* Y.H. Mu & H.S. Yuan (Fig. 3). However, *H. sulcatum* can be distinct from *H. tarda* by its dark brown pileal surface, brown spines, and shorter basidia (20–30 × 4–8 µm, Mu et al. 2021).

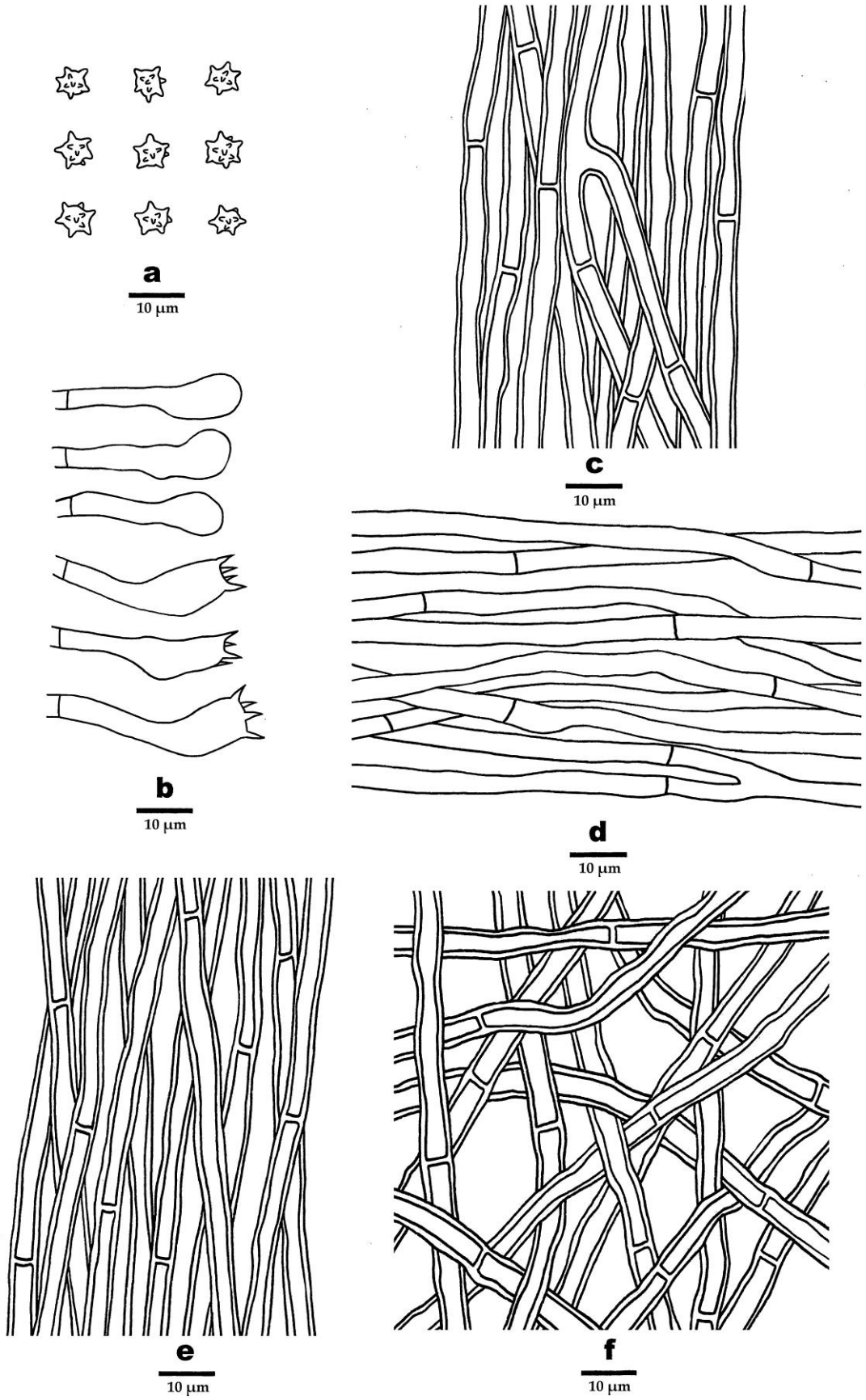

Fig. 27 Microscopic structures of *Hydnellum tarda* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Hydnellum xanthopus B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 9 b, c; 12 a, b; 28).

Index Fungorum number: IF 902693; Facesoffungi number: FoF 16254

Diagnosis – Differs from other *Hydnellum* species by its fawn to orange brown and zonate pileal surface, and clay buff spines.

Type – **CHINA.** Sichuan Province, Xiaojin County, Meiwo, on the ground of angiosperm forest, approx. 102° 29' 24" E 30° 52' 2" N, alt 3200 m, 1 August 2020, Cui 18618 (holotype in BJFC, isotype in IFP).

Etymology – *xanthopus* (Lat.), refers to the fawn to orange brown pileal surface.

Fruiting body – Basidiomata annual, centrally or eccentrically stipitate, single to concrescent, odorless when dry. Pileus circular, up to 2.4 cm in diam, 0.5 cm thick at center. Pileal surface fawn to orange brown when fresh and becoming greyish brown to vinaceous grey upon drying, zonate, fibrillose to tomentose, with radially aligned stripes, fawn to light brown near margin when fresh and becoming brown upon drying; margin white when fresh, becoming greyish brown to black upon drying, up to 0.3 cm wide. Spines soft, clay buff when fresh, becoming fragile, dark brown to fuscous upon drying, up to 2 mm long. Context greyish brown upon drying, tough, up to 0.2 cm thick. Stipes cylindrical, glabrous to fibrillose, greyish brown, up to 1.3 cm long, 0.5 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae with simple-septa; all the hyphae IKI–, CB–; all tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff, thick-walled, occasionally branched, with simple-septa, regularly arranged, 2–5 µm in diam.

Spines – Generative hyphae clay-buff, thin-walled, occasionally branched, with simple-septa, regularly arranged, with clamp connections, 2–3.5 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 18–38 × 5–7 µm; sterigmata 1.5–3 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, slightly thick-walled in the surface layer, rarely branched, with simple-septa, regularly arranged, 2–4 µm in diam.

Spores – Basidiospores, brown, subglobose to globose, thin-walled, warted, IKI–, CB–, 3.5–4.8 × 4–5.5 µm, L = 4.86 µm, W = 4.26 µm, Q = 1.14 (n = 30/1, without the ornamentation).

Notes – *Hydnellum xanthopus* was collected from southwest China under a temperate alpine climate. In this study, *H. xanthopus* was clustered with *H. concentricum* B.K. Cui & C.G. Song in our phylogenetic analysis (Fig. 3). Morphologically, *H. xanthopus* resembles *H. concentricum* in having concentric bands on pileal surface. However, *H. xanthopus* can be distinguished by its fawn to orange brown, fibrillose to tomentose pileal surface, and clay buff spines (Song et al. 2023).

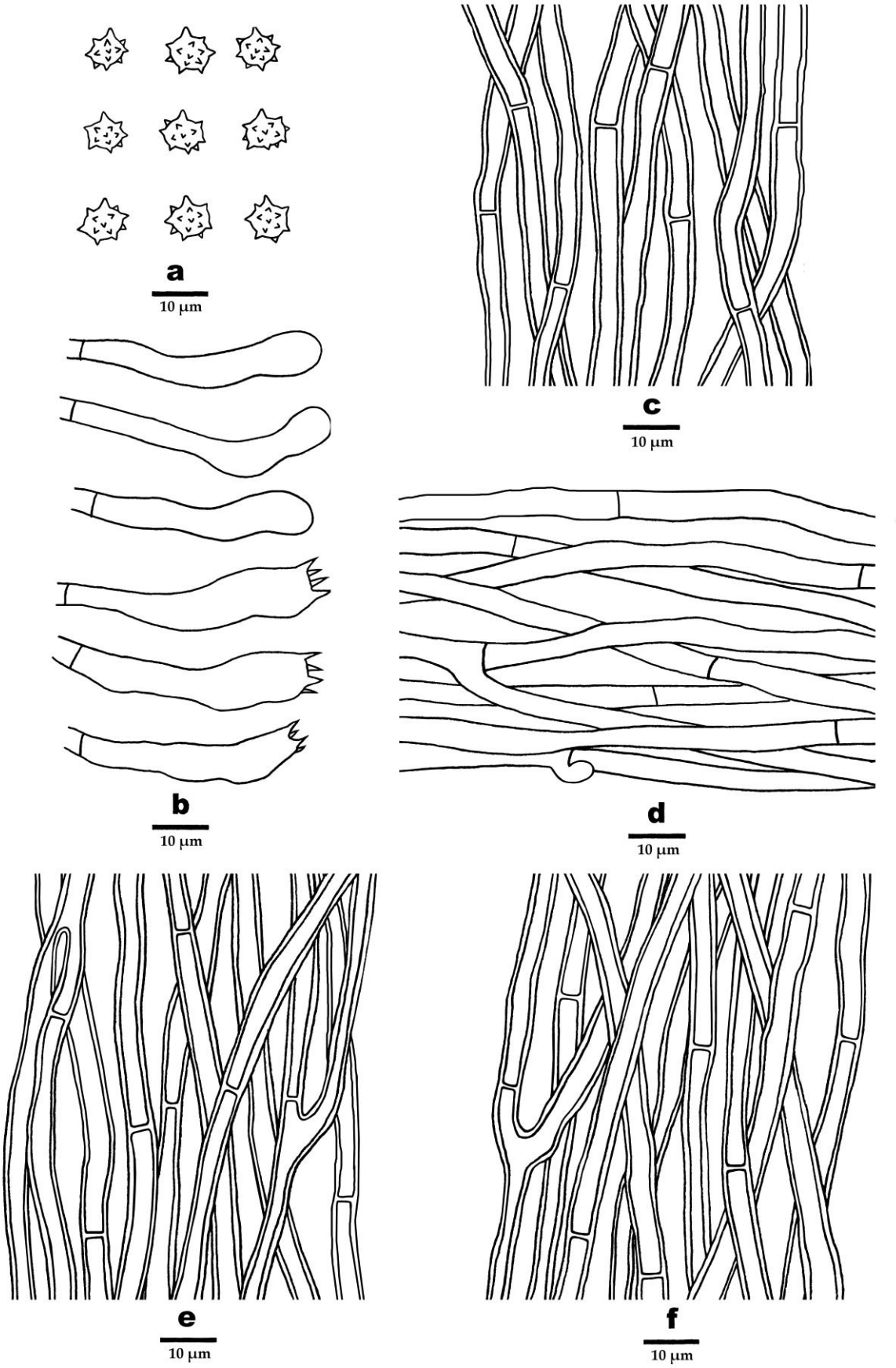

Fig. 28 Microscopic structures of *Hydnellum xanthopus* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Neosarcodon Xiao-L. He, Di Wang & W.H. Peng

Type species – *Neosarcodon pakaraimensis* (A. Grupe & T.W. Henkel) Xiao-L. He, Di Wang & W. H. Peng.

Description – Basidiomata annual, pileate, centrally stipitate, single to gregarious. Pileus conic, broadly conic to planoconvex or nearly plain with age, never infundibuliform. Pileal surface brown to black, glabrous, sometimes scaly. Hymenophores, white to brown, aculeate. Context soft, brittle, whitish to pale grayish, fleshy. Stipes hollow to solid, concolorous with pileus or slightly paler, glabrous to coarse. Hyphal system monomitic; generative hyphae with clamp connections, inflated. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores brown, ellipsoid, subglobose to globose, warted. For a detailed description of *Neosarcodon*, see Grupe et al. (2015, 2016) and Wang et al. (2024).

Notes – *Neosarcodon* was separated from *Sarcodon* as a new genus by Wang et al. (2024), and nine species have been described and transferred to the genus. Originally, *Neosarcodon* species were discovered in Belize, Guyana, Puerto Rico, and Colombia, all belonging to the Neotropics (Grupe et al. 2015, 2016). They mostly grow in broad-leaved tree forests dominated by trees of Caesalpinioideae, Dipterocarpaceae, Fagaceae, and Papilionoideae (Grupe et al. 2015, 2016). However, this study collected a new species from China, indicating that the genus was also distributed in China. Morphologically, *Neosarcodon* species can be characterized by conic, broadly conic to planoconvex or nearly plain pileus, brown to blackpileal surface, hollow to solid stipes, brown and warted basidiospores. In this study, *Neosarcodon* formed an independent lineage with high support (100% ML, 1.00 BPP, Figs. 1, 2) and was closely related to *Sarcodon*. Morphologically, *Neosarcodon* is similar to *Sarcodon* in having brown to dark brown pileus, fleshy context, and numerous clamp connections in generative hyphae. However, *Neosarcodon* can be distinguished by its conic, broadly conic to planoconvex pileus. With the addition of morphological evidence, one new species was described.

Neosarcodon melanocarpus B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 9 d, e; 12 c, d; 29).

Index Fungorum number: IF 902694; Facesoffungi number: FoF 16255

Diagnosis – Differs from other *Neosarcodon* species by its black pileal surface and black stipe.

Type – **CHINA**. Yunnan Province, Xichou County, Xiaoqiaogou, on the ground of forest, approx. 104° 41' 33" E 23° 21' 52" N, alt. 1500 m, 29 June 2019, Dai 19964 (holotype in BJFC, isotype in IFP).

Etymology – *melanocarpus* (Lat.), refers to the black pileal surface.

Fruiting body – Basidiomata annual, centrally stipitate, pileate, single, and odorless when dry. Pileus umbelliferous, margin often valgus after maturity, up to 2 cm in diam, and 0.2 cm thick at the center. Pileal surface black when fresh and becoming fuscous to black upon drying, azonate, glabrous; margin black when fresh and becoming fuscous to black upon drying, and up to 1.8 cm wide. Spines soft, brown to greyish brown when fresh, dark grey upon drying, fragile, and up to 2.5 mm long. Context olive grey to fuscous upon drying, fragile, and up to 0.15 cm thick. Stipes cylindrical, glabrous, black in the outer layer, dark grey to fuscous in the inner layer, and up to 4 cm long, 0.2 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae most with simple-septa, occasionally with clamp connections; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae olive green to black, thick-walled, rarely branched, regularly arranged, and 4–12 µm in diam.

Spines – Generative hyphae clay-buff, thick-walled, rarely branched, regularly arranged, and 3–13 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 26–42 × 8–10 µm; sterigmata 4–10 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff to black, thick-walled, rarely branched, regularly arranged, and 3–17 µm in diam.

Spores – Basidiospores, brown, subglobose, thin-walled, warted, IKI–, CB–, 6.5–9 × 6–8.5 µm, L = 7.87 µm, W = 7.02 µm, Q = 1.11–1.14 (n = 60/2, without the ornamentation).

Additional specimen (paratype) examined – **CHINA**. Yunnan Province, Xichou County, Xiaoqiaogou, on the ground of forest, approx. 104° 41' 33" E 23° 21' 52" N, alt. 1500 m, 29 June 2019, Dai 19978 (BJFC, duplicate in IFP).

Notes – *Neosarcodon melanocarpus* was collected from southwest China under a subtropical climate. Morphologically, *N. melanocarpus* can be distinguished by its black pileal surface and black stipe. In this study, *N. melanocarpus* was shown to be a distinct well-supported lineage within *Neosarcodon* (100% ML, 1.00 BPP, Figs. 1, 2).

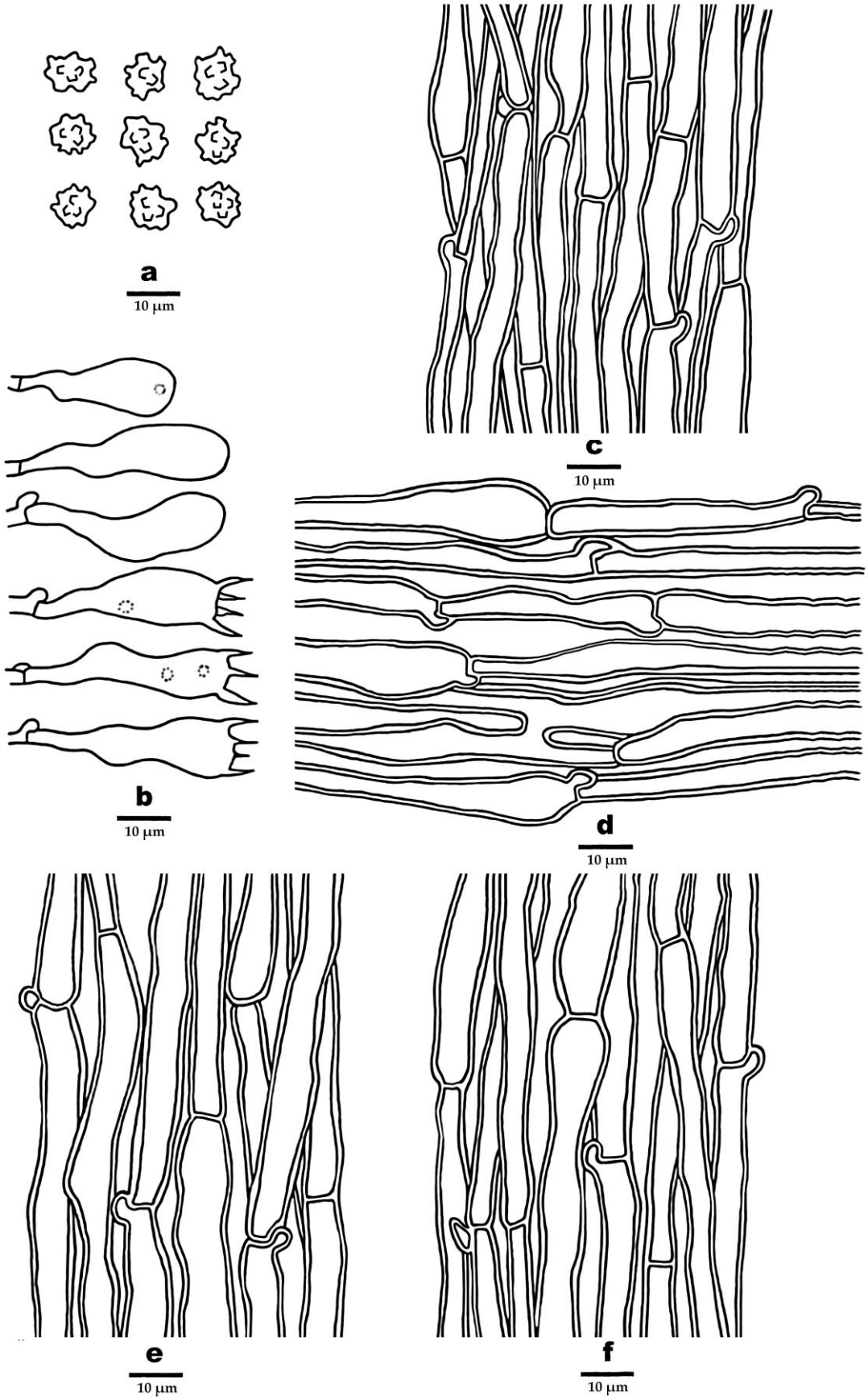

Fig. 29 Microscopic structures of *Neosarcodon melanocarpus* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Sarcodon Quél. ex P. Karst., Revue Mycologique Toulouse 3 (9): 20, 1881.

Type species – *Sarcodon imbricatus* (L.) P. Karst.

Description – Basidiomata annual, pileate, centrally or laterally stipitate, single to gregarious. Pileus circular to irregular, pale brown to dark brown, tomentum of the pileus develops into coarse scales with the tips upturned or turning into a pellicle, which becomes cracked and may form appressed scales. Hymenophores white to grey, aculeate. Stipes cylindrical, sometimes hollow, glabrous to fibrillose, surface similar to pileus or paler. Hyphal system monomitic; generative hyphae with clamp connections, context hyphae inflated. Cystidia and cystidioles absent. Basidia clavate, 4–spored. Basidiospores brown, ellipsoid, subglobose to globose, warted. For a detailed description of *Sarcodon*, see Karsten (1881) and Baird et al. (2013).

Notes – *Sarcodon* was established by Karsten (Karsten 1881). *Sarcodon* species were often collected and observed in hardwood forests with scattered conifers, especially Pinaceae and Fagaceae (Baird et al. 2013, Mu et al. 2020). *Sarcodon* species have been reported in Europe (Agerer 1991, Maas Geesteranus 1956, 1975, Hrouda 1999, Walleyn & Verbeken 2000, Hrouda 2005, Nitare 2006, Komura et al. 2015), America (Harrison 1964, 1984, Baird 1985, Bononi1981, Coker & Beers 1951, Baird et al. 2013, Magnago et al. 2015), Asia (Mu et al. 2021, Wang et al. 2024), New Zealand (Maas Geesteranus 1964, 1971, 1975) and Australia (Mleczko et al. 2011, Magnago et al. 2015, Hahn et al. 2018). It is characterized by stipitate and pileate basidiomata, scaly pileus, and brown and warted basidiospores. Morphologically, *Sarcodon* species are relatively similar to *Hydnellum* in having fleshy pileus and spines. In previous studies, the two genera were thought to be syngeneic (Baird 2013, Mu et al. 2020). However, Larsson et al. (2019) transferred twelve species from *Sarcodon* to *Hydnellum* to make the two genera monophyletic. In this study, twelve species of *Sarcodon* were included to construct the phylogenetic trees, and they form an independent lineage with proper support (83% ML, 1.00 BPP, Fig. 1; 98% ML, 1.00 BPP, Fig. 2) except *S. scabripes*. *Sarcodon scabripes* formed a separate branch and may represent an independent genus. In addition, with the addition of morphological evidence, one new species was described.

Sarcodon yunnanensis B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 9 f, g; 12 g, h; 30).

Index Fungorum number: IF 902695; Facesoffungi number: FoF 16256

Diagnosis – Differs from other *Sarcodon* species by its light greyish brown pileal surface and the clay pink spines.

Type – **CHINA**. Yunnan Province, Chuxiong, on the ground of forest, approx. 101° 30' 50" E 25° 3' 8" N, alt. 1800 m, 15 September 2011, He 1078 (holotype in BJFC, isotype in IFP).

Etymology – *yunnanensis* (Lat.), refers to the holotype locality of the species in Yunnan Province.

Fruiting body – Basidiomata annual, centrally stipitate, single to concrescent, with a fenugreek odor when dry. Pileus circular and depressed, scaly, up to 5.8 cm in diam, and 0.5 cm thick at the center. Pileal surface light greyish brown when fresh and becoming light brown to dark brown upon drying, azonate, glabrous; margin dark brown when fresh and becoming light brown upon drying, and up to 0.4 cm wide. Spines soft, fawn to clay pink when fresh, light brown upon drying, fragile, and up to 3 mm long. Context light brown upon drying, fragile, and up to 0.3 cm thick. Stipes cylindrical, glabrous, light brown in the outer layer and cream to light brown in the inner layer, and up to 6 cm long, 1 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae mostly with simple-septa, occasionally with clamp connections in hyphal of pileus and stipe, with simple-septa in hyphal of the spines; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff to brown, thick-walled, occasionally branched, regularly arranged, and 3–12 µm in diam.

Stipe – Generative hyphae clay-buff, thick-walled, occasionally branched, regularly arranged and 2–13 µm in diam.

Spines – Generative hyphae clay-buff, thin-walled, branched, rarely regularly arranged, and 2–6 µm in diam. Cystidia and cystidioles absent. Basidia clavate, 4–spored, 26–45 × 5–7 µm; sterigmata 2–4 µm; basidioles similar to basidia in shape.

Spores – Basidiospores, yellow, subglobose, thin-walled, warted, IKI–, CB–, 5–6.5 × 4.5–5.5 µm, L = 5.75 µm, W = 4.98 µm, Q = 1.15 (n = 30/1, without the ornamentation).

Notes – *Sarcodon yunnanensis* was collected from southwest China under a north subtropical monsoon climate. In this study, *S. yunnanensis* was closely related to *S. flavidus* Xiao L. He & D. Wang (Figs. 1, 2). Morphologically, *S. yunnanensis* differs by its fawn to greyish brown pileal surface and the clay pink spines (Wang et al. 2024).

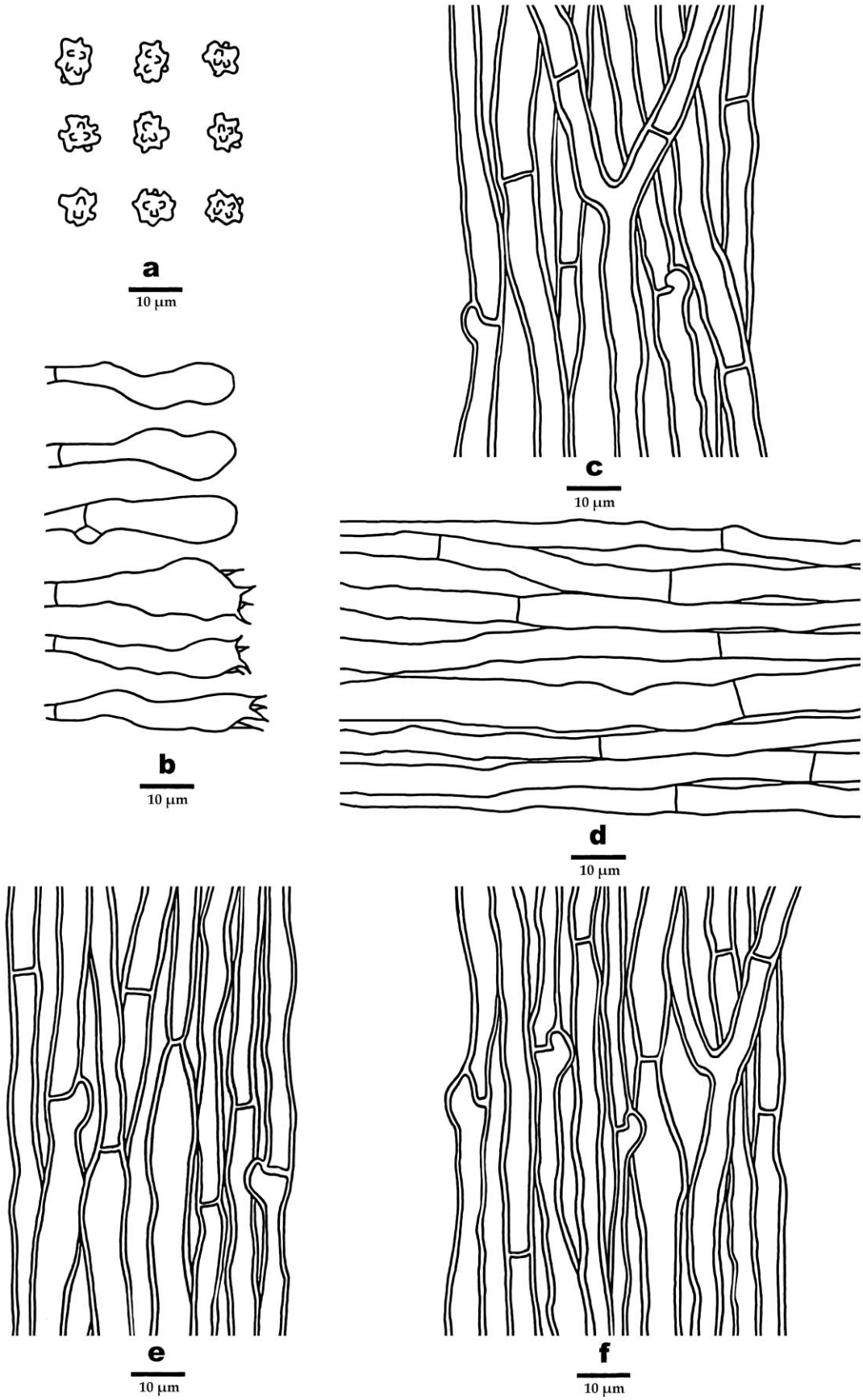

Fig. 30 Microscopic structures of *Sarcodon yunnanensis* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from spines; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Thelephoraceae Chevall., Flore Générale des Environs de Paris 1: 84, 1826.

Type genus – *Thelephora* Ehrh. ex Willd.

Description – Basidiomata annual, diverse forms: clavarioid, cantharelloid, spathulate, pleuropodally, pileate or resupinate, effused, byssoid, arachnoid, mucedinoid or pelliculose, adherent to separable, colored in a wide variety of tints. Hymenophores white, cinnamon buff to brown or darker, smooth, partially wrinkled, granulose, to aculeate. Hyphal system monomitic or dimitic; generative hyphae with simple-septate or clamp connections. Cystidia absent or present, acuminate, clavate, obclavate or capitulate. Basidia clavate, 4–spored. Basidiospores normally pigmented some shade of brown, green or red, ellipsoid to irregular globose or globose, echinulate or warted.

Notes – In this study, species of *Thelephora* and *Odontia* grouped together and formed a distinct clade with high support (71% ML, 0.98 BPP, Fig. 1; 68% ML, 1.00 BPP, Fig. 2) within Thelephorales. Morphologically, it was characterized by diverse forms of basidiomata, smooth to partially wrinkled, granulose, colliculose, aculeate hymenophores, and muricate, warted or echinulate basidiospores. Species of *Thelephora* and *Odontia* could not be placed in any of the presently known families of Thelephorales. Besides, the divergence time estimation results showed that the ancestor of this clade evolved at 253.98 Mya, which was in line with the time range for the differentiation of other families in Thelephorales (Fig. 6). Thus, we recommend the two genera as members of the family Thelephoraceae.

Key to genera of Thelephoraceae

1. Hymenophores smooth to partially wrinkled ..... *Thelephora*
1. Hymenophores aculeate ..... *Odontia*

Odontia Pers., Neues Magazin für die Botanik 1: 110, 1794.

Type species – *Odontia ferruginea* Pers.

Description – Basidiomata annual, continuous, arachnoid to resupinate, brown. Hymenophores light brown or darker, aculeate. Rhizomorphs present in the subiculum and margins, rhizomorph surface rather smooth. Hyphae system monomitic or dimitic; generative hyphae with clamp connections. Cystidia and cystidioles absent. Basidia subclavate to clavate, 4–spored. Basidiospores light brown, ellipsoid to irregular globose, lobed to warted. For a detailed description of *Odontia*, see Persoon (1794).

Notes – *Odontia* was established by Persoon (Persoon 1794). Tedersoo et al. (2014) suggest that *Odontia* species are nonmycorrhizal, but their nutrition differs from typical wood-rotting Basidiomycota. *Odontia* species have been found on rotten angiosperm wood branches and reported in Europe and Asia (Banker 1929, Miller 1933, Yuan et al. 2018). Morphologically, *Odontia* can be characterized by resupinate basidiomata, aculeate hymenophores, the presence of rhizomorphs and irregular globose, warted basidiospores. In the phylogenetic analyses, eight species of *Odontia* were included to construct the phylogenetic tree, these species formed a separate lineage within Thelephoraceae (74% ML, 0.99 BPP, Fig. 1; 73% ML, 1.00 BPP, Fig. 2).

Thelephora Florae Berolinensis Prodromus: 397, 1787.

Type species – *Thelephora terrestris* Ehrh., Pl. crypt. exsicc., no 178: no. 178, 1787. MB 193195

Description – Basidiomata annual, arachnoid to pelliculose, resupinate, or pileate, diverse forms, colored in a wide variety of tints. Hymenophores white, cinnamon buff to brown or darker, smooth, partially wrinkled, granulose, or aculeate. Hyphal system monomitic or dimitic, generative hyphae with simple-septate or clamp connections; cordons present or absent. Cystidia and cystidioles absent or present, subclavate, with obtuse apex. Basidia chiastic to clavate, 2(–4)–spored. Basidiospores normally pigmented some shade of brown, green or red, ellipsoid to globose echinulate to warted.

Notes – *Thelephora* was established by Willdenow (Willdenow 1787; Corner 1968, 1976). It can be characterized by pileate, stipitate, sessile or resupinate, clavarioid, cantharelloid, spathulate basidiomata; hyphal system monomitic; generative hyphae hyaline to brown, thin- to thick-walled; basidiospores subhyaline to brownish, ornamented (Cunningham 1957, Corner 1966, 1968, 1976, Stalpers 1993, Vizzini et al. 2016). The name *Tomentella* was firstly proposed by Persoon in 1799 as an infrageneric name under *Corticium*, with two species: *C. ferrugineum* and *C. chalibaeum* (Stalpers 1993). Patouillard (1887) validly published the name *Tomentella* and accepted the taxon in the sense of Persoon, as he cited it with Persoon's name in brackets. Quélet (1886) characterized the genus as having resupinate, effused basidiomes, and aculeate or echinulate spores. The two genera were closely related within Thelephoraceae (Patouillard 1887) and were usually intermixed in the same evolutionary branch (Vizzini et al. 2016). There is considerable evidence that taxonomically, *Thelephora* and *Tomentella* are quite similar (Yorou 2008, Ramírez-López et al. 2015, Li et al. 2020, Lu et al. 2022, Yang et al. 2023). Morphologically, the two genera share similar characteristic, such as the monomitic hyphal system with clamp connections in generative hyphae and warted or echinulate basidiospores. However, *Tomentella* differs in having resupinate, effused, and adherent basidiomata (Stalpers 1993, Kõljalg 1996, Zecchin 2008, Li et al. 2020). Ramírez-López et al. (2015) revealed that some *Thelephora* species, *T. versatilis* Ram. -Lóp. & Villegas and *T. pseudoversatilis* Ram. -Lóp. & Villegas, also have resupinate basidiomata. In addition, there were considerable evidence that taxonomically, the boundary between *Thelephora* and *Tomentella* is delicate (Yorou 2008, Ramírez-López et al. 2015, Li et al. 2020, Lu et al. 2022, Yang et al. 2023). Until recently, Kõljalg et al. (2024) merged the genus *Tomentella* into *Thelephora*. In this study, 143 species were included to construct the phylogenetic trees. Samples of *Thelephora* clustered together and formed a strongly supported monophyletic lineage (100 % ML, 1.00 BPP, Figs. 1, 2), which supports the classification proposed by Kõljalg et al. (2024). In addition, 4 new combinations were proposed based on available subsequences and were listed in Table 3.

Species of *Thelephora* can form ectomycorrhiza, and have been found in forests dominated by trees of Achatocarpaceae, Apocynaceae, Betulaceae, Cistaceae, Dipterocarpaceae, Ericaceae, Fabaceae, Fagaceae, Orchidaceae, Pinaceae, Myrtaceae, Nothofagaceae, Nyctaginaceae, Papilionoideae, Polygonaceae, Pyrolaceae, Rhamnaceae, Rosaceae, Salicaceae, Ticodendraceae, and Tiliaceae (Tedersoo et al. 2007, 2008, Smith et al. 2011, Jakucs et al. 2015, Salgado Salomón et al. 2017, Alvarez-Manjarrez et al. 2018, Malysheva et al. 2018, Lu et al. 2022). According to the previous studies, approximately 452 accepted species of *Thelephora* have been described worldwide (Lu et al. 2018a, b, Lu et al. 2022, Yang et al. 2023). The reconstituted genus *Thelephora* has been reported in America (Wakefield 1962, Larsen 1974, Kuhar et al. 2016), UK (Wakefield 1969), Africa (Yorou et al. 2007, 2012a, b, Yorou & Agerer 2008, Wakefield 1966), India (Welden 1968; Thind & Rattan 1971), Italy (Yorou & Agerer 2011a, b, Natarajan & Chandrashekara 1978), Europe (Kõljalg 1996, Wakefield 1966, Yorou & Agerer 2011a, b), and Asia (Yuan et al. 2020, Lu & Yuan 2021, Li et al. 2020, Liu et al. 2021). Morphologically, the reconstituted genus *Thelephora* can be characterized by smooth, partially wrinkled, granulose, colliculose or aculeate hymenophores, monomitic or dimitic hyphal system, and warted to echinulate basidiospores. In this study, 143 species were included to construct the phylogenetic tree (Fig. 5). Two new species were described and illustrated, based on morphological characters and phylogenetic evidence.

Thelephora bubalinomarginata B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 9 h, i, j; 12 i, j; 31).

Index Fungorum number: IF 902696; Facesoffungi number: FoF 16257

Diagnosis – Differs from other *Thelephora* species by its imbricated pileus, white, buff, cinnamon buff to greyish brown hymenial surface, downy, tomentose to rugulose pileal surface, and short stipe.

Type – **CHINA**. Yunnan Province, Xichou County, Xiaoqiaogou, on the ground of forest, approx. 104° 41' 33" E 23° 21' 53" N, alt. 1580 m, 29 September 2019, Dai 19931 (holotype in BJFC, isotype in IFP).

Etymology – *bubalinomarginata* (Lat.), refers to the white margin.

Fruiting body – Basidiomata annual, eccentrically stipitate, single to concrescent, with strong fenugreek odor when dry. Pileus circular to irregular, often imbricated, up to 6.8 cm in diam, 0.4 cm thick at the center. Pileal surface light brown when fresh, and becoming pinkish buff to light brown upon drying, zonate, downy; margin white to cream when fresh, and becoming pinkish buff to light brown upon drying, downy, tomentose to rugulose, up to 0.5 cm wide. Hymenophores smooth, greyish brown at the center, buff, pinkish buff to cinnamon buff near the margin, white at the margin when fresh. Context cream to pinkish buff upon drying, tough, up to 0.2 cm thick. Stipes cylindrical, downy, surface layer light brown to greyish-brown, inner layer cream, up to 0.5 cm long, 0.7 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae mostly with simple-septa, occasionally with clamp connections; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff, slightly thick-walled, occasionally branched, mostly with simple-septa, occasionally with clamp connections, regularly arranged, 2.5–5 µm in diam.

Hymenophore – Cystidia and cystidioles absent. Basidia clavate, 4–spored, 33–64 × 5–7.5 µm; sterigmata 3–6 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae clay-buff, thick-walled, branched, mostly with simple-septa, occasionally with clamp connections, regularly arranged, 2–7 µm in diam.

Spores – Basidiospores, hyaline to light yellow or light brown, globose to irregularly elliptical, warted, IKI–, CB–, 6.5–8.5 × 5.5–7 µm, L = 7.32 µm, W = 6.04 µm, Q =1.2–1.23 (n = 90/3, without the ornamentation).

Additional specimens (paratypes) examined – **CHINA**. Yunnan Province, Mengla County, Shangyong Nature Reserve, on the ground of forest, approx. 101° 34' 2" E 21° 27' 55" N, alt. 800 m, 20 August 2019, Dai 20606 (BJFC, duplicate in IFP) & Dai 20608 (BJFC, duplicate in IFP); Yunnan Province, Xichou County, Xiaoqiaogou, on the ground of forest, approx. 104° 41' 33" E 23° 21' 53" N, alt. 1580 m, 29 September 2019, Dai 19919 (BJFC, duplicate in IFP) & Dai 19932 (BJFC, duplicate in IFP).

Notes – *Thelephora bubalinomarginata* was collected from southwest China under a subtropical monsoon climate. This study closely relates to *Thelephora sikkimensis* K. Das, Hembrom & Kuhar (Fig. 5). Morphologically, *T. bubalinomarginata* differs by its light brown pileal surface and greyish brown, buff to cinnamon buff hymenophores (Kanad et al. 2018).

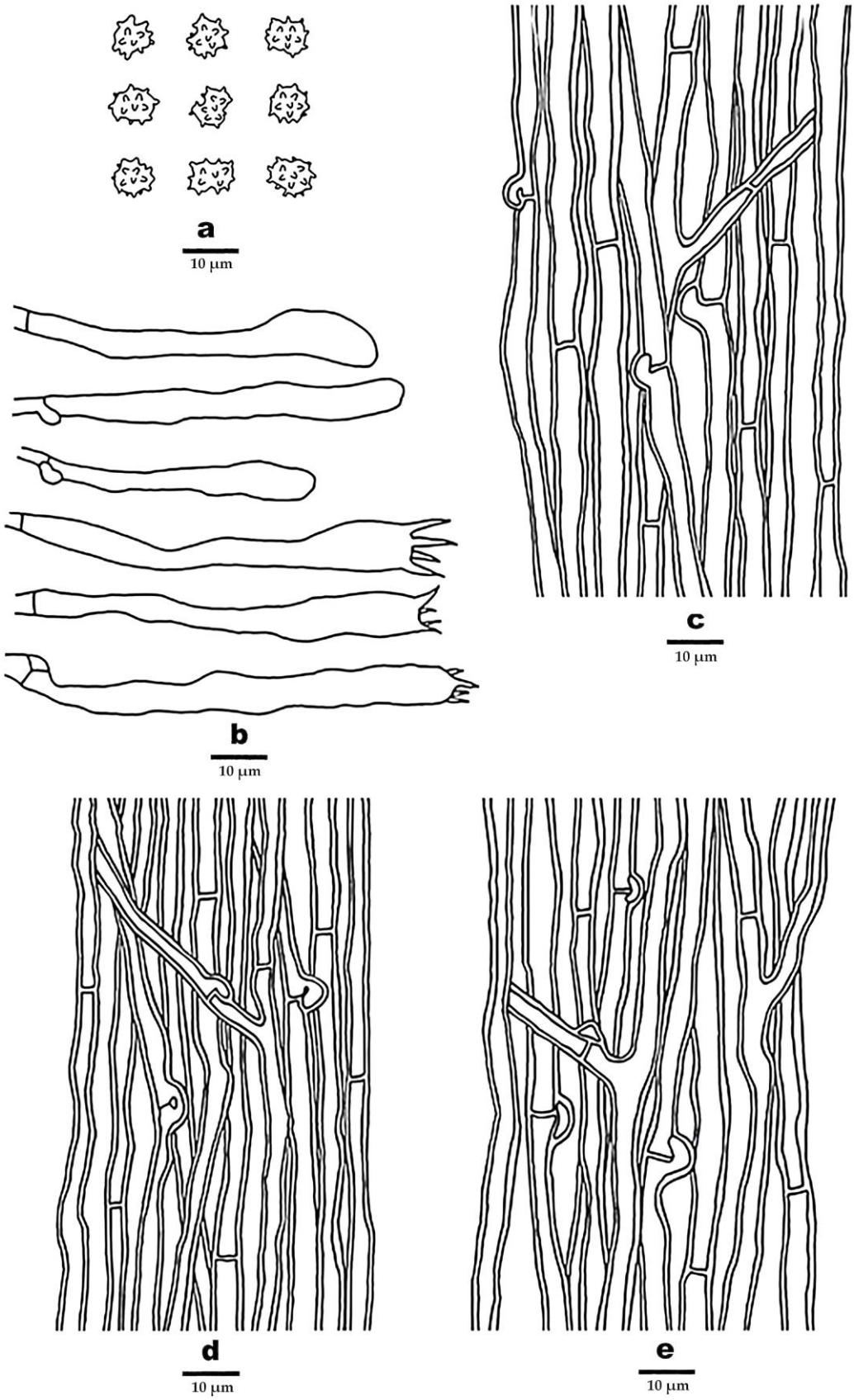

Fig. 31 Microscopic structures of *Thelephora bubalinomarginata* (drawn from the holotype). **a** Basidiospores; **b** Basidia and basidioles; **c** Hyphae from context; **d** Hyphae from the inner layer of stipe; **e** Hyphae from the surface layer of stipe. Bars: 10 μm.

Thelephora macrospora B.K. Cui, Y.F. Sun and C.G. Song, **sp. nov.** (Figs. 9 k, l; 12 k, l; 32).

Index Fungorum number: IF 902697; Facesoffungi number: FoF 16482

Diagnosis – Differs from other *Thelephora* species by its truncate to subacute or sub-cristate tips of pileus, and light brown to dark brown pileal surface.

Type – **USA.** Connecticut, Hebron and Bolton, Gay City State Park, on the ground of mixed forest, approx. 73° 3' 9" W 41° 34' 41" N, alt. 400 m, 3 September 2019, Cui 23037 (holotype in BJFC, isotype in IFP).

Etymology – *macrospora* (Lat.), refers to the big basidiospores.

Fruiting body – Basidiomata annual, centrically stipitate, single, with fenugreek odor when dry. Pileus truncate to subacute or sub-cristate tips, flattened or sub-cylindrical, palmatifid or multifid, up to 3.6 cm in diam, 0.3 cm thick at the center. Pileal surface light brown to dark brown when fresh, and becoming light brown to fuscous upon drying, azonate, finely fibrillose; margin inconspicuous. Hymenophores smooth, brown to greyish brown when fresh, becoming light brown upon drying. Context dark brown to fuscous upon drying, fragile, up to 0.1 cm thick. Stipes cylindrical, fibrillose, surface layer light brown to fuscous, inner layer fuscous, up to 1.4 cm long, 0.4 cm in diam.

Hyphal structure – Hyphal system monomitic; generative hyphae mostly with simple-septa, occasionally with clamp connections; all the hyphae IKI–, CB–; tissues turned olive green in KOH.

Pileus – Generative hyphae clay-buff to light brown, thick-walled, occasionally branched, mostly with simple-septa, occasionally with clamp connections, regularly arranged, 3.5–6 µm in diam.

Hymenophore – Cystidia present, subclavate, with obtuse apex, 26–57 × 6–10 µm. Basidia clavate, 4–spored, 50–79 × 9–11 µm; sterigmata 5–10 µm; basidioles similar to basidia in shape.

Stipe – Generative hyphae light brown to fuscous, thick-walled, occasionally branched, mostly with simple-septa, occasionally with clamp connections, regularly arranged, 3–6 µm in diam.

Spores – Basidiospores, hyaline to light yellow or light brown, globose to elliptical, echinulate, IKI–, CB–, 7–11(–12) × 6–8 µm, L = 8.96 µm, W = 6.81 µm, Q =1.17–1.2 (n = 60/2, without the ornamentation).

Additional specimen (paratype) examined – **USA.** Connecticut, Hebron and Bolton, Gay City State Park, on the ground of mixed forest, approx. 73° 3' 9" W 41° 34' 41" N, alt. 470 m, 3 September 2019, Cui 23038 (BJFC, duplicate in IFP).

Notes – *Thelephora macrospora* was collected from the east-central United States under a temperate humid continental climate. In this study, *T. macrospora* grouped together with *Thelephora palmata* (Scop.) Fr. and *Thelephora regularis* Schwein. (Fig. 5). Morphologically, *T. macrospora* is similar to *T. palmata* and *T. regularis* in having flattened, palmatifid or multifid pileus (Corner 1968). However, *T. macrospora* differs by its light brown to dark brown pileal surface and brown to greyish brown hymenophores (Corner 1968).

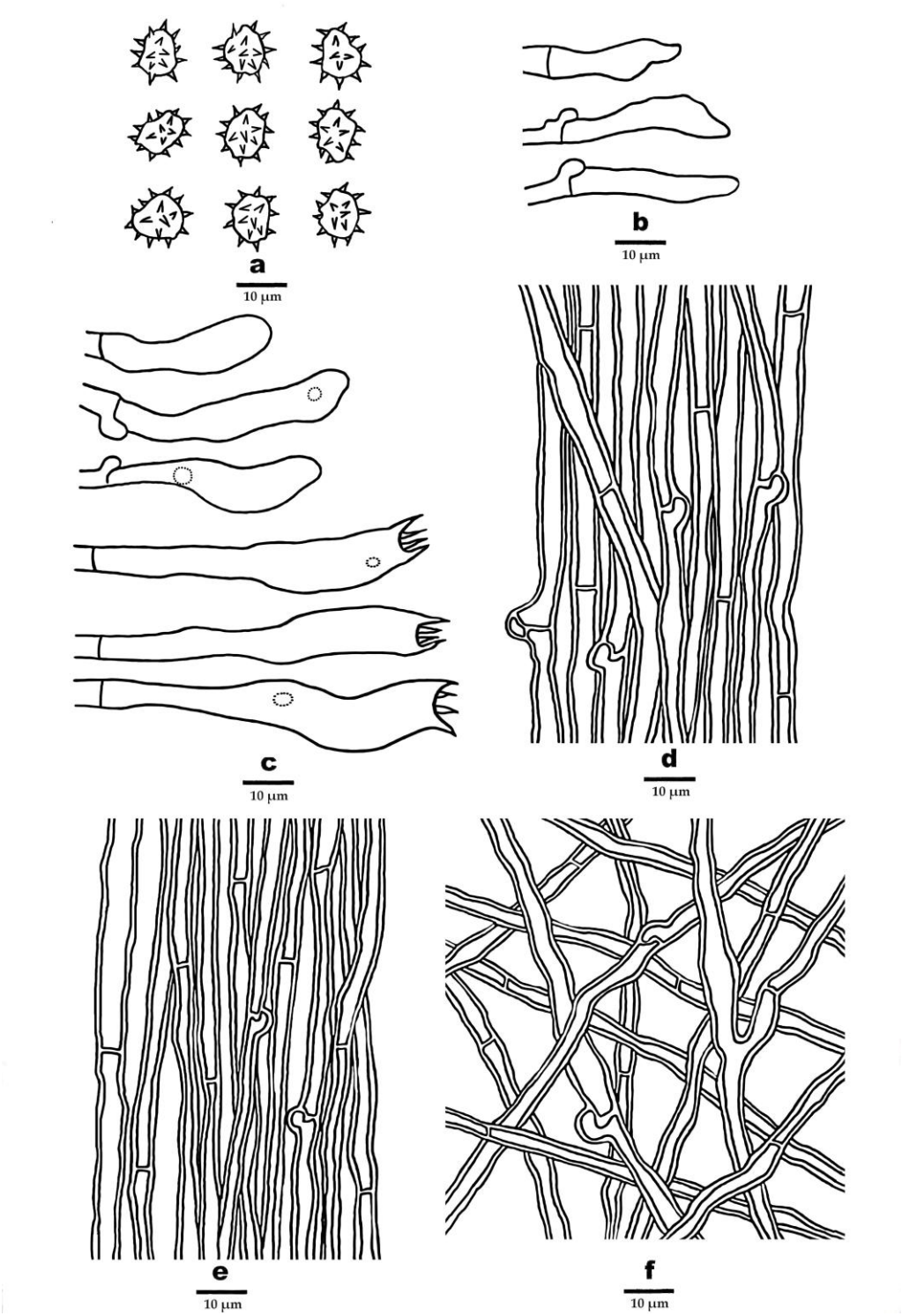

Fig. 32 Microscopic structures of *Thelephora macrospora* (drawn from the holotype). **a** Basidiospores; **b** Cystidia; **c** Basidia and basidioles; **d** Hyphae from context; **e** Hyphae from the inner layer of stipe; **f** Hyphae from the surface layer of stipe. Bars: 10 μm.

Table 3 New combinations of *Thelephora*

Species	IF	FOF	Basionym	Reference
Thelephora botryoides (Schwein.) B.K. Cui, Y.F. Sun and C.G. Song, comb. nov.	902717	16146	*Tomentella botryoides* (Schwein.) Bourdot & Galzin, Bulletin de la Société Mycologique de France 40 (2): 159, 1924.	Bourdot & Galzin (1924).
Thelephora fuscocinerea (Pers.) B.K. Cui, Y.F. Sun and C.G. Song, comb. nov.	902745	16173	*Tomentella fuscocinerea* (Pers.) Donk, Mededelingen van het botanisch Museum en Herbarium van de Rijksuniversiteit Utrecht 9: 30, 1933.	Donk (1933).
Thelephora punicea (Alb. & Schwein.) B.K. Cui, Y.F. Sun and C.G. Song, comb. nov.	902794	16219	*Tomentella punicea* (Alb. & Schwein.) J. Schröt., Kryptogamen-Flora von Schlesien 3-1(4): 420, 1888.	Schröter (1888).
Thelephora sublilacina (Ellis & Holw.) B.K. Cui, Y.F. Sun and C.G. Song, comb. nov.	902805	16229	*Tomentella sublilacina* (Ellis & Holw.) Wakef., Mycologia 52 (6): 931, 1962.	Wakefield (1962).

Note: IF: Index Fungorum number, FOF: Facesoffungi number, comb. nov.: new combination.

Tomentellopsidaceae B.K. Cui, Y.F. Sun and C.G. Song, **fam. nov.**

Index Fungorum number: IF 902849; Facesoffungi number: FoF 16755

Type genus – *Tomentellopsis* Hjortstam

Descrip tion – Basidiomata resupinate, separable, dark-colored. Hymenophores pallid yellow, ochre yellow or chestnut in age, smooth, fibrillar, or arachnoid. Hyphae system monomitic; generative hyphae with simple-septa. Cystidia and cystidioles absent. Basidia clavate to utriform, sometimes sinuous, 4–spored. Basidiospores hyaline to very pale brown, slightly globose or ellipsoid, strongly echinulate to warted.

Notes – In this study, species of *Tomentellopsis* grouped together within Thelephorales and formed a single clade with high support (79% ML, 0.95 BPP, Fig. 1; 86% ML, 1.00 BPP, Fig. 2). However, *Tomentellopsis* could not be placed in any recognized families. Morphologically, *Tomentellopsis* species can be characterized by echinulate, hyaline to pale brown spores, simple-septa, and light-colored basidiomata. *Tomentellopsis* species have different morphology and are distant from the presently known families of the Thelephorales. Besides, the divergence time estimation results showed that the ancestor of *Tomentellopsis* evolved at 174.89 Mya, which was in line with the time range for the differentiation of other families in Thelephorales (Fig. 6). Thus, a new family, Tomentellopsidaceae was proposed to accommodate this genus.

Tomentellopsis Hjortstam, Svensk Botanisk Tidskrift 64 (4): 425, 1970

Type species – *Tomentellopsis echinospora* (Ellis) Hjortstam

Description – Basidiomata annual, resupinate, separable or rarely adherent to the substratum, pelliculose to arachnoid, continuous, light-colored. Hymenophores concolorous with subiculum or paler, smooth, fibrillar and arachnoid. Hyphal system monomitic, generative hyphae with simple-septate. Cystidia and cystidioles absent. Basidia clavate to utriform, sometimes sinuous, 4–spored. Basidiospores hyaline or rarely very pale brown, slightly globose or ellipsoid, warted to strongly echinulate. For a detailed description of *Tomentellopsis*, see Kõljalg (1996) and Kuhar et al. (2022).

Notes – *Tomentellopsis* was established by Hjortstam (Kõljalg 1996). Kõljalg et al. (2002, 2009) suggested that *Tomentellopsis* species are ectomycorrhizal fungi and can form mycorrhiza with conifers and deciduous trees. *Tomentellopsis* species have been reported in Europe (Menolli & Capellari 2014, Kõljalg 2002), the Northern Hemisphere (Greslebin 2002), the Southern Gondwana (Truong et al. 2017), and the South America (Kuhar et al. 2022). According to previous studies, nine species have been described and transferred to *Tomentellopsis* (Kõljalg et al. 2009, Kuhar et al. 2022). It can be characterized by resupinate and light-colored basidiomata, hyaline to pale

brown, and echinulate basidiospores. In this study, six species of *Tomentellopsis* were included to construct the phylogenetic trees. They formed an independent clade within Thelephorales with high support (79% ML, 0.95 BPP, Fig. 1; 86% ML, 1.00 BPP, Fig. 2). Phylogenetically, *Tomentellopsis* was closely related to *Amaurodon* and *Phellodon* (Figs. 1, 2). Morphologically, *Tomentellopsis* can be distinct by its resupinate, separable basidiomata, smooth hymenophores, fibrillar and arachnoid hymenophore margin, and echinulate basidiospores (Kuhar et al. 2022).

DISCUSSION

In this study, taxonomic, phylogenetic analyses and divergence time of Thelephorales were carried out. The phylogenetic analyses revealed that six clades at the family level were obtained in Thelephorales, including eleven genera viz., *Amaurodon*, *Boletopsis*, *Hydnellum*, *Lenzitopsis*, *Neosarcodon*, *Odontia*, *Sarcodon*, *Phellodon*, *Polyozellus*, *Thelephora*, *Tomentellopsis*, representing six families: Bankeraceae, Lenzitopsidaceae, Polyozellaceae, Sarcodonaceae, Thelephoraceae and Tomentellopsidaceae (Figs. 1, 2, 6). This division was also supported by morphology and ultrastructural features. In addition, *Corneroporus* was not included in the phylogenetic analyses since there were no available sequences, and it was treated as an independent genus within Sarcodonaceae since it was separated from *Boletopsis* (Hattori 2001). Thus, the classification system of Thelephorales was revised. Among the six families, Bankeraceae and Thelephoraceae were accepted in the previous studies (Stalpers 1993, He et al. 2019). Lenzitopsidaceae, Polyozellaceae, Sarcodonaceae and Tomentellopsidaceae were proposed as new families in this study. The main morphological characters of genera in Thelephorales were provided (Table 4). In addition, 20 new species were described, and 4 new combinations were proposed (Table 3). SEM micrographs of basidiospores of the new species were presented (Figs. 10–12).

The divergence time of Thelephorales was estimated with ITS, nLSU, nSSU and RPB2 sequences based on the calibrations of two fossils of Agaricales and Hymenochaetales. All main lineages in Basidiomycota were contained in the divergence time estimation (Fig. 6). The ancestor of Agaricales, Amylocorticiales, Atheliales, Boletales, Geastrales, Gloeophyllales, Hymenochaetales, Jaapiales, Polyporales and Russulales, split at about 133.15 Mya, 133.15 Mya, 127.3 Mya, 127.3 Mya and 139.85 Mya, 81.32 Mya, 165.65 Mya, 81.32 Mya, 131.98 Mya, 165.65 Mya (Fig. 6), respectively, which generally consistent with the previous studies (Zhao et al. 2017; He et al. 2019; Ji et al. 2022).

In this study, the divergence time estimation results showed that families in Thelephorales diverged at 145.95–269.07 Mya. Thelephorales was estimated to have a common ancestor that evolved during the Permian; among them, Thelephoraceae was the first to appear (about 269.07 Mya), Sarcodonaceae appeared immediately (about 216.52 Mya). The next were Tomentellopsidaceae and Bankeraceae (about 174.89 Mya), Lenzitopsidaceae and Polyozellaceae (about 145.95 Mya). According to the divergence time estimation of Thelephorales in this study, eleven genera were well supported as allied lineages. The divergence times of these genera could effectively support their existence. The estimated divergence times of the families and genera in Thelephorales were summarized in Table 2. This comprehensive analysis provides a deeper understanding of the evolutionary history and divergence times of Thelephorales. Further research may continue to refine these estimates and provide more detailed insights into the evolutionary relationships among these fungi.

Donk (1961) introduced Bankeraceae as a family, consisting of only two genera: *Bankera* and *Phellodon*. Jülich (1981) revised the classification system of Basidiomycetes and classified *Hydnellum* and *Sarcodon* into the Bankeraceae. Hattori (2001) separated *Boletopsis subcitrina* Corner from *Boletopsis* as a new genus, *Corneroporus*, and combined *Boletopsis* and *Corneroporus* into Bankeraceae. In addition, in the recent study of Wang et al. (2024), *Neosarcodon* was formally

Table 4 The distribution and main morphological differences of accepted genera in Thelephorales

Genus	Family	Basidiomata	Hymenophores	Hyphal system	Cystidia	Basidiospores	Reference
Amaurodon	Phellodonaceae	Resupinate	Poroid, aculeate or smooth	Monomitic	Absent	Hyaline to pale yellow or blue; smooth to warted	Kõljalg (1996).
Boletopsis	Sarcodonaceae	Stipitate, pileate	Poroid	Monomitic	Absent	Pale buff to pale brownish; warted	Ryvarden and Gilbertson (1993).
Corneroporus	Sarcodonaceae	Stipitate, pileate	Poroid	Monomitic	Absent	Hyaline; subangular to warted	Hattori (2001).
Hydnellum	Sarcodonaceae	Stipitate, pileate	Aculeate	Monomitic	Absent	Brown; warted	Karsten (1879), Baird et al. (2013).
Lenzitopsis	Phellodonaceae	Resupinate	Irregular, sinuous to lenzitoid	Monomitic	Absent	Pale brown; warted	Malençon and Bertault (1963), Ryvarden and Gilbertson (1993).
Neosarcodon	Sarcodonaceae	Stipitate, pileate	Aculeate	Monomitic	Absent	Brown; warted	Grupe (2015, 2016), Wang et al. (2024).
Odontia	Thelephoraceae	Resupinate	Aculeate	Monomitic to dimitic	Absent	Light brown; lobed to warted	Persoon (1794).
Polyozellus	Phellodonaceae	sessile or stipitate, resupinate or pileate	Reticulate or almost poroid to corticioid	Monomitic or dimitic	Absent	White to brown; angular, lobed, or warted	Svantesson et al. (2021).
Phellodon	Phellodonaceae	Stipitate, pileate	Aculeate	Monomitic	Absent	Hyaline; echinulate	Karsten (1881), Maas Geesteranus (1971).
Sarcodon	Sarcodonaceae	Stipitate, pileate	Aculeate	Monomitic	Absent	Brown; warted	Karsten (1881), Baird et al. (2013).
Thelephora	Thelephoraceae	Arachnoid to pelliculose, resupinate, or pileate	Smooth, granulose, colliculose, or aculeate	Monomitic or dimitic	Absent or present	Subhyaline to brown; echinulate to warted	Willdenow (1787), Stalpers (1993).
Tomentellopsis	Tomentellopsidaceae	Resupinate	Smooth	Monomitic	Absent	Hyaline to very pale brown; echinulate to warted	Kõljalg (1996).

introduced as a genus of Bankeracea by moving nine species from *Sarcodon* to *Neosarcodon*. However, in this study, *Phellodon* clustered together with *Amaurodon* (Figs. 1, 2, 6). They formed a distinct clade with high support (69% ML, 1.00 BPP, Fig. 1; 55% ML, 1.00 BPP, Fig. 1). Morphologically, species in this clade were characterized by pileate or resupinate basidiomata, smooth, aculeate, or poroid hymenophores, and hyaline to pale yellow or blue basidiospores. Therefore, we propose that the existing family Bankeraceae consist of *Phellodon* and *Amaurodon*. In addition, *Boletopsis*, *Hydnellum*, *Neosarcodon*, and *Sarcodon* clustered together and formed a distinct clade with high support (52% ML, 1.00 BPP, Fig. 1; 78% ML, 1.00 BPP, Fig. 2). Morphologically, species in this clade can be characterized by pileate basidiomata, aculeate or poroid hymenophores, and echinulate or warted basidiospores. Therefore, *Boletopsis*, *Corneroporus*, *Hydnellum*, *Neosarcodon*, and *Sarcodon* were transferred to the new family Sarcodonaceae.

In this study, 193 fungal samples of 83 species of *Hydnellum* with available molecular data were involved in the phylogenetic analyses and divided into 17 subclades. Subclade I contains 19 species (99% ML, 1.00 BPP, Fig. 3), viz., *Hydnellum atrorubrum* Y.H. Mu & H.S. Yuan, *Hydnellum bomiense* Y.H. Mu & H.S. Yuan, *Hydnellum concentricum* B.K. Cui & C.G. Song, *H. concrescens*, *H. dianthifolium*, *H. nitida*, *Hydnellum parvum* Banker, *H. qinghaiensis*, *H. rubidofuscum*, *Hydnellum scrobiculatum* (Fr.) P. Karst., *Hydnellum* sp.3, *Hydnellum* sp.4, *Hydnellum* sp.5, *Hydnellum squamulosum* Y.H. Mu & H.S. Yuan, *Hydnellum subsuccosum* K.A. Harrison, *Hydnellum sulcatum* Y.H. Mu & H.S. Yuan, *H. tarda*, *H. xanthopus*, *Hydnellum yunnanense* Y.H. Mu, X.H. Wang & H.S. Yuan, four of which are new species in this study. Species in this subclade are characterized by zonate pileal surface. Subclade II contains seven species (94% ML, 1.00 BPP, Fig. 3), viz., *H. chocolatum* B.K. Cui & C.G. Song, *Hydnellum crassipileatum* B.K. Cui & C.G. Song, *Hydnellum ferrugineum* (Fr.) P. Karst., *Hydnellum melanocarpum* B.K. Cui & C.G. Song, *Hydnellum pineticola* K.A. Harrison, *Hydnellum spongiosipes* (Peck) Pouzar, *Hydnellum* sp.2, and all of them have spongy pileal surface. Subclade III contains only one species (100% ML, 1.00 BPP, Fig. 3), *Hydnellum geogenium* (Fr.) Banker mainly has concrescent and imbricate basidiomata. Subclade IV contains two species (100% ML, 1.00 BPP, Fig. 3), *Hydnellum radiatum* B.K. Cui & C.G. Song and *Hydnellum cumulatum* K.A. Harrison, which have radial pileal surfaces. Six species were contained in subclade V (100% ML, 1.00 BPP, Fig. 3), viz., *Hydnellum aurantiacum* (Batsch) P. Karst., *Hydnellum auratile* (Britzelm.) Maas Geest., *Hydnellum brunneorubrum* Y.H. Mu & H.S. Yuan, *Hydnellum chrysinum* K.A. Harrison, *H. cinnamomea*, *Hydnellum earlianum* Banker, and all of them have orange pileal surface. *H. complicatum* was contained in subclade VI (100% ML, 1.00 BPP, Fig. 3) and has complicated basidiomata. Subclade VII contains seven species (99% ML, 1.00 BPP, Fig. 3), viz., *H. caeruleum*, *H.* sp., *Hydnellum ferrugipes* Coker, *Hydnellum fibulatum* Y.H. Mu & H.S. Yuan, *H. luteocaesia*, *Hydnellum martioflavum* (Snell, K.A. Harrison & H.A.C. Jacks.) E. Larss., K.H. Larss. & Kõljalg, *H. subcaeruleum*, two of which are new species in this study. Species in this subclade are characterized by white pileal margins. The type species *H. suaveolens* and its related species *Hydnellum atrospinosum* Y.H. Mu & H.S. Yuan were contained in subclade VIII (100% ML, 1.00 BPP, Fig. 3), and both species have dark blue context. Subclade IX contains *Hydnellum scleropodium* K.A. Harrison and *Hydnellum cyanopodium* K.A. Harrison (100% ML, 1.00 BPP, Fig. 3), which have blue spines. A single species, *Hydnellum versipelle* (Fr.) E. Larss., K.H. Larss. & Kõljalg, formed subclade X (100% ML, 1.00 BPP, Fig. 3), which has various shapes of pileus. *Hydnellum subalpinum* Xiao L. He & D. Wang formed subclade XI (100% ML, 1.00 BPP, Fig. 3), which was discovered in the subalpine region. Subclade XII contains six species (100% ML, 1.00 BPP, Fig. 3), viz., *Hydnellum cristatum* (Bres. ex G.F. Atk.) Stalpers, *Hydnellum granulosum* Y.H. Mu & H.S. Yuan, *Hydnellum inflatum* Y.H. Mu, X.H. Wang & H.S. Yuan, *Hydnellum lundellii* (Maas Geest. & Nannf.) E. Larss., K.H. Larss. & Kõljalg, *Hydnellum mirabile* (Fr.) P. Karst., and *Hydnellum piperatum* Coker ex Maas Geest. Species in this subclade are characterized by depressed and lobed pileus and brownish orange to brown pileal surface. Subclade XIII contains two species (100% ML, 1.00 BPP, Fig. 3), *Hydnellum gracilipes* (P. Karst.) P. Karst. and a notable

species, *Hydnellum* sp.1. Species in this subclade are characterized by rhizomorph-like stipe. Subclade XIV contains seven species (100% ML, 1.00 BPP, Fig. 3), viz., *Hydnellum fuligineoviolaceum* (Kalchbr.) E. Larss., K.H. Larss. & Kõljalg, *Hydnellum fuscoindicum* (K.A. Harrison) E. Larss., K.H. Larss. & Kõljalg, *Hydnellum glaucopus* (Maas Geest. & Nannf.) E. Larss., K.H. Larss. & Kõljalg, *Hydnellum ioeides* (Pass.) E. Larss., K.H. Larss. & Kõljalg, *Hydnellum roseoviolaceum* Nitare, *Hydnellum* sp., *H. succulentus*. Species in this subclade are characterized by violaceous basidiocarps. Subclade XV contains a single species (100% ML, 1.00 BPP, Fig. 3), *Hydnellum peckii*, with reddish droplets on young pileus (Baird et al. 2013). Subclade XVI contains one species (100% ML, 1.00 BPP, Fig. 3), *H. diabolus*, which has spongy tomentose pileus with strigose hairy, collapsing in age rarely becomes matted. Subclade XVII (100% ML, 1.00 BPP, Fig. 3), the largest clade of *Hydnellum*, contains 16 species, viz., *Hydnellum amygdaliolens* (Rubio Casas, Rubio Roldán & Català) E. Larss., K.H. Larss. & Kõljalg, *Hydnellum coactum* (Y.H. Mu & H.S. Yuan) Della Maggiora, *H. decurrata*, *Hydnellum edulium* Xiao L. He & D. Wang, *Hydnellum fagiscabrosum* A.M. Ainsw. & Nitare, *Hydnellum grosselepidotum* (Y.H. Mu & H.S. Yuan) Della Maggiora, *Hydnellum fennicum* (P. Karst.) E. Larss., K.H. Larss. & Kõljalg, *Hydnellum illudens* (Maas Geest.) Nitare, *Hydnellum lepidum* (Maas Geest.) E. Larss., K.H. Larss. & Kõljalg, *H. lidongensis*, *Hydnellum nemorosum* A.M. Ainsw. & E. Larss., *Hydnellum scabrosellum* Nitare, *Hydnellum scabrosum* (Fr.) E. Larss., K.H. Larss. & Kõljalg, *H. subedulium*, *Hydnellum subscabrosellum* Xiao L. He & D. Wang, *Hydnellum underwoodii* (Banker) E. Larss., K.H. Larss. & Kõljalg. Species in this subclade are characterized by the fresh and scaly pileal surface. Moreover, *Hydnellum regium* K.A. Harrison formed a distinct branch within *Hydnellum* (Fig. 3). *Hydnellum regium* can be characterized by large size of pileus, violaceous black basidiomata, long spines measuring as 1–6 µm, and the solid to woody stipe (Harrison 1964). Since there is only one available sequence, we cannot specify its position on the phylogenetic tree at this time, more specimens will be needed for further study in the future.

Mu et al. (2021) conducted a phylogenetic analysis for *Hydnellum* based on ITS+nLSU+nSSU+RPB2 sequences, and *Hydnellum* were divided into ten clades representating ten subgenera: subg. *Caesispinosum*, subg. *Croceum*, subg. *Hydnellum*, subg. *Inflatum*, subg. *Rhizomorphum*, subg. *Scabrosum*, subg. *Spongiosum*, subg. *Subindufibulatum*, subg. *Violaceum* and subg. *Zonatum*. Subg. *Caesispinosum* consisted of two species with blue spines in corresponding to subclade IX in this study. Subg. *Croceum* included five species with orange basidiocarps, which is corresponding to subclade V in this study. Subg. *Hydnellum* consisted of two species in which the type species of the genus is located, which is corresponding to subclade VIII in this study. Subg. *Inflatum* consisted of five species with the presence of inflated generative hyphae in the context of the pileus, which is corresponding to subclade XII in this study. Subg. *Rhizomorphum* consisted of *Hydnellum gracilipes* and a notable species *Hydnellum* sp.1, with rhizomorph-like stipe being the typical common characteristics of them, which form subclade XIII in this study. Subg. *Scabrosum* consisted of twelve species with scabrosity on pileal surface, which is corresponding to subclade XVII in this study. Subg. *Spongiosum* consisted of four species with spongy pileal surface in corresponding to subclade II in this study. Subg. *Subindufibulatum* consisted of three species with occasional presence of clamped hyphae in the context of the pileus, which is corresponding to subclade VII in this study. Subg. *Violaceum* consisted of five species with violaceous basidiocarps in corresponding to subclade XIV in this study. Subg. *Zonatum* consisted of 14 species with the concentrically zonate pileal surface, which is corresponding to subclade I in this study. This indicated that the division of *Hydnellum* species by Mu et al. (2021) is different from the division of *Hydnellum* species by our multiple gene-based analysis (Fig. 2). The ten subgenera they have divided can roughly in corresponding to our ten subclades (subclade I, subclade II, subclade V, subclade VII, subclade VIII, subclade IX, subclade XII, subclade XIII, subclade XIV, subclade XVII), while our subclades contain five species descripted by Song et al. (2023) and the ten new species in this study. In addition, seven undivided separate branches of Mu et al. (2021) are also listed as single clades (subclade III, Subclade IV, Subclade VI, Subclade X, Subclade XI, Subclade XV, Subclade XVI) in this study.

Thelephoraceae was established by Chevaller in 1826, and contains species with effused, effuse-reflexed, resupinate, apodal pileate basidiomata and colorless to strongly pigmented, warted to typically echinulate basidiospores (Corner 1968, Stalpers 1993, Kõljalg 1996, Larsen 1968, 1974, Dämmrich 2006, Vizzini et al. 2016). In our phylogenetic analyses (Figs. 1, 2, 6), species in the original sense of Thelephoraceae (*Lenzitopsis*, *Polyozellus*, *Pseudotomentella*, *Thelephora*-*Tomentella*, and *Tomentellopsis*) formed separate clades. Meanwhile, in our phylogenetic analyses (Figs. 1, 2, 6), *Thelephora*, the original type genus of Thelephoraceae, clustered together with *Odontia*, and the two genera form an independent clade. Morphologically, this clade can be characterized by diverse forms of basidiomata, smooth to partially wrinkled, granulose, colliculose, aculeate hymenophores, and muricate, warted or echinulate basidiospores. Consequently, this study confirm that the family Thelephoraceae encompasses two genera: *Thelephora* and *Odontia*. In this study, three genera include *Lenzitopsis*, *Polyozellus*, and *Tomentellopsis* form separate clades within Thelephorales (Figs. 1, 2, 6). In addition, the results from the divergence time estimation indicated that the ancestors of *Lenzitopsis*, *Polyozellus*, and *Tomentellopsis* diverged approximately 145.95 Mya, 145.95 Mya, and 174.89 Mya respectively. These estimations coincide with the differentiation timeline of other families within Thelephorales (Fig. 6), and provide support for the classification of these as three distinct families. Phylogenetically, *Lenzitopsis* is closely related to *Polyozellus* (Figs. 1, 2, 6). Morphologically, *Lenzitopsis* is similar to *Polyozellus* in having resupinate basidiomata, and brown basidiospores sometimes with warted. However, *Lenzitopsis* can be distinct by dark basidiomata, and sinuous to lenzitoid hymenophores. Phylogenetically, *Polyozellus* formed a separate clade with moderate support (Figs. 1, 2, 6) within Thelephorales. Morphologically, *Polyozellus* can be distinct by its pileate or resupinate, fleshy to woody basidiomata, and poroid to corticioid hymenophores. Therefore, three new families Lenzitopsidaceae, Polyozellaceae, and Tomentellopsidaceae were established in this study.

In summary, we performed a comprehensive study on the taxonomy and phylogeny of Thelephorales. In this study, twelve genera belonging to six families are accepted in Thelephorales, including four new families. This study not only fills in the blank of multiple gene fragments of Thelephorales but also enriches the species diversity of the order, promoting the taxonomy and phylogeny of Thelephorales. Therefore, this study provides a basis for further research on Thelephorales. However, there are still some species of Thelephorales lacking molecular data, which limits the phylogenetic analysis of Thelephorales. More specimens are needed for an in-depth study of Thelephorales, and more clades at the family or genus level of Thelephorales might be discovered in the future.

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