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ORIGINAL ARTICLE





A new genus and two new species of *Auriculariales* (*Basidiomycota*) from southwest China, evidenced by morphological characteristics and phylogenetic analyses

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Abstract

Wood-inhabiting fungi, a remarkably diverse group morphologically, phylogenetically, and ecologically, play a fundamental role in ecosystem processes, particularly in wood degradation and the recycling of organic matter. Recognized as pivotal contributors to the intricate balance of forest ecosystems, these fungi are renowned as "key players" due to their enzymatic prowess, effectively breaking down woody components like lignin, cellulose, and hemicellulose. In the present study, a new wood-inhabiting fungal genus *Nodulochaete*, and two new species *N. fissurata* and *N. punctata*, collected from southwest China, are proposed based on a combination of morphological features and molecular evidence. The new genus *Nodulochaete* is characterized by the resupinate basidiomata with smooth to tuberculate hymenophore, a dimitic hyphal system with clamped generative hyphae, presence of abundantly nodulose hyphidia, ellipsoid to ovoid, longitudinally septate basidia, and cylindrical to allantoid basidiospores. Sequences of the internal transcribed spacers (ITS) and the large subunit (nrLSU) of the nuclear ribosomal DNA (rDNA) markers of the studied samples were generated. Phylogenetic analyses were performed with maximum likelihood, maximum parsimony, and Bayesian inference methods. Phylogenetic analyses of ITS + nrLSU nuclear RNA gene regions show that *Nodulochaete* forms a monophyletic lineage within the order *Auriculariales*. Furthermore, two new species *N. fissurata* and *N. punctata* were assigned to the genus *Nodulochaete*.

Keywords Biodiversity · Molecular systematics · New taxa · Taxonomy · Wood-inhabiting fungi

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Introduction

Fungi represent one of the most diverse groups of organisms on the earth, with an indispensable role in the processes and functioning of ecosystems (Hyde 2022). The order *Auriculariales* is a group mainly composed of wood-inhabiting fungi in *Agaricomycetes* (*Basidiomycota*) (Hibbett et al. 2007). The type genus of this order is *Auricularia* Bull., in which several other gelatinous genera *Exidia* Fr., *Guepinia* Fr., and *Pseudohydnum* P. Karst., comprise important edible and medicinal fungi (Wu et al. 2019; Liu et al. 2022b). Therefore, species diversity in gelatinous genera have increased significantly in recent years (Chen et al. 2020; Shen and Fan 2020; Ye et al. 2020; Wang and Thorn 2021; Wu et al. 2021; Tohtirjap et al. 2023).

Species of the order *Auriculariales* belong to woodinhabiting fungi, and they have industrial, medicinal, edible, and economic value while some others contain toxic metabolites (Cheng et al. 2023; Niego et al. 2023; Wang et al. 2023; Zhou et al. 2023). They produce ligninolytic and cellulolytic enzymes that break down lignins, celluloses, and hemicelluloses, underscores their significance in the recycling of organic matter and nutrient cycling, typically categorized as the white-rot and brown-rot fungi (Cui et al. 2019; Liu et al. 2022a). Besides the gelatinous genera, most species in the order *Auriculariales* bear stereoid, corticioid, or hydnoid, basidiomata (Wells and Bandoni 2001; Miettinen et al. 2012; Hibbett et al. 2014; Malysheva and Spirin 2017; Alvarenga et al. 2019; Spirin et al. 2019a, b; Guan et al. 2020; Li et al. 2022a; Li and Zhao 2022; Liu et al. 2022b; Tohtirjap et al. 2023; Dong et al. 2024b). Species with steroid basidiocarps are widely distributed in many orders of the *Agaricomycetes*, and also in the order *Auriculariales* (Malysheva and Spirin 2017).

Classification of the kingdom of fungi has been updated continuously, based on the frequent inclusion of data from DNA sequences in many phylogenetic studies (Cui et al. 2019; Wijayawardene et al. 2020, 2022; Hyde et al. 2024). Based on the early embrace of molecular systematics by mycologists, both the discovery and classification of fungi, among the more basal branches of the tree, are now coming to light from genomic analyses and environmental DNA surveys that have been conducted (James et al. 2020). The corticoid species of the order Auriculariales were traditionally placed in Eichleriella Bres., Exidiopsis (Bref.) Möller, and Heterochaete Pat. according to morphological characteristics (Burt 1915; Wells 1961; Raitviir and Wells 1966; Wells and Raitviir 1980). Based on both morphological and phylogenetic evidence, the genus concepts of Eichleriella, Hirneolina (Pat.) Bres., and Tremellochaete Raitv. were revised, in which Malysheva and Spirin (2017) proposed that Heteroradulum Lloyd ex. Spirin and Malysheva was validated. The genus Eichleriella was accepted to be a monophyletic genus, while both genera Exidiopsis and Heterochaete seemed to be synonymous with a priority of the latter genus (Malysheva and Spirin 2017; Alvarenga et al. 2019; Alvarenga and Gibertoni 2021). However, certain species of *Exidiopsis*, even sequenced ones such as E. calcea (Pers.) K. Wells and E. grisea (Bres.) Bourdot and Maire, still have no appropriate placement at the generic level (Malysheva and Spirin 2017; Li et al. 2022b; Liu et al. 2022b; Dong et al. 2024b). With the continuously study of the order Auriculariales, several corticioid genera, e.g., Adustochaete Alvarenga and K.H. Larss., Alloexidiopsis L.W. Zhou and S.L. Liu, Amphistereum Spirin and Malysheva, Crystallodon Alvarenga, Heteroradulum, Metulochaete Alvarenga, Proterochaete Spirin adn Malysheva, and Sclerotrema Spirin and Malysheva have been established and described based on morphological and phylogenetic studies (Malysheva and Spirin 2017; Alvarenga et al. 2019; Alvarenga and Gibertoni 2021; Liu et al. 2022b).

During investigations on wood-inhabiting fungi in the Yunnan-Guizhou Plateau, China, many corticioid specimens were collected. To clarify the placement and relationships of these specimens, molecular phylogenetic along with taxonomic studies were carried out on the order *Auriculariales* based on the combined ITS + nrLSU data analyses.

Materials and methods

Sample collection and herbarium specimen preparation

The basidiomata were collected on fallen angiosperm branches from Lincang, Qujing, and Zhaotong of Yunnan Province, China. The samples were photographed in situ, and fresh macroscopic details were recorded. Photographs were recorded by a Nikon D7100 camera. All the photos were focus stacked using Helicon Focus software. Macroscopic observations were noted. Collected basidiomata were dried on an electric food dryer at 45 °C. Dried specimens were sealed in an envelope and zip-lock plastic bags and labeled with voucher number (Hu et al. 2022). The voucher specimens were deposited in the herbarium of the Southwest Forestry University, Kunming, Yunnan Province, China (SWFC).

Morphological study

The macro-morphological descriptions were based on field notes and photos captured in the field and lab. The color terminology follows Petersen (1996). The macro-morphological data were obtained from the dried specimens after observation under a light microscope with a magnification of 1000×oil (Zhao et al. 2023a, b; Dong et al. 2024a). Sections mounted in 5% KOH and 2% phloxine B ($C_{20}H_2Br_4C_{14}Na_2O_5$), and we also used other reagents, including Cotton Blue and Melzer's reagent to observe micromorphology following Wu et al. (2022b). To show the variation in spore sizes, 5% of measurements were excluded from each end of the range and shown in parentheses. At least 30 basidiospores from each specimen were measured. Stalks were excluded from basidium measurements, and the hilar appendage was excluded from basidiospores measurements. The following abbreviations are used: KOH = 5%potassium hydroxide water solution, CB-=acyanophilous, IKI-=both inamyloid and indextrinoid, L=mean spore length (arithmetic average for all spores), W = mean spore width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied, Q_m represented the average Q of basidiospores measured \pm standard deviation, and n = a/b (number of spores (a) measured from given number (b) of specimens).

Molecular phylogenetic studies

The CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to obtain genomic DNA from the dried specimens according to the manufacturer's instructions. The nuclear ribosomal of the internal transcribed spacer (ITS) region was amplified with ITS5 and ITS4 primers (White et al. 1990). The nuclear large subunit (nrLSU) region was amplified with the LROR and LR7 primer pair (Vilgalys and Hester 1990; Rehner and Samuels 1994). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and a final extension of 72 °C for 10 min. The PCR procedure for nrLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 48 °C for 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. The PCR products were purified and sequenced at Kunming Tsingke Biological Technology Limited Company (Yunnan Province, P.R. China). The newly generated sequences were deposited in NCBI GenBank (Table 1).

The sequences were aligned in MAFFT version 7 (Katoh et al. 2019) using the G-INS-i strategy. The alignment was adjusted manually using AliView version 1.27 (Larsson 2014). The dataset was aligned first, and then the sequences of ITS + nrLSU were combined with Mesquite version 3.51. The alignment datasets were deposited in TreeBASE (Submission ID 31903). The combined ITS + nrLSU sequence datasets were used to infer the position of the new genus and related species in the order *Auriculariales*. Sequences of *Sistotrema brinkmannii* (Bres.) J. Erikss. were retrieved from GenBank and used as an outgroup in the ITS + nrLSU (Fig. 1) analysis (Tohtirjap et al. 2023).

Maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) analyses were applied to the combined three datasets following a previous study (Zhao and Wu 2017; Dong et al. 2024a), and the tree construction procedure was performed in PAUP* v.4.0b10 (Swofford 2002). All of the characters were equally weighted, and gaps were treated as missing data. Using the heuristic search option with TBR branch swapping and 1000 random sequence additions, trees were inferred. Max trees were set to 5000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics, tree length (TL), the consistency index (CI), the retention index (RI), the rescaled consistency index (RC), and the homoplasy index (HI) were calculated for each maximum parsimonious tree generated. The multiple sequence alignment was also analyzed using

ML in RAxML-HPC2 on XSEDE v.8.2.8 with default parameters (Miller et al. 2012). Branch support (BS) for ML analysis was determined by 1000 bootstrap replicates.

jModelTest v2 (Darriba et al. 2012) was used to determine the best-fit evolution model for each dataset for the purposes of BI, BI was performed using MrBayes 3.2.7a with a GTR + I + G model of DNA substitution and a gamma distribution rate variation across sites (Ronquist et al. 2012). The first one-fourth of all the generations were discarded as burn-ins. The majority-rule consensus tree of all the remaining trees was calculated. Branches were considered significantly supported if they received a ML bootstrap value (BS) of ≥ 70%, a MP bootstrap value (BT) of ≥ 70%, or Bayesian posterior probabilities (BPP) of ≥ 0.95.

Results

Molecular phylogeny

The aligned dataset comprised 65 specimens representing 47 species. Four Markov chains were run for two runs from random starting trees, each for three million generations for the combined ITS + nrLSU (Fig. 1) data set with trees and parameters sampled every 1000 generations. The dataset had an aligned length of 2239 characters, of which 1308 characters are constant, 314 are variable and parsimony uninformative, and 617 are parsimony informative. MP analysis yielded 140 equally parsimonious trees (TL = 3701, CI = 0.4191, HI = 0.5809, RI = 0.5179, and RC = 0.2171). The best model for the ITS + nrLSU dataset, estimated and applied in the Bayesian analysis, was SYM + I + G. Both Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.022695 (BI), and the effective sample size (ESS) for Bayesian analysis across the two runs is the double of the average ESS (avg. ESS) = 528.5.

The phylogram based on the combined ITS + nrLSU data set (Fig. 1) analysis showed that the new fungal collections formed an independent monophyletic group with two different lineages (91% BS, 91% BP, 1.00 BPP) within *Auriculariales* and grouped with the two genera *Adustochaete* and *Proterochaete*.

Taxonomy

Nodulochaete J.H. Dong & C.L. Zhao, gen. nov.

MycoBank No.: MB 855375.

Etymology: Nodulochaete (Lat.): referring to the abundant nodulose hyphidia in hymenium.

Description: Basidiomata annual, resupinate, adnate, membranaceous, without odor or taste when fresh, becoming coriaceous upon drying. Hymenial surface smooth to

Table 1 List of species, specimens, and GenBank accession number of sequences used in this study

Species name	Specimen voucher/collection no.	GenBank acce	ession no.	References
		ITS	nrLSU	
Adustochaete rava	RC 841	MK391516	_	Alvarenga et al. (2019)
Adustochaete rava	KHL 15526	MK391517	MK391526	Alvarenga et al. (2019)
Alloexidiopsis australiensis	LWZ 20180513-22	OM801933	OM801918	Liu et al. (2022b)
Alloexidiopsis calcea	MW 331	AF291280	AF291326	Weiß and Oberwinkler (2001)
Amphistereum leveilleanum	FP-106715	KX262119	KX262168	Malysheva and Spirin (2017)
Amphistereum schrenkii	HHB 8476	KX262130	KX262178	Malysheva and Spirin (2017)
Aporpium caryae	Miettinen 14774	JX044145	_	Miettinen et al. (2012)
Aporpium caryae	WD 2207	AB871751	AB871730	Sotome et al. (2014)
Auricularia auricula-judae	JT 04	KT152099	KT152115	Tohtirjap et al. (2023)
Auricularia cornea	Dai 13621	MZ618936	MZ669905	Tohtirjap et al. (2023)
Auricularia mesenterica	Oberwinkler 25132	AF291271	AF291292	Weiß and Oberwinkler (2001)
Auricularia polytricha	TUFC 12920	AB871752	AB871733	Sotome et al. (2014)
Auricularia tibetica	Dai 13336	MZ618943	MZ669915	Tohtirjap et al. (2023)
Bourdotia galzinii	Otto MiettinenX3067	MG757511	MG757511	Malysheva et al. (2018)
Crystallodon subgelatinosum	RC 1609-URM93444	MN475884	MN475888	Alvarenga and Gibertoni (2021)
Crystallodon subgelatinosum	TBG BF-18001-URM93445	MN475885	MN475889	Alvarenga and Gibertoni (2021)
Eichleriella bactriana	TAAM 55071	KX262121	KX262170	Malysheva and Spirin (2017)
Eichleriella leucophaea	Barsukova LE 303261	KX262111	KX262161	Malysheva and Spirin (2017)
Elmerina cladophora	Miettinen 14314	MG757509	MG757509	Malysheva et al. (2018)
Elmerina sclerodontia	Miettinen 16431	MG757512	MG757512	Malysheva et al. (2018)
Exidia glandulosa	Dai 21232	MT663362	MT664781	Wu et al. (2020)
Exidia glandulosa	Dai 21233	MT663363	MT664782	Wu et al. (2020)
Exidia pithya	MW 313	AF291275	AF291321	Weiß and Oberwinkler (2001)
Exidiopsis effusa	OM 19136	KX262145	KX262193	Tohtirjap et al. (2023)
Grammatus labyrinthinus	Yuan 1600	KM379139	KM379140	Alvarenga et al. (2019)
Grammatus semis	OM10618	KX262146	KX262194	Malysheva and Spirin (2017)
Heteroradulum adnatum	LR 23453	KX262116	KX262165	Tohtirjap et al. (2023)
Heteroradulum kmetii	VS 6466	KX262104	KX262152	Malysheva and Spirin (2017)
Heterochaete hirneoloides	USJ 55480	AF291283	AF291334	Weiß and Oberwinkler (2001)
Hyalodon piceicola	Spirin 2689	MG735414	MG735422	Spirin et al. (2019a)
Hyalodon piceicola	Spirin 11063	MG735415	MG735423	Spirin et al. (2019a)
Metulochaete sanctae-catharinae	AM 0678	MK484065	MK480575	Spirin et al. (2019a)
Mycostilla vermiformis	Spirin 11330	MG735417	MG735425	Spirin et al. (2019a)
Mycostilla vermiformis	OF 188059	MG735418	_	Spirin et al. (2019a)
Myxarium cinnamomescens	O F160494	KY801882	KY801909	Spirin et al. (2018)
Myxarium hyalinum	TL2012 443455	KY801880	KY801907	Spirin et al. (2018)
Nodulochaete fissurata	CLZhao 27512	PQ166571	PQ166563	Present study
Nodulochaete fissurata	CLZhao 27528	PQ166572	PQ166564	Present study
Nodulochaete fissurata	CLZhao 27533 *	PQ166573	PQ166565	Present study
Nodulochaete fissurata	CLZhao 31349	PQ166574	PQ166566	Present study
Nodulochaete fissurata	CLZhao 31360	PQ166575	_	Present study
Nodulochaete fissurata	CLZhao 31402	PQ166576	PQ166567	Present study
Nodulochaete fissurata	CLZhao 31477	PQ166577	_	Present study
Nodulochaete fissurata	CLZhao 31612	PQ166578	_	Present study
Nodulochaete fissurata	CLZhao 31616	PQ166579	_	Present study
Nodulochaete fissurata	CLZhao 31625	PQ166580	PQ166568	Present study
Nodulochaete fissurata	CLZhao 31783	PQ166581	_	Present study
Nodulochaete fissurata	CLZhao 31923	PQ166582	_	Present study

Table 1 (continued)

Species name	Specimen voucher/collection no.	GenBank acces	sion no.	References
		ITS	nrLSU	
Nodulochaete fissurata	CLZhao 31970	PQ166583	_	Present study
Nodulochaete fissurata	CLZhao 32030	PQ166584	—	Present study
Nodulochaete fissurata	CLZhao 32076	PQ166585	_	Present study
Nodulochaete fissurata	CLZhao 32329	PQ166586	_	Present study
Nodulochaete fissurata	CLZhao 32337	PQ166587	_	Present study
Nodulochaete fissurata	CLZhao 32747	PQ166588	_	Present study
Nodulochaete fissurata	CLZhao 33065	PQ166589	_	Present study
Nodulochaete fissurata	CLZhao 33078	PQ166590	_	Present study
Nodulochaete fissurata	CLZhao 33223	PQ166591	_	Present study
Nodulochaete fissurata	CLZhao 33847	PQ166592	_	Present study
Nodulochaete fissurata	CLZhao 35479	PQ166593	_	Present study
Nodulochaete fissurata	CLZhao 35524	PQ166594	_	Present study
Nodulochaete punctata	CLZhao 22803 *	PQ166569	PQ166561	Present study
Nodulochaete punctata	CLZhao 25480	PQ166570	PQ166562	Present study
Proterochaete adusta	CNOM 10519	MK391519	_	Alvarenga et al. (2019)
Proterochaete adusta	VS 9021	MK391520	MK391528	Alvarenga et al. (2019)
Protodaedalea foliacea	Miettinen 13 054	MG757507	MG757507	Malysheva et al. (2018)
Protodaedalea hispida	Spirin 5139	MG757510	MG757510	Malysheva et al. (2018)
Protodontia africana	AS 171126 1104	MK098978	MK098973	Spirin et al. (2019b)
Protohydnum cartilagineum	SP 467240	MG735419	MG735426	Malysheva et al. (2018)
Protomerulius dubius	VS 3019	MK484041	MK480553	Spirin et al. (2019a)
Protomerulius minor	KHL 15937	MK484060	MK480569	Spirin et al. (2019a)
Protomerulius substuppeus	O 19171	JX134482	JQ764649	Spirin et al. (2019a)
Pseudohydnum gelatinosum	F14063	AF384861	AF384861	Weiß and Oberwinkler (2001)
Sclerotrema griseobrunneum	Niemela 2722	KX262144	KX262192	Malysheva and Spirin (2017)
Sclerotrema griseobrunneum	Spirin 7674	KX262140	KX262188	Malysheva and Spirin (2017)
Sistotrema brinkmannii	isolate 236	JX535169	JX535170	Alvarenga and Gibertoni 2021
Stypellopsis farlowii	Larsson 12337	MG857095	MG857099	Spirin et al. (2018)
Stypellopsis hyperborea	J Norden 9751	MG857097	MG857101	Spirin et al. (2018)
Tremellochaete atlantica	URM90199	MG594381	MG594383	Tohtirjap et al. (2023)
Tremellochaete japonica	TAA 42689	AF291274	AF291320	Weiß and Oberwinkler (2001)

New species shown in bold

*Indicates type material

tuberculate, white to cream when fresh, turning to cream to slightly pink upon drying. Hyphal system monomitic, generative hyphae with clamp connections, colorless, thinwalled. Cystidia subclavate to subcylindrical, fusiform, thinwalled. Hyphidia arising from generative hyphae, abundant, nodulose. Basidia ellipsoid to ovoid, longitudinally septate, two to four-celled. Basidiospores cylindrical to allantoid, slightly curved, colorless, thin-walled, smooth, IKI–, CB–.

Typus generis: Nodulochaete fissurata J.H Dong & C.L. Zhao.

Nodulochaete fissurata J.H. Dong & C.L. Zhao, sp. nov. Figs. 2, 3, and 4 MycoBank No.: MB 855376. *Holotype*: CHINA, Yunnan Province, Qujing, Zhanyi District, Dapo Town, Lijiafen Village, GPS coordinates 25° 68' N, 103° 66' E, altitude 1800 m asl., on fallen branch of angiosperm, leg. C.L. Zhao, 7 March 2023, CLZhao 27533 (SWFC).

Etymology: fissurata (Lat.): referring to the cracked hymenial surface of the type specimen.

Basidiomata: Annual, resupinate, closely adnate, soft coriaceous, very hard to separate from substrate, without odor or taste when fresh, becoming coriaceous upon drying, up to 5 cm long, 2 cm wide, 100–150-µm thick. Hymenial surface tuberculate, cracked, white to cream when fresh, turning to cream to slightly pink upon drying. Sterile margin cream, narrow, up to 1 mm wide.

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<Fig. 1 Maximum parsimony strict consensus tree illustrating the phylogeny of *Nodulochaete* and related genera in the order *Auriculariales* based on ITS + nrLSU sequences. Branches are labelled with maximum likelihood bootstrap value \geq 70%, parsimony bootstrap value \geq 50%, and Bayesian posterior probabilities \geq 0.95

Hyphal structure: Monomitic, generative hyphae with clamp connections, colorless, thin-walled, branched, interwoven, $2-3 \mu m$ in diameter; IKI–, CB–, tissues unchanged in KOH.

Hymenium: Cystidia numerous, thin-walled, subcylindrical to fusiform, occasionally sinuous in the basal, $14.5-22.5 \times 4-6.5 \mu m$, with a clamp connection at base; cystidioles absent. Hyphidia arising from generative hyphae, nodulose, rarely branched, colorless, thin-walled, 2–4.5 μ m in diameter. Basidia ellipsoid to ovoid, longitudinally septate, two to four-celled, 13.5–24 × 10.5–13 μ m; basidioles dominant, similar to basidia in shape, but slightly smaller.

Basidiospores: Subcylindrical to allantoid, slightly curved, colorless, smooth, thin-walled, with one oil drop, IKI-, CB-, (9.7-)10.5-13.8(-14) × (5-)5.5-7.5(-8) μ m, *L*=12.34 μ m, *W*=6.23 μ m, *Q*=1.85-2.15, *Q*_m=1.99±0.07 (*n*=300/10).

Additional specimens (paratypes) examined: China, Yunnan Province, Qujing, Zhanyi District, Dapo Town, Lijiafen Viliage, GPS coordinates 25° 68' N, 103° 66' E, altitude 1800 m asl., on fallen branch of angiosperm, leg. C.L. Zhao, 7 March 2023, CLZhao 27512, CLZhao 27528. Zhaotong,



Fig. 2 Basidiomata of *Nodulochaete fissurata*. **a**, **b** CLZhao 27533 (holotype). **c**, **d** CLZhao 27512. **e**, **f** CLZhao 31923. Scale bars: **a**, **c**, $\mathbf{e} = 1$ cm; **b**, **d**, $\mathbf{f} = 1$ mm



Fig. 3 Sections of hymenium of *Nodulochaete fissurata* (CLZhao 27533, holotype). **a** Basidiospores. **b** Hyphae. **c** Basidia. **d** Cystidia. **e** Hyphidia. Scale bars: **a**, **b**, **c**, **d**=10 μ m; 1000×oil

Wumengshan National Nature Reserve, GPS coordinates 28° 58' N, 104° 20' E, altitude 2000 m asl., on fallen branch of angiosperm, leg. C.L. Zhao, 25 August 2023, CLZhao 31349, CLZhao 31360, CLZhao 31402, CLZhao 31477; same location, 26 August 2023, CLZhao 31612, CLZhao 31616, CLZhao 31625, CLZhao 31783; same location, 27 August 2023, CLZhao 31923, CLZhao 31970, CLZhao 32030, CLZhao 32076; same location, 28 August 2023, CLZhao 32255, CLZhao 32329, CLZhao 32337, CLZhao 32405; same location, 29 August 2023, CLZhao 32747; same location, 18 September 2023, CLZhao 33065, CLZhao

1477; CLZhao 35524 (SWFC).
Zhao
on, 27 Nodulochaete punctata J.H. Dong & C.L. Zhao, sp. nov.
Zhao Figs. 5, 6, and 7

MycoBank No.: MB 855377.

Holotype: CHINA, Yunnan Province, Lincang, Fengqing County, Yaojie Town, Xingyuan Village, GPS coordinates 24° 40′ N, 100° 10′ E, altitude 1500 m asl., on fallen branch

33078; same location, 19 September 2023, CLZhao 33133,

CLZhao 33223; same location, 21 September 2023, CLZhao

33847; same location, 7 November 2023, CLZhao 35479,



Fig. 4 Microscopic structures of *Nodulochaete fissurata* (CLZhao 27533, holotype). **a** Basidiospores. **b** Basidia. **c** Basidioles. **d** Cystidia. **e** Hyphidia. **f** Part of the vertical section of hymenium. Scale bars: **a**, **b**, **c**, **d**, **e**, **f** = 10 μ m

of angiosperm, leg. C.L. Zhao, 20 July 2022, CLZhao 22803 (SWFC).

Etymology: punctata (Lat.): referring to the punctate hymenial surface of the type specimen.

Basidiomata: Annual, resupinate, closely adnate, soft membranaceous, very hard to separate from substrate, without odor or taste when fresh, becoming membranaceous upon drying, up to 4 cm long, 2 cm wide, $50-100 \mu m$

thick. Hymenial surface smooth, white to cream when fresh, turning to cream to slightly pinkish to salmon upon drying. Sterile margin cream, narrow, up to 0.5 mm wide.

Hyphal structure: Monomitic, generative hyphae with clamp connections, colorless, thin-walled, occasionally branched, interwoven, $1.5-3 \mu m$ in diameter; IKI–, CB–, tissues unchanged in KOH.

Hymenium: Cystidia numerous, thin-walled, clavate to cylindrical, occasionally sinuous in the basal, $13-23 \times 4.5-6.5 \mu m$, with a clamp connection at base; cystidioles absent. Hyphidia arising from generative hyphae, nodulose, rarely branched, colorless, thin-walled, $1-4.5 \mu m$ in diameter. Basidia ellipsoid to ovoid, longitudinally septate, two to four-celled, $13-15 \times 11.5-13 \mu m$; basidioles dominant, similar to basidia in shape, but slightly smaller.

Basidiospores: Cylindrical to allantoid, slightly curved, colorless, smooth, thin-walled, with one oil drops, IKI–, CB–, (10–)10.5–13.5×(4.7–)5–6.3(–6.5) µm, L=12.34 µm, W=5.60 µm, Q=2.07-2.26, $Q_m=2.20\pm0.05$ (n=60/2).

Additional specimen (paratype) examined: China, Yunnan Province, Lincang, Fengqing County, Yaojie Town, Xingyuan Village, GPS coordinates 24°40'N, 100°10'E, altitude 1500 m asl., on fallen branch of angiosperm, leg. C.L. Zhao, 22 October 2022, CLZhao 25480 (SWFC).

Discussion

In the present study, a new genus *Nodulochaete* and two new species *N. fissurata* and *N. punctata* are described based on phylogenetic analyses and morphological characteristics.

A multilocus-based phylogeny with a wider sampling of various morphological groups in *Auriculariales* is urgently needed to achieve a more natural classification of this order, as in other orders within *Agaricomycetes* (Wang et al. 2021). Our result based on the combined ITS + nrLSU analyses demonstrated the new genus formed an independent monophyletic group comprising two new species within the order *Auriculariales* with strong support (91% BS, 91% BP, 1.00 BPP; Fig. 1). Therefore, a new genus is proposed with description and illustrations based on the morphological characteristics and phylogenetic analyses, including two new species.

Although phylogenetically *Nodulochaete* formed a single lineage it grouped with the well-known genera *Adustochaete* and *Proterochaete* (Fig. 1). However, morphologically *Adustochaete* differs from *Nodulochaete* in having grayish to brownish basidiomata, spiny or tuberculate hymenial surface, and variably branched hyphidia (Alvarenga et al. 2019). *Proterochaete* differs from



Fig. 5 Basidiomata of *Nodulochaete punctata* in general and detailed views. **a**, **b** CLZhao 22803 (holotype). **c**, **d** CLZhao 25480. Scale bars: **a**, $\mathbf{c} = 1 \text{ cm}$; **b**, $\mathbf{d} = 1 \text{ mm}$



Fig. 6 Sections of hymenium of *Nodulochaete punctata* (CLZhao 22803, holotype). **a** Basidiospores. **b** Basidia. **c** Cystidia. **d** Hyphidia. Scale bars: **a**, **b**, **c**, **d** = 10 μ m; 1000×oil

Nodulochaete by having cream-colored to grayish or pale ochraceous basidiomata, and a smooth or irregularly spiny hymenial surface (Alvarenga et al. 2019). The new species *N. fissurata* is revealed as a close sister to *N. punctata* with strong support (91% BS, 91% BP, 1.00 BPP; Fig. 1). However, *N. fissurata* can be distinguished from *N. punctata* by its cracked, tuberculate hymenial surface and longish basidia (13.5–24 × 10.5–13 µm).

Morphologically, *Nodulochaete* resembles *Adustochaete*, *Alloexidiopsis*, *Amphistereum*, *Crystallodon*, *Heteroradulum*, *Metulochaete*, *Proterochaete*, and *Sclerotrema* because of the corticioid basidiomata. However, they are distinguished molecularly and clustered apart from *Nodulochaete*. A morphological comparison between *Nodulochaete* and its related corticioid genera in *Auriculariales* is presented in Table 2.

New DNA sequencing techniques have revolutionized the researches of fungal taxonomy and diversity, in which about 155,000 species of fungi have been described (Hyde 2022). In recent years, the wood-inhabiting fungi are a group of species that have been extensively studied, which includes species with poroid, smooth, grandinoid, odontioid, and hydnoid basidiomata in China (Dai et al. 2021; Wu et al. 2022a, b; Dong et al. 2023a, b, 2024a, b; Guan et al. 2023; Liu et al. 2023; Mao et al. 2023; Yang et al. 2023, 2024; Deng et al. 2024; Li et al.



Fig.7 Microscopic structures of *Nodulochaete punctata* (CLZhao 22803, holotype). **a** Basidiospores. **b** Basidia. **c** Basidioles. **d** Cystidia. **e** Hyphidia. **f** Part of the vertical section of hymenium. Scale bars: **a**, **b**, **c**, **d**, **e**, **f** = 10 μ m

2024; Luo et al. 2024; Wang et al. 2024; Yuan and Zhao 2024; Zhang et al. 2023, 2024; Zhao et al. 2024; Zhou et al. 2024a, b). Up to now, several corticioid genera have been reported and described in the order *Auriculariales* (Malysheva and Spirin 2017; Alvarenga et al. 2019; Alvarenga and Gibertoni 2021; Liu et al. 2022b), but many new taxa have not yet been discovered. So, the

corticioid species diversity of the order *Auriculariales* is still not well known in China, especially in the subtropical and tropical areas. This paper enriches our knowledge of fungal diversity in this area. We anticipate that more undescribed corticioid taxa will be discovered throughout China after extensive collection combined with morphological and molecular analyses.

Table 2 Morph	ological comparison betwo	een <i>Nodulochaete</i> and relat	ted genera in the ord	ler Auriculariales			
Genus name	Basidiomata	Hymenial surface	Hyphal system	Basidiospores	Cystidia	Hyphidia	References
Adustochaete	Annual, small-sized, orbicular, waxy	Spiny or tuberculate, grayish to brownish	Monomitic	Cylindrical to broadly cylindrical, straight or curved	Clavate to fusiform, thin-walled	Variably branched	Alvarenga et al. (2019)
Alloexidiopsis	Annual, effused, leathery	Smooth or with sterile spines, more or less grayish	Monomitic	Cylindrical to broadly cylindrical, slightly curved	Cylindrical to clavate, thin-walled	Nodulose or richly branched	Liu et al. (2022a, b)
Amphistereum	Annual or perennial, cupulate-orbicular, hard leathery	Smooth, pale-colored	Dimitic	Cylindrical to broadly cylindrical, slightly curved	Rare, narrowly clavate, thin-walled	Richly branched	Malysheva and Spirin (2017)
Crystallodon	Annual, effused, gelatinous to crustaceous	Covered by sharp- pointed sterile spines, brownish	Monomitic	Cylindrical to broadly cylindrical, slightly curved	Fusiform to cylindrical, often sinuous, thin- walled	Branched	Alvarenga and Gibertoni (2021)
Heteroradulum	Annual or perennial, effused-reflexed, leathery	Smooth, with sterile spines, pinkish or reddish	Mono- or dimitic	Cylindrical to broadly cylindrical, sometimes curved	Clavate to fusiform, thin to thick-walled	Richly branched	Malysheva and Spirin (2017)
Metulochaete	Effused, gelatinous to waxy-arid	Smooth or covered by sterile spines, pale- colored	Monomitic	Allantoid, straight to slightly curved	Metuloid, covering hymenial spines, thick-walled	Richly branched	Alvarenga et al. (2019)
Nodulochaete	Annual, resupinate, membranaceous to coriaceous	Smooth to tuberculate, cream to slightly pink	Monomitic	Cylindrical to allantoid, slightly curved	Subclavate to subcylin- drical, fusiform	Nodulose or rarely branched	Present study
Proterochaete	Annual, orbicular, arid	Smooth or irregularly spiny, cream-colored to grayish or pale ochraceous	Monomitic	Cylindrical to broadly cylindrical, slightly curved	Occasional, sinuous, accidentally dichoto- mously branched, thin-walled	Richly or sparsely branched	Alvarenga et al. (2019)
Sclerotrema	Perennial, orbicular, leathery	Smooth or irregularly spiny, cream-colored to grayish or pale ochraceous	Monomitic	Allantoid, distinctly curved	Hyphoid to fusiform, thick-walled	Richly branched	Malysheva and Spirin (2017)

Author contribution Conceptualization, CZ and JD; methodology, CZ, MIH, and JD; software, CZ, JD, and YX; validation, CZ and JD; formal analysis, CZ, JD, and MIH; investigation, CZ, JD, and YX; resources, CZ; writing—original draft preparation, CZ, JD, YX, QJ, and MIH; review and editing, CZ and JD; visualization, CZ and JD; supervision, CZ and JD; project administration, CZ; funding acquisition, CZ. All authors have read and agreed to the published version of the manuscript.

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Data availability Publicly available datasets were analyzed in this study. This data can be found here: [https://www.ncbi.nlm.nih.gov/; https://www.mycobank.org/page/Simple%20 names%20 search; https:// treebase.org/treebase-web/home.html (TreeBase ID 31903)].

Declarations

Competing interests The authors declare no competing interests.

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