


Article

The Morphological Characteristics and Phylogenetic Analyses Revealed an Additional Taxon in *Heteroradulum* (Auriculariales)

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Abstract: Auriculariales is diverse, embracing a number of corticioid, poroid, and hydroid genera. The present study covers a new wood-inhabiting fungal species of *Heteroradulum niveum* sp. nov. that is proposed on the basis of a combination of morphological features and molecular evidence. The species is characterized by the resupinate basidiomata, a monomitic hyphal system with generative hyphae with clamp connections; tubular cystidia; two- to four-celled basidia; and allantoid, colorless, thin-walled, smooth, IKI–, CB–, basidiospores (6.5–13.5 × 2.7–5.5 μm). Sequences of ITS and nLSU rRNA gene regions of the specimens were generated, and phylogenetic analyses were carried out with methods of maximum parsimony, maximum likelihood, and Bayesian inference. These phylogenetic analyses inferred from ITS+nLSU indicated that *H. niveum* is nested in *Heteroradulum* within Auriculariales. Further study within *Heteroradulum* on the basis of ITS+nLSU dataset revealed that it formed a monophyletic lineage with a strong support (100% BS, 100% BP, 1.00 BPP) and then grouped with *H. yunnanensis*.

Keywords: corticioid fungi; phylogeny; wood-inhabiting fungi; taxonomy; Yunnan Province



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1. Introduction

The Auriculariales is a characteristic order of Agaricomycetes (Basidiomycota), in which it has been introduced to embrace a number of corticioid, poroid, and hydroid genera on the basis of a result of morphological, phylogenetic, and cytological studies [1–3]. The Auriculariales are wood decomposers inhabiting various hosts, from the tropics to the subarctic zone, in which some of them are able to survive under extreme climatic conditions [4]. Currently, the delimitation of Auriculariales has been principally based on the characteristics observed under optical and electron microscopy and supports by molecular analyses [5].

Heteroradulum Lloyd ex Spirin & Malysheva was typified by *H. kmetii* (Bres.) Spirin & Malysheva [4], which is characterized by a combination of annual or perennial, resupinate, or effused-reflexed basidiomata with a leathery consistency; hymenophore smooth to odontoid; a monomitic hyphal structure (rare dimitic) with clamp connections on generative hyphae; and the presence of cystidia, basidia narrowly ovoid to obconical, longitudinally septate with a well-developed enucleate stalk and basidiospores hyaline, thin-walled, smooth, cylindrical, acyanophilous, and negative in Melzer's reagent [4]. Currently, seven species have been accepted in *Heteroradulum* worldwide [4,6–11].

The molecular systematics involving *Heteroradulum* based on the internal transcribed spacer (ITS) regions and the large subunit nuclear ribosomal RNA gene (nLSU) sequences

revealed that the taxonomy and phylogeny of the Auriculariales with steroid basidiocarps were employed, in which *H. adnatum* Spirin & Malysheva and *H. semis* Spirin & Malysheva were described as new taxa [4]. The genus *Protohydnum* A. Möller [12] was revised, which showed that *Heteroradulum* grouped with *Exidiopsis* (Bref.) Möller [13] and *Tremellochaete* Raitv [14]. Phylogenetic analyses based on ITS+nLSU DNA sequence data indicated that *Heteroradulum* belonged to Auriculariaceae, which showed that *Heteroradulum* was to be related to *Grammatus* H.S. Yuan & C. Decock [15]. Sequences of ITS and LSU nrRNA gene regions of the studied samples were generated, which showed that *H. yunnanensis* C.L. Zhao formed a monophyletic lineage with a strong support and then grouped with *H. adnatum* [11].

In the present study, we collected the material supposedly belonging to an undescribed species of corticioid fungi from Yunnan Province, P.R. China. We present morphological and molecular phylogenetic evidence that supports the recognition of a new species within the *Heteroradulum*, on the basis of the internal transcribed spacer (ITS) region nLSU sequences.

2. Materials and Methods

2.1. Morphological Studies

The studied specimens are deposited at the herbarium of Southwest Forestry University (SWFC), Yunnan Province, China. Macromorphological descriptions are based on photos captured in the field and lab and field notes. Color terminology follow Petersen [16]. Micromorphological data were obtained from the dried specimens and observed under a light microscope following Dai [17]. The following abbreviations were used: KOH = 5% potassium hydroxide water solution, CB− = acyanophilous, CB = Cotton Blue, IKI− = both inamyloid and indextrinoid, IKI = Melzer's reagent, 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, $n = a/b$ (number of spores (a) measured from given number (b) of specimens).

2.2. Molecular Methods

CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to obtain genomic DNA from dried specimens, according to the manufacturer's instructions followed previous study [18]. ITS region was amplified with primer pair ITS5 and ITS4 [19]. Nuclear LSU region was amplified with primer pair LR0R and LR7 (<http://lutzonilab.org/nuclear-ribosomal-dna/>; accessed on 5 January 2022). The PCR procedure for ITS and nLSU followed previous study [18]. All newly generated sequences in the present study were deposited in NCBI GenBank (Table 1).

Table 1. List of species, samples, and GenBank numbers of sequences employed in present study.

Species Name	Sample No.	GenBank Accession No.		References	Country
		ITS	nLSU		
<i>Amphistereum leveilleanum</i>	FP 106715	KX262119		[4]	Russia
			KX262168	[4]	USA
<i>A. schrenkii</i>	HHB 8476	KX262130	KX262178	[4]	USA
<i>Auricularia americana</i>	Cui 11509	KT152094	KT152110	[20]	China
<i>A. auricula-judae</i>	MW 446	AF291268	AF291289	[20]	Germany
<i>Basidioidendron eyrei</i>	TUFC 14484	AB871753	AB871734	[4]	Japan
<i>Bjerkandera adusta</i>	HHB-12826-Sp	KP134983	KP135198	[21]	North America
<i>Ductifera sucina</i>	KW 3886	AY509551	AY509551	[22]	New Zealand
<i>Eichleriella alliciens</i>	HHB 7194	KX262120	KX262169	[4]	USA
<i>E. bactriana</i>	TAAM 104431	KY262138	KY262186	[4]	Germany
<i>Elmerina caryae</i>	Dai 5215	JQ764654	JQ764633	[23]	Italy
<i>E. cladophora</i>	Wei 5621	JQ764659	JQ764634	[23]	China

Table 1. Cont.

Species Name	Sample No.	GenBank Accession No. ITS	nLSU	References	Country
<i>Exidia glandulosa</i>	MW 355	AF291273	AF291319	[24]	Germany
<i>E. pithya</i>	MW 313	AF291275	AF291321	[24]	Germany
<i>Exidiopsis effusa</i>	OM 19136	KX262145	KX262193	[4]	Finland
<i>Heteroradulum adnatum</i>	LR 23453	KX262116	KX262165	[4]	Mexico
<i>H. deglubens</i>	TAAM 064782	KX262101	KX262148	[4]	Russia
<i>H. niveum</i>	CLZhao 11204	MZ352947	MZ352932	this study	China
<i>H. niveum</i>	CLZhao 11210	MZ352948	MZ352933	this study	China
<i>H. niveum</i>	CLZhao 16260	MZ352940	MZ352934	this study	China
<i>H. niveum</i>	CLZhao 16280	MZ352941	MZ352935	this study	China
<i>H. niveum</i>	CLZhao 16398	MZ352942	MZ352936	this study	China
<i>H. niveum</i>	CLZhao 16424	MZ352943	MZ352937	this study	China
<i>H. niveum</i>	CLZhao 16432	MZ352944		this study	China
<i>H. niveum</i>	CLZhao 16472	MZ352945	MZ352938	this study	China
<i>H. niveum</i>	CLZhao 16483	MZ352946	MZ352939	this study	China
<i>H. yunnanensis</i>	CLZhao 4023	MT215564	MT215568	[11]	China
<i>H. yunnanensis</i>	CLZhao 8106	MT215565	MT215569	[11]	China
<i>H. yunnanensis</i>	CLZhao 9132	MT215566	MT215570	[11]	China
<i>H. yunnanensis</i>	CLZhao 9200	MT215567	MT215571	[11]	China
<i>Sclerotrema griseobrunneum</i>	VS 7674	KX262140	KX262188	[4]	Russia
<i>Sistotrema brinkmannii</i>	Isolate 236	JX535169	JX535170	[4]	Russia
<i>Tremellochaete japonica</i>	LE 303446	KX262110	KX262160	[4]	Russia

Sequences were aligned in MAFFT 7 (<https://mafft.cbrc.jp/alignment/server/>; accessed on 5 January 2022) using G-INS-i strategy for ITS+nLSU datasets, and manually adjusted in BioEdit [25]. Aligned dataset was deposited in TreeBase (submission ID 28346). *Sistotrema brinkmannii* (Bres.) J. Erikss. and *Bjerkandera adusta* (Willd.) P. Karst. were selected as an outgroup for phylogenetic analyses of ITS+nLSU dataset following a previous study [26] (Figure 1); *Exidiopsis effusa* (Bref. ex Sacc.) Möller and *Tremellochaete japonica* (Lloyd) Raitv [14] obtained from GenBank were used as an outgroup to root trees following Guan et al. [11] in the ITS+nLSU analysis (Figure 2).

Maximum parsimony analysis was applied to two combined ITS+nLSU datasets. Its approaches followed Zhao and Wu [18], and the tree construction procedure was performed in PAUP* version 4.0b10 [27]. All characters were equally weighted, and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. 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 [28]. Descriptive tree statistics: tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each maximum parsimonious tree generated on the basis of PAUP* version 4.0b10 [27]. Datamatrix was also analyzed using maximum likelihood (ML) approach with RAxML-HPC2 through the Cipres Science Gateway (www.phylo.org, accessed on 5 January 2022) [29]. Branch support (BS) for ML analysis was determined by 1000 bootstrap replicates.

MrModeltest 2.3 [30] was used to determine the best-fit evolution model for each dataset for Bayesian inference (BI). The soft of MrBayes 3.1.2 was calculated for BI [31]. Four Markov chains were run for 2 runs from random starting trees for 1.1 million generations for ITS+nLSU (Figure 1), or for 0.25 million generations for ITS+nLSU (Figure 2). The first quarter of all generations was discarded as burn-in. The majority rule consensus tree of all remaining trees was calculated.

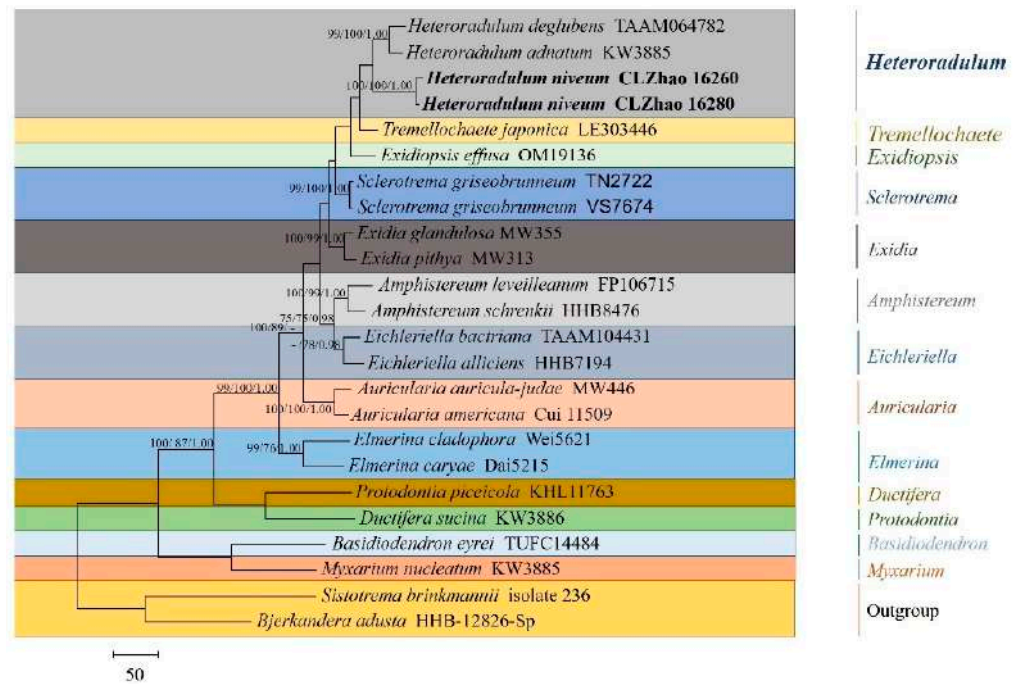


Figure 1. Maximum parsimony strict consensus tree illustrating the phylogeny of *Heteroradulum niveum* and related species in Auriculariaceae based on ITS+nLSU sequences. Branches are labeled with maximum likelihood bootstrap higher than 70%, parsimony bootstrap proportions higher than 50%, and Bayesian posterior probabilities more than 0.95.

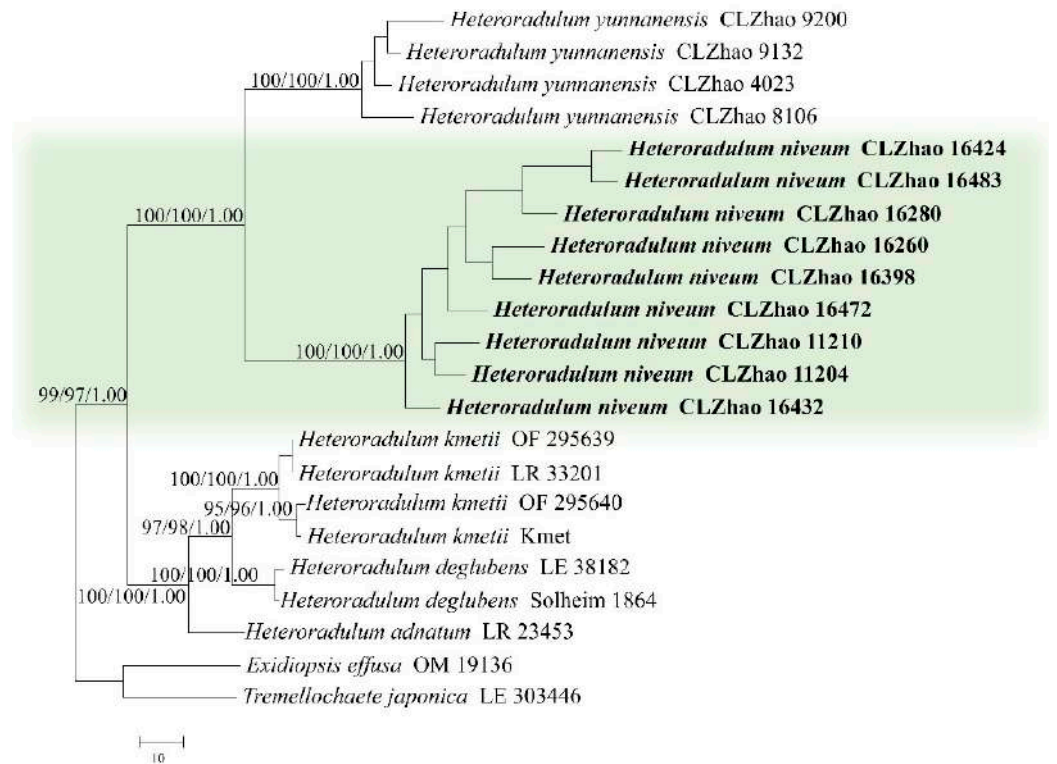


Figure 2. Maximum parsimony strict consensus tree illustrating the phylogeny of *Heteroradulum niveum* and related species in genus *Heteroradulum* on the basis of ITS+nLSU sequences. Branches are labeled with maximum likelihood bootstrap higher than 70%, parsimony bootstrap proportions higher than 50%, and Bayesian posterior probabilities more than 0.95.

3. Results

3.1. Molecular Phylogeny

The dataset of ITS+nLSU included sequences from 24 fungal specimens representing 22 species (Figure 1). The dataset includes 1922 characters an aligned for the length, of which 1350 characters are constant, 410 are parsimony-informative, and 309 are variable and parsimony-uninformative. Maximum parsimony analysis yielded one equally parsimonious tree (TL = 1922, CI = 0.5723, RI = 0.4207, HI = 0.4277, RC = 0.2408). The best model for the dataset of ITS+nLSU estimated and applied in the Bayesian analysis was GTR+I+G (Iset nst = 6, prset statefreqpr = dirichlet (1,1,1,1), rates = invgamma). ML analysis and Bayesian analysis resulted in a similar topology to MP analysis, and Bayesian analysis has an average standard deviation of split frequencies = 0.008747 (BI), and the effective sample size (ESS) across the two runs was the double of the average ESS (avg ESS) = 1108. The phylogram based on ITS+nLSU sequences (Figure 1) demonstrated that the new taxon clustered into genus *Heteroradulum* and formed a well-supported lineage within Auriculariales.

As shown in Figure 2, the ITS+nLSU dataset included 22 fungal specimens representing 7 species. The dataset had an aligned length of 1967 characters, of which 1724 characters are constant, 159 are parsimony-informative, and 84 are variable and parsimony-uninformative. Maximum parsimony analysis yielded 42 equally parsimonious trees (TL = 412, HI = 0.2694, RI = 0.8490, CI = 0.7306, RC = 0.6202). The best model for the ITS+nLSU dataset estimated and applied in the Bayesian analysis was GTR+I+G (Iset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1)). ML analysis and Bayesian analysis resulted in a similar topology to MP analysis, Bayesian analysis had an average standard deviation of split frequencies = 0.009184 (BI), and the effective sample size (ESS) across the two runs was double the average ESS (avg ESS) = 247. The phylogenetic tree (Figure 2) inferred from ITS+nLSU sequences revealed that *Heteroradulum niveum* sp. nov. formed a monophyletic lineage with high supports of 100% BS, 100% BP, and 1.00 BPP, and then grouped with *H. yunnanensis*.

3.2. Taxonomy

Heteroradulum niveum J.J. Li & C.L. Zhao sp. nov. Figures 3 and 4.

Mycobank no.: 841986

Holotype—China. Yunnan Province, Wenshan, Pingba Town, Wenshan National Nature Reserve, 104.25° E, 23.37° N, 2195.6 m asl., on the fallen angiosperm branch, on the broad-leaved forest, mainly with oak, leg. C.L. Zhao, 25 July 2019, CLZhao 16280 (SWFC).

Etymology—*niveum* (Lat.): referring to the white hymenial surface of type specimens.

Fruiting body—Basidiomata annual, resupinate, leathery, without odor or taste when fresh, becoming membranaceous upon drying, up to 15 cm long, 4 cm wide, 100–200 µm thick. Hymenial surface smooth, white when fresh, becoming white to slightly cream upon drying, older basidiomata with more or less pronounced black stains. Sterile margin white.

Hyphal system—Monomitic, generative hyphae with clamp connections, IKI–, CB–; tissues unchanged in KOH; subiculum indistinct; hymenium thicken, generative hyphae colorless, thin-walled, unbranched, more or less interwoven, 2.5–4 µm in diameter.

Hymenium—Cystidia tubular, 15–34 × 2.5–7 µm; basidia narrowly ovoid to obconical, longitudinally septate, two- to four-celled, embedded, with a well-developed enucleate stalk, 9–19 × 8–15 µm.

Spores—Basidiospores allantoid, colorless, smooth, thin-walled, IKI–, CB–, (6.2–)6.5–13.5(–14) × (2.5)2.7–5.5(–5.8) µm, L = 10.02 µm, W = 4.38 µm, Q = 2.1–2.4 (*n* = 150/5).

Additional specimens examined—China. Yunnan Province, Wenshan, Xichou County, Xiaomiaogou, Wenshan National Nature Reserve, 104.46° E, 23.22° N, 1541.5 m asl., on the fallen angiosperm branch, leg. C.L. Zhao, 16 January 2019, CLZhao 11204 (SWFC 011204), CLZhao 11210 (SWFC 011210); Pingba Town, Wenshan National Nature Reserve, 104.25° E, 23.37° N, 2195.6 m asl., on the fallen angiosperm branch, leg. C.L. Zhao, 25 July 2019, CLZhao 16260 (SWFC 016260); 26 July 2019, CLZhao 16398 (SWFC 016398), CLZhao

16424 (SWFC 016424), CLZhao 16432 (SWFC 016432), CLZhao 16472 (SWFC 016472); on the angiosperm trunk, leg. C.L. Zhao, 26 July 2019, CLZhao 16483 (SWFC 016483).

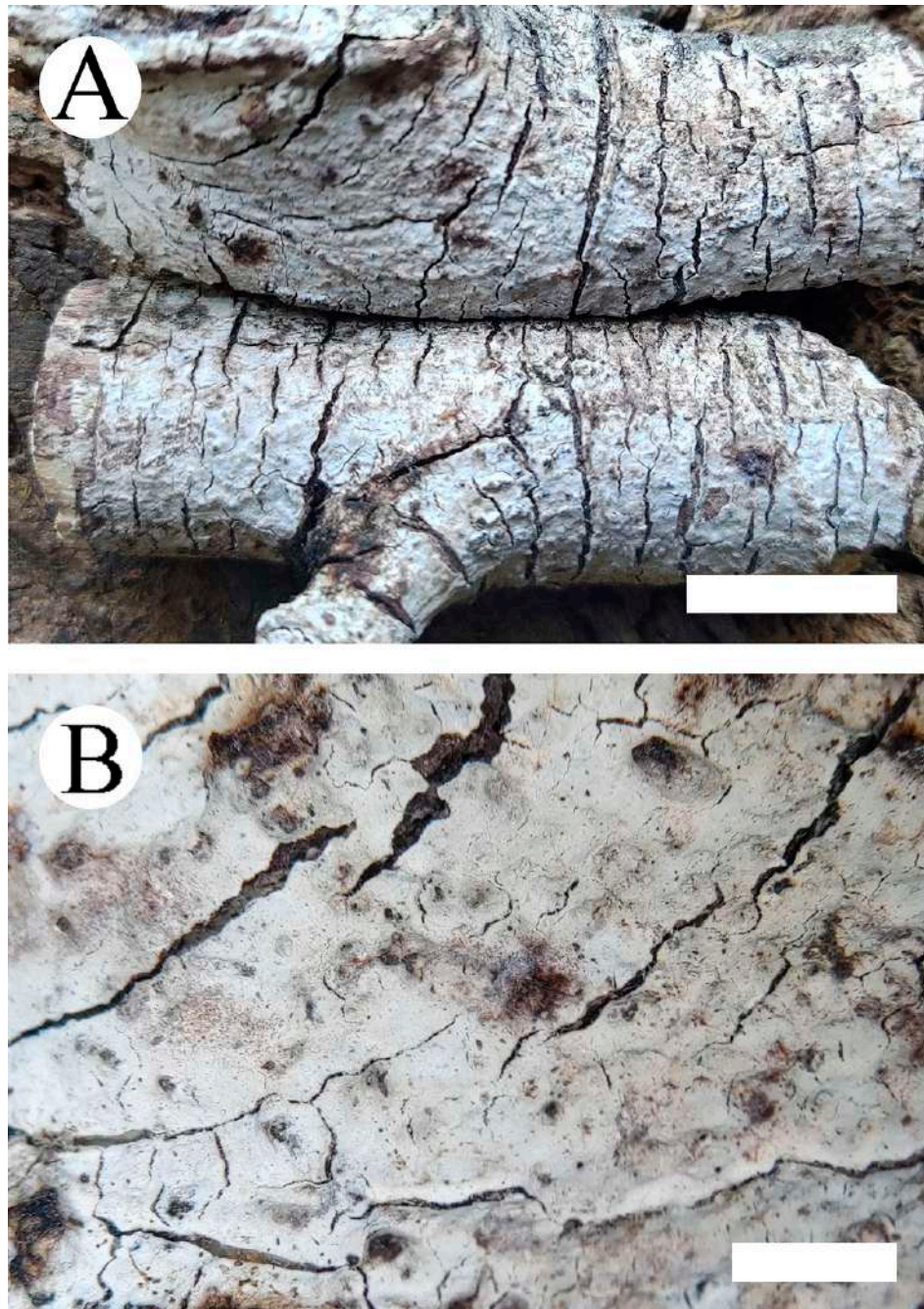


Figure 3. Basidiomata of *Heteroradulum niveum*. Bars: (A) = 1 cm; (B) = 2 mm (holotype).

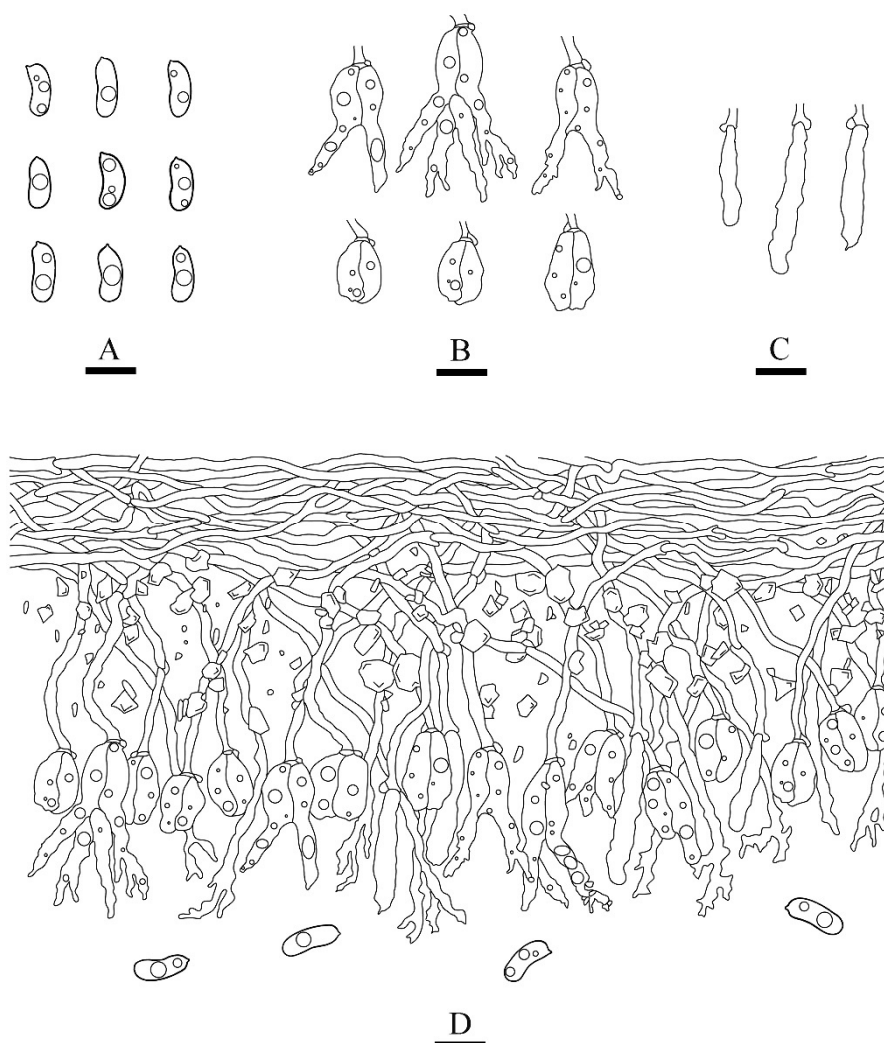


Figure 4. Microscopic structures of *Heteroradulum niveum* (holotype): basidiospores (A); basidia and basidioles (B); cystidia (C); A section of hymenium (D). Bars: (A–D) = 10 μ m.

4. Discussion

In the present study, a new species, *Heteroradulum niveum*, is described on the basis of phylogenetic analyses and morphological characters.

Phylogenetically, Alvarenga and Gibertoni [5] employed the phylogenetic reconstruction using ITS+nLSU topology in the lineages of Auriculariales, showing that *Heteroradulum* grouped closely with *Adustochaete* Alvarenga & K.H. Larss., *Amphistereum* Spirin & Malyshева, and *Exidiopsis* (Bref.) Möller. In the present study, the new species formed a monophyletic lineage with high supports of 100% BS, 100% BP, and 1.00 BPP and then grouped with *H. yunnanensis*. However, morphologically, *H. yunnanensis* differs from *H. niveum* by its odontoid hymenial surface (50–100 μ m long) and larger basidiospores (17–24 \times 5–8 μ m) [11].

Morphologically, *Heteroradulum niveum* is similar to *H. adnatum* on the basis of presence of the white hymenial surface. However, *H. adnatum* differs from *H. niveum* by having the hydroid hymenophore and wider basidiospores (11.4–14.2 \times 5.2–7.2 μ m) [4].

Heteroradulum niveum is reminiscent of two species of *Heteroradulum*, *H. deglubens* and *H. kmetii*, on the basis of the character by the smooth hymenophore, but *H. deglubens* differs from *H. niveum* by having a greyish pink hymenial surface with reddish tints and larger basidiospores (13.1–19.8 \times 6.1–8.1 μ m) [4], whereas *H. kmetii* differs in its perennial, pileal basidiomata; pinkish or reddish hymenial surface; and larger basidiospores (14.3–22.3 \times 6–9.2 μ m) [4].

Heteroradulum niveum shares the similar characteristics of the allantoid basidiospores with *H. lividofuscum*. However, *H. lividofuscum* differs from *H. niveum* by having the hydroid hymenophore, a dimitic hyphal structure, the presence of abundant gloeocystidia, and larger basidiospores ($17.6\text{--}23.1 \times 7.3\text{--}9 \mu\text{m}$) [4].

On the basis of biogeography of *Heteroradulum* (Figure 5), the species is mainly distributed in Europe, such as in Austria, Russia, France, Germany, Poland, the United Kingdom, the Netherlands, Portugal, Sweden, Italy, Denmark, Norway, Finland, and Spain [32]. On the other hand, *H. adnatum* has been found in Mexico, *H. brasiliense* has been found in Brazil, *H. spinulosum* has been found in North America, and *H. yunnanensis* was discovered as a new species by Guan et al. in China [4,11].

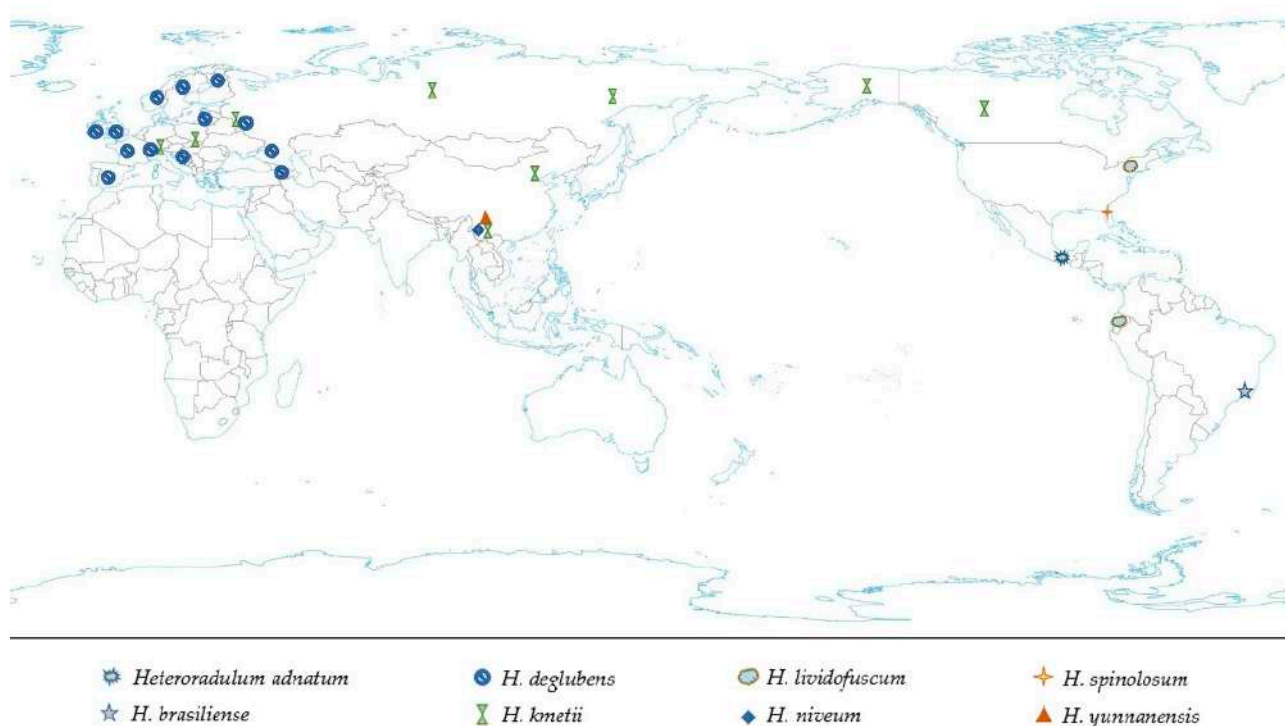


Figure 5. Geographic distribution of *Heteroradulum* species worldwide.

In addition, the results of BLAST queries in NCBI based on ITS and nLSU separately showed the sequences producing significant alignment descriptions: in ITS BLAST results, the top 10 records for *Heteroradulum yunnanensis* (maximum record descriptions: max score 765; total score 765; query cover 95%; E value 0; ident 90.39%), *Exidiopsis calcea* (maximum record descriptions: max score 769; total score 769; query cover 85%; E value 0; ident 93.49%), *Adustochaete rava* (maximum record descriptions: max score 745; total score 745; query cover 93%; E value 0; ident 90.07%), *Sebacina filicicola* (maximum record descriptions: max score 713; total score 713; query cover 97%; E value 0; ident 89.10%), and *E. grisea* (maximum record descriptions: max score 699; total score 699; query cover 71%; E value 0; ident 96.25%). In nLSU BLAST results, the top 10 records for *H. yunnanensis* (maximum record descriptions: max score 2457; total score 2457; query cover 99%; E value 0; ident 99.19%), *Auricularia fuscosuccinea* (maximum record descriptions: max score 2377; total score 2377; query cover 98%; E value 0; ident 98.17%), and *A. subglabra* (maximum record descriptions: max score 2375; total score 2375; query cover 99%; E value 0; ident 97.96%).

Wood-rotting fungi are an extensively studied group of Basidiomycota [17,32–34], but Chinese wood-rotting fungal diversity is still not well known, especially in the subtropics and tropics. Many recently described taxa of fungi are from subtropical and tropical areas [17,35–38]. The new species presented in the current study is also from the subtropics. It is possible that new taxa will be found after further investigations and molecular analyses.

Author Contributions: Conceptualization, C.-L.Z.; methodology, C.-L.Z. and J.-J.L.; software, C.-L.Z., C.-M.L. and J.-J.L.; validation, C.-L.Z. and J.-J.L.; formal analysis, C.-L.Z. and J.-J.L.; investigation, C.-L.Z. and C.-M.L.; resources, C.-L.Z. and C.-M.L.; writing—original draft preparation, C.-L.Z. and J.-J.L.; writing—review and editing, C.-L.Z. and J.-J.L.; visualization, C.-L.Z. and J.-J.L.; supervision, C.-L.Z.; project administration, C.-L.Z.; funding acquisition, C.-L.Z. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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