

## RESEARCH ARTICLE

# *Clavulina mollis*, sp. nov. (Hydnaceae, Cantharellales), a New Fungal Species from Southwest China Revealed by Morphology and Phylogenetic Analyses

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## ABSTRACT

A new basidiomycete, *Clavulina mollis*, is described based on morphological features and DNA sequence analyses. This fungus, collected in Yunnan Province, China, is characterized by its coralloid basidiomata growing in caespitose clusters, branching two to five times, polychotomous toward the apices and irregularly dichotomous to polychotomous at the base; a monomitic hyphal system with clamped generative hyphae; pale yellow, subclavate to subcylindrical basidia with two sterigmata; and subglobose basidiospores measuring 7–8.5 × 6–8 μm. Phylogenetic analyses based on three loci—the internal transcribed spacer region, the large subunit nuclear ribosomal RNA gene (nrLSU), and the small subunit mitochondrial rRNA gene (mtSSU)—revealed that the studied material represents a new lineage within the genus *Clavulina*, closely related to *C. cirrhata* and *C. livida*. In addition to a detailed description, illustrations, and a phylogeny reconstruction showing the placement of the new species, a key to *Clavulina* species reported from China is provided.

## 1 | Introduction

The order *Cantharellales* Gäum. was erected by Gäumann (1926) in the pursuit of a natural classification based on evolutionary relationships. This order originally included three genera, i.e., *Cantharellus* Adans. ex Fr., *Clavulina* J. Schröt., and *Craterellus* Pers. These genera produce stichic basidia, but their basidiomata are remarkably diverse, clavarioid to coralloid in *Clavulina*, and cantharelloid in *Cantharellus* and *Craterellus*. Currently, the order *Cantharellales* comprises about 725 recognized species, but its diversity is considered to be significantly high, with a worldwide distribution (He et al. 2024). The order contains economically important fungi (Watling 1997), such as *Cantharellus*, *Craterellus* and *Hydnum* L., which produce edible basidiomata, and important plant pathogens that cause economic losses, like *Ceratobasidium* D.P. Rogers (Veldre et al. 2013). *Cantharellales* is a highly heterogeneous monophyletic assemblage of fungi that lacks shared characters across the order. The family *Hydnaceae*

Chevall. is referred to as the core cantharelloid clade (Moncalvo et al. 2006), in which it is the only family with species that produce complex fleshy basidiomata (e.g. cantharelloid, clavarioid-coralloid, polyporoid, clavarioid), predominantly ectomycorrhizal, that are usually slow growing and long-lived due to resistance against invertebrate predation (Pilz et al. 2003).

*Clavulina* J. Schröt. is a monophyletic genus within the order *Cantharellales* and represents a prominent component of the coral fungi (Yuan et al. 2020; De Meiras-Ottoni and Gibertoni 2023; Liu et al. 2024). Typical characteristics of the genus are simple or branched, clavarioid to coralloid basidiomata, and an amphigenous hymenium with two-spored basidia, which often are septated with postpartal septa after the release of the mature spores (Corner 1970; Petersen 1988; Huang et al. 2023; Liu et al. 2024). The taxonomy of *Clavulina* has undergone several revisions. Initially, members of *Clavulina* were classified in the *Clavariaceae* Chevall., as were all genera with clavarioid or

coralloid basidiomata (Persoon 1797). Schröter (1888) retained the genus within the *Clavariaceae* based on its distinctive morphological characters, including the two horn-shaped sterigmata, smooth basidiospores, and the presence of clamp connections. Subsequently, Donk (1933) established the subfamily *Cantharelloideae* (R. Maire) and transferred *Clavulina* to the new subfamily. A revision by Donk (1961) erected the new family *Clavulinaceae* Donk, into which *Clavulina* was classified as the sole genus. Corner (1970) agreed with the revised classification of *Clavulina*. Hibbett et al. (2014) provided a comprehensive phylogeny based on a multiple-marker dataset (ITS, nrLSU, mtSSU, *TEF1*, and *RPB2*) for the entire *Hydnaceae* sensu stricto, and confirmed seventeen genera in this family, including *Clavulina*.

Species of the genus *Clavulina* are globally distributed and frequently found in diverse ecosystems, but with higher species diversity in the Neotropics (Thacker and Henkel 2004; Uehling et al. 2012a; Uehling et al. 2012b; Yuan et al. 2020). Species of *Clavulina* have been reported to quantitatively be very important in ectomycorrhizal communities, especially in temperate regions where *Clavulina* species are being detected in environmental sequencing and ectomycorrhizal community studies (De Meiras-Otoni and Gibertoni 2023; He et al. 2024). According to Index Fungorum (accessed on 22 July 2025), 182 names have been published under the genus *Clavulina*, of which 117 species are currently accepted worldwide (De Meiras-Otoni and Gibertoni 2023; Liu et al. 2024). Currently, only 23 *Clavulina* species have been described from specimens collected in China, including *C. baiyunensis* X. X. Huang & L. H. Qiu, *C. bessonii* (Pat.) Corner, *C. castaneipes* (G.F. Atk.) Corner, *C. chengdeensis* Yue Gao, Hao Zhou & C. L. Hou, *C. cinerea* (Bull.) J. Schröt., *C. coralloides* (L.) J. Schröt., *C. curva* P. Zhang & X. F. Liu, *C. eburnea* P. Zhang & P. T. Deng, *C. flava* P. Zhang, *C. griseoviolacea* Yue Gao, Hao Zhou & C. L. Hou, *C. hainanensis* P. Zhang & P. T. Deng, *C. lilaceorosea* X. X. Huang & L. H. Qiu, *C. livida* Shu Z. Yan, G. He & Shuang L. Chen, *C. minor* X. X. Huang & L. H. Qiu, *C. pallida* Yue Gao, Hao Zhou & C. L. Hou, *C. pallidorosea* P. Zhang & P. T. Deng, *C. purpurascens* P. Zhang, *C. rugosa* (Bull.) J. Schröt., *C. spinosa* P. Zhang & X. F. Liu, *C. thindii* U. Singh, *C. tomentosa* P. Zhang & P. T. Deng, *C. tropica* (Dogma) P. Zhang, and *C. yunnanensis* P. Zhang & X. F. Liu (Teng 1963; Li et al. 2015; He et al. 2016; Wu et al. 2019a; Cao et al. 2021; Deng et al. 2022, 2024; Huang et al. 2023; Gao et al. 2024; Liu et al. 2024).

During investigations on basidiomycetes in Yunnan Province, China, some *Clavulina* specimens were collected. To assess the taxonomic placement and phylogenetic relationships of these specimens, we carried out a polyphasic characterization, including the analysis of multilocus sequence data and morphological features. This taxon is identified as a previously undescribed species of *Clavulina* and named *C. mollis*. A description, illustrations, and phylogenetic analyses of the new species are provided.

## 2 | Materials and Methods

### 2.1 | Specimen Collection and Morphological Studies

Fresh basidiomata were collected from the moist soil of broad-leaved forests in Dehong and Zhaotong, Yunnan Province, in

July 2023. 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 details were recorded, and basidiomata were transported to a field station and dried on an electronic food drier at 45°C (Dong et al. 2024). Once dried, the specimens were sealed in an envelope and zip-lock plastic bags and labelled (Senanayake et al. 2020; Rathnayaka et al. 2024). The dried specimens were deposited in the herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, China.

The macromorphological descriptions were based on field notes and photos captured in the field and lab. Petersen (1996) was followed for the color terminology. Micromorphological data were obtained from dried specimens using a light microscope at 1000× magnification. Sections of the hymenium were mounted in 5% KOH, 2% phloxine B, Cotton Blue, and Melzer's reagent. To show the variation in spore sizes, 5% of measurements were excluded from each end of the range and shown in parentheses. At least thirty basidiospores from each specimen were measured. Stalks were excluded from basidia 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 nondextrinoid, 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, and  $n = a/b$  (number of spores (a) measured from given number (b) of specimens). The new species was registered in the MycoBank database (<http://www.mycobank.org>).

### 2.2 | Molecular Phylogeny

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 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 LR0R and LR7 primer pair (Vilgalys and Hester 1990; Rehner and Samuels 1994). The mitochondrial mtSSU region was amplified with primer pairs MS1 and MS2 (White et al. 1990). 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 procedure for mtSSU was as follows: initial denaturation at 94°C for 2 min, followed by 35 cycles at 94°C for 45 s, 52°C for 45 s, and 72°C for 1 min, and a final extension of 72°C for 10 min (White et al. 1990). The PCR products were purified and sequenced at Kunming Tsingke Biological Technology Limited Company (Yunnan Province, P.R. China). Consensus sequences were generated using SnapGene (version 4.2.4; from Insightful Science; available at [snapgene.com](http://snapgene.com)). The newly generated sequences were deposited in NCBI GenBank (Table 1).

**TABLE 1** | Names, sample numbers, references, and corresponding GenBank accession numbers of the taxa used in the phylogenetic analyses of this study.

Species	Specimen voucher	GenBank accession no.			Country	References
		ITS	nLSU	mtSSU		
<i>Bergerella atrofusca</i>	Berger 34 240	MN902070	MN902070	—	Austria	Lawrey et al. 2020
<i>Bryoclavula phycophia</i>	S-287-FB3	LC544109	LC544110	—	Japan	Masumoto and Degawa 2020
<i>B. phycophila</i>	S-293-FB5	LC508117	LC508118	—	Japan	Masumoto and Degawa 2020
<i>Bulbilla applanata</i>	Flakus16422 SV2	KC336079	OR471070	—	Bolivia	Diederich et al. 2014
<i>B. applanata</i>	Flakus16422 SV1	OR471315	OR471069	—	Bolivia	Diederich et al. 2014
<i>Burgella favoparmeliae</i>	JL192-01	—	DQ915469	—	USA	Lawrey et al. 2007
<i>B. lutea</i>	Etayo 27 623	KC336076	KC336075	—	Bolivia	Diederich et al. 2014
<i>Cantharellus cibarius</i>	479/GE 07.025	KX907204	KF294658	KF294585	France	Olariaga et al. 2017
<i>C. cibarius</i>	BIO-Fungi 10 986	KR677501	KR677539	—	Sweden	Olariaga et al. 2017
<i>C. laevihymeninus</i>	KUN-HKAS 125 910 (LEI693)	OP909722	OP909722	—	China	Cao et al. 2021
<i>C. lateritius</i>	BB 07.058	—	KF294633	KF294562	USA	Buyck et al. 2014
<i>C. lewisii</i>	BB 02.197	—	KF294623	KF294551	USA	Buyck et al. 2014
<i>C. lewisii</i>	BB 07.003	JN944021	JN940597	KF294554	USA	Cao et al. 2021
<i>C. magnus</i>	IFP 019444	—	MW979517	MW980525	China	Cao et al. 2021
<i>C. magnus</i>	IFP 019443	—	MW979516	MW980524	China	Cao et al. 2021
<i>C. platyphyllus</i>	BB 98.126	—	KF294620	KF294549	Tanzania	Buyck et al. 2014
<i>C. platyphyllus</i>	BB 08.160	—	KF294648	KF294579	Tanzania	Buyck et al. 2014
<i>C. subincarnatus</i>	BB 06.096	KF981372	KF294602	KF294537	Madagascar	Cao et al. 2021
<i>C. subminor</i>	IFP 019446	MW980546	MW979523	MW980529	China	Cao et al. 2021
<i>C. subminor</i>	IFP 019447	MW980547	MW979524	MW980530	China	Cao et al. 2021
<i>C. symoensii</i>	BB 98.011	—	KF294618	KF294547	Tanzania	Buyck et al. 2014
<i>C. symoensii</i>	BB 98.113	—	KF294619	KF294548	Tanzania	Buyck et al. 2014
<i>Clavulina amazonensis</i>	TH 9191	HQ680356	—	—	Guyana	Henkel et al. 2011
<i>C. caespitosa</i>	TH 8709	DQ056371	—	—	Guyana	Henkel et al. 2005
<i>C. castaneipes</i>	TENN056432	JX287357	—	—	Costa Rica	Uehling et al. 2012a
<i>C. castaneipes</i>	OSC 108 705	EU669209	—	—	USA	De Meiras-Otoni and Gibertoni 2023
<i>C. cerebriformis</i>	MCA4022	NR121504	JN228222	—	Guyana	Uehling et al. 2012a
<i>C. cinereoglebosa</i>	TH8561 clone C	JN228217	—	—	Guyana	Uehling et al. 2012a
<i>C. cinereoglebosa</i>	TH8561 clone E	JN228218	JN228232	—	Guyana	Uehling et al. 2012a
<i>C. cirrhata</i>	RAS323 SV1	OR464379	—	—	USA	Swenie et al. 2024
<i>C. cirrhata</i>	RAS323 SV4	OR464382	—	—	USA	Swenie et al. 2024
<i>C. craterelloides</i>	TH 8234	JQ911749	—	—	Guyana	Smith et al. 2013
<i>C. cristata</i>	JKU8	JN228227	JN228227	—	USA	Uehling et al. 2012a
<i>C. dicymbetorum</i>	TH 8730	DQ056364	—	—	Guyana	Henkel et al. 2005
<i>C. effusa</i>	TH 8511	JN228231	—	—	Guyana	Uehling et al. 2012a
<i>C. guyanensis</i>	BRG TH9245	JQ677056	—	—	Guyana	Uehling et al. 2012a
<i>C. guyanensis</i>	TH 9257	JQ677057	—	—	Guyana	Uehling et al. 2012a
<i>C. humicola</i>	TH 8737	DQ056368	—	—	Guyana	Henkel et al. 2005

(Continues)

TABLE 1 | (Continued).

Species	Specimen voucher	GenBank accession no.			Country	References
		ITS	nLSU	mtSSU		
<i>C. kunmudlutsa</i>	TH 9206	HQ680358	—	—	Guyana	Henkel et al. 2011
<i>C. kunmudlutsa</i>	TH 8932	HQ680359	—	—	Guyana	Henkel et al. 2011
<i>C. livida</i>	MCCNNU00959	KU219603	—	—	China	He et al. 2016
<i>C. monodiminutiva</i>	TH 8738	DQ056365	—	—	Guyana	Henkel et al. 2005
<i>C. nigricans</i>	TH 8284	JN228224	—	—	Guyana	Uehling et al. 2012a
<i>C. pakaraimensis</i>	TH 9244	JQ677054	—	—	Guyana	Uehling et al. 2012b
<i>C. rosiramea</i>	BRG: TH8954	JQ677064	—	—	Guyana	Uehling et al. 2012b
<i>C. rugosa</i>	BIO 9668	EU862224	—	—	Spain	Olariaga et al. 2009
<i>C. rugosa</i>	BIO 11 162	EU862229	—	—	Spain	Olariaga et al. 2009
<i>C. samuelsii</i>	PDD: 89 881	GU222317	—	—	New Zealand	He et al. 2016
<i>C. samuelsii</i>	TENN065723	JQ638712	—	—	USA	Uehling et al. 2012a
<i>C. sprucei</i>	TH 9120	HQ680353	—	—	Guyana	Henkel et al. 2011
<i>C. subrugosa</i>	TN 43 395	JN228221	—	—	New Zealand	Uehling et al. 2012b
<i>C. subrugosa</i>	TENN043395	JQ638711	—	—	USA	Uehling et al. 2012b
<i>C. tepurumenga</i>	TH 8217	HQ680357	—	—	Guyana	Henkel et al. 2011
<b><i>C. mollis</i></b>	<b>CLZhao 29 645</b>	<b>PP356581</b>	<b>PP785345</b>	—	<b>China</b>	<b>Present study</b>
<b><i>C. mollis</i></b>	<b>CLZhao 29 648*</b>	<b>PP356582</b>	<b>PP785344</b>	<b>PP785354</b>	<b>China</b>	<b>Present study</b>
<b><i>C. mollis</i></b>	<b>CLZhao 29 684</b>	<b>PP356583</b>	—	—	<b>China</b>	<b>Present study</b>
<i>Craterellus badiogriseus</i>	IFP 019452	MW980548	MW979532	—	China	Cao et al. 2021
<i>C. badiogriseus</i>	IFP 019453	MW980549	MW979533	—	China	Cao et al. 2021
<i>C. croceialbus</i>	IFP 019455	MW980573	MW979530	—	China	Cao et al. 2021
<i>C. croceialbus</i>	IFP 019456	MW980574	MW979531	—	China	Cao et al. 2021
<i>C. fallax</i>	AFTOL-ID 286	DQ205680	AY700188	—	USA	Cao et al. 2021
<i>C. squamatus</i>	IFP 019458	MW980570	MW979535	—	China	Cao et al. 2021
<i>C. tubaeformis</i>	BB 07.293	—	KF294640	KF294571	Slovakia	Buyck et al. 2014
<i>C. tubaeformis</i>	TM 0268	—	DQ898741	DQ898651	Canada	Moncalvo et al. 2006
<i>Craterelus squamatus</i>	IFP 019457	MW980571	MW979534	—	China	Cao et al. 2021
<i>Dacrymyces australis</i> Lloyd	FPL8953	DQ205684	—	—	USA	Matheny et al. 2007
<i>Hydnum albomagnum</i>	AFTOL-ID 471	DQ218305	AY700199	—	USA	Matheny et al. 2007
<i>H. flavidocanum</i>	IFP 019460	MW980559	MW979545	MW980535	China	Cao et al. 2021
<i>H. flavidocanum</i>	IFP 019461	MW980560	MW979546	MW980536	China	Cao et al. 2021
<i>H. longibasidium</i>	IFP 019463	MW980555	MW979542	MW980534	China	Cao et al. 2021
<i>H. longibasidium</i>	IFP 019462	MW980556	MW979541	MW980533	China	Cao et al. 2021
<i>H. pallidocroceum</i>	IFP 019466	MW980568	MW979554	—	China	Cao et al. 2021
<i>H. pallidocroceum</i>	IFP 019467	MW980569	MW979555	—	China	Cao et al. 2021
<i>H. pallidomarginatum</i>	IFP 019469	MW980567	MW979553	MW980540	China	Cao et al. 2021
<i>H. pallidomarginatum</i>	IFP 019468	MW980566	MW979552	MW980539	China	Cao et al. 2021
<i>H. repandum</i>	H 6 003 710	NR_164553	—	—	Finland	Niskanen et al., 2018
<i>H. repandum</i>	LJU GIS 1337	AJ547871	—	—	Slovenia	Grebenc et al. 2009
<i>H. repandum</i>	MA-Fungi 3457	AJ547879	—	—	Spain	Grebenc et al. 2009

(Continues)

TABLE 1 | (Continued).

Species	Specimen voucher	GenBank accession no.			Country	References
		ITS	nLSU	mtSSU		
<i>H. sphaericum</i>	IFP 019470	MW980563	MW979549	—	China	Cao et al. 2021
<i>H. sphaericum</i>	IFP 019471	MW980565	MW979551	—	China	Cao et al. 2021
<i>H. ventricosum</i>	IFP 019478	MW980561	MW979547	MW980537	China	Cao et al. 2021
<i>H. ventricosum</i>	IFP 019479	MW980562	MW979548	MW980538	China	Cao et al. 2021
<i>Minimedusa polyspora</i>	SH-Ecto-3	MG833806	MG833798	—	China	Cao et al. 2021
<i>M. polyspora</i>	CBS 113.16	MH854646	MH866167	—	USA	Vu et al. 2019
<i>Multiclavula caput-serpentis</i>	KaiR699	MW386064	MW369074	—	Panama	Reschke et al. 2021
<i>M. corynoides</i>	Lutzoni 930 804–2	U66440	U66440	—	USA	Lutzoni 1997
<i>M. mucida</i>	RAS392	OR464363	OR460863	—	USA	Swenie et al. 2024
<i>M. vernalis</i>	Lutzoni 930 806–1	U66439	U66439	—	USA	Lutzoni 1997
<i>Neoburgoa freyi</i>	EZ4455	OR471314	OR471068	—	USA	Swenie et al. 2024
<i>N. freyi</i>	JL596-16	KX423755	KX423755	—	USA	Lawrey et al. 2016
<i>Rogersiomyces malaysianus</i>	LE-BIN 3507–10	KT779285	KU820986	—	Vietnam	Psurtseva et al. 2016
<i>R. malaysianus</i>	LE-BIN 3507	KT779284	KT779286	—	Vietnam	Psurtseva et al. 2016
<i>Sistotrema confuens</i>	PV174	AY463466	AY586712	—	Sweden	Larsson et al. 2004
<i>S. confuens</i>	AFTOL-ID 613	DQ267125	AY647214	—	USA	Cao et al. 2021
<i>S. subconfluens</i>	Dai 12 577	JX076812	JX076810	—	China	Zhou and Qin 2012
<i>Tulasnella asymmetrica</i>	AFTOL-1D1678	DQ520101	DQ520101	—	Germany	Cao et al. 2021

Note: Specimens from this study are in bold, – means not available and \*represents the ex-type specimens.

The sequences were aligned in MAFFT version 7 (Katoh et al. 2019) using the G-INS-i strategy. Alignments were manually adjusted using AliView version 1.27 (Larsson 2014). Alignments of different loci were combined with Mesquite version 3.51 (Maddison and Maddison 2018). Two datasets were used for the phylogenetic analyses. The first comprised a concatenated ITS + nLSU + mtSSU alignment including species from 13 genera within the *Cantharellales*, and was used to determine the genus-level placement of the studied material. The second dataset included ITS sequences of 25 *Clavulina* species and was used to evaluate the species-level identity and phylogenetic position of the studied specimens within that genus.

Maximum parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI) analyses were applied to the combined three datasets following a previous study (Dong et al. 2024). 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 pseudo-replicates (Felsenstein 1985). Descriptive tree statistics—tree length (TL), composite consistency index (CI), composite retention index (RI), composite rescaled consistency index (RC), and composite homoplasy index (HI)—were calculated for each maximum parsimonious tree generated. The combined dataset was also analysed

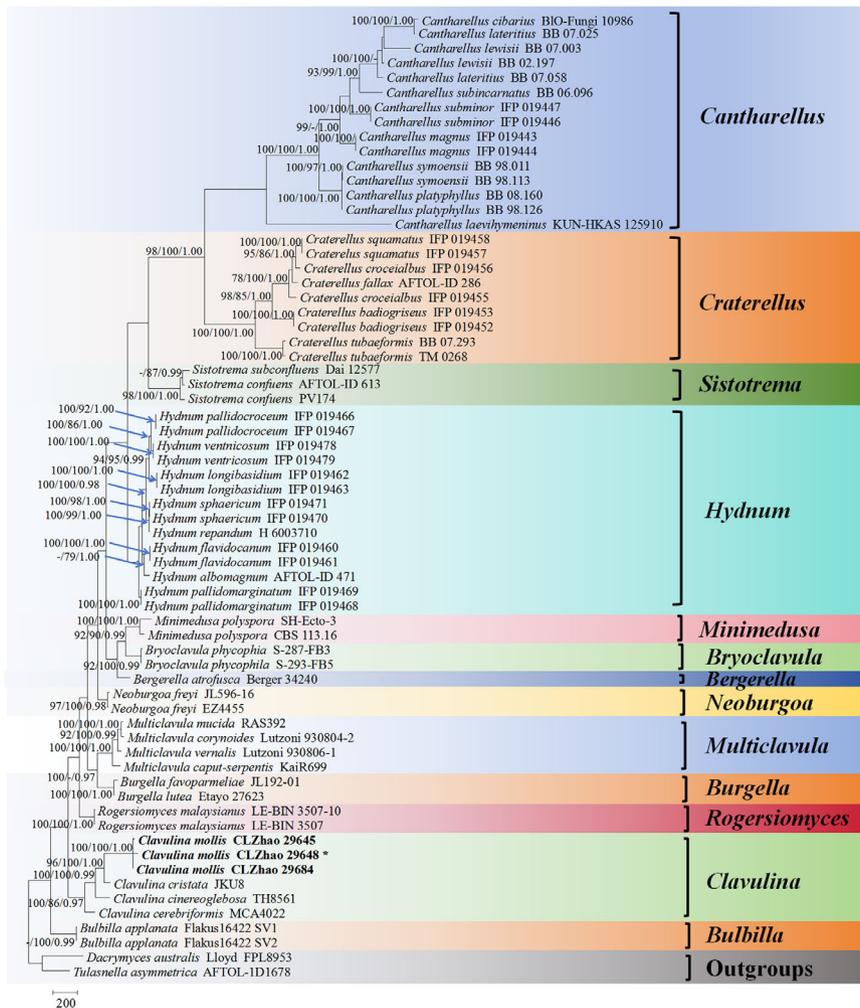
using maximum likelihood (ML) in RAxML-HPC2 through the CIPRES Science Gateway (Miller et al. 2012). Branch support (BS) for the ML analysis was determined by 1000 bootstrap pseudo-replicates.

MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each dataset for the purposes of Bayesian inference (BI), which 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 quarter of all the generations was discarded as burn-ins. A majority rule consensus tree was computed from the remaining trees. Branches were considered significantly supported if they received a maximum likelihood bootstrap support value (BS) of  $\geq 70\%$ , a maximum parsimony bootstrap support value (BT) of  $\geq 70\%$  or a Bayesian posterior probability (BPP) of  $\geq 0.95$ .

### 3 | Results

#### 3.1 | Molecular Phylogeny

The Bayesian phylogram for the combined dataset of ITS + nLSU + mtSSU is shown in Figure 1. The aligned dataset encompassed 66 specimens representing 44 taxa, including a new *Clavulina* species. *Dacrymyces australis* Lloyd and *Tulasnella asymmetrica* Warcup & P.H.B. Talbot were used as outgroup taxa in the phylogenetic analysis (Figure 1). The trees from the three

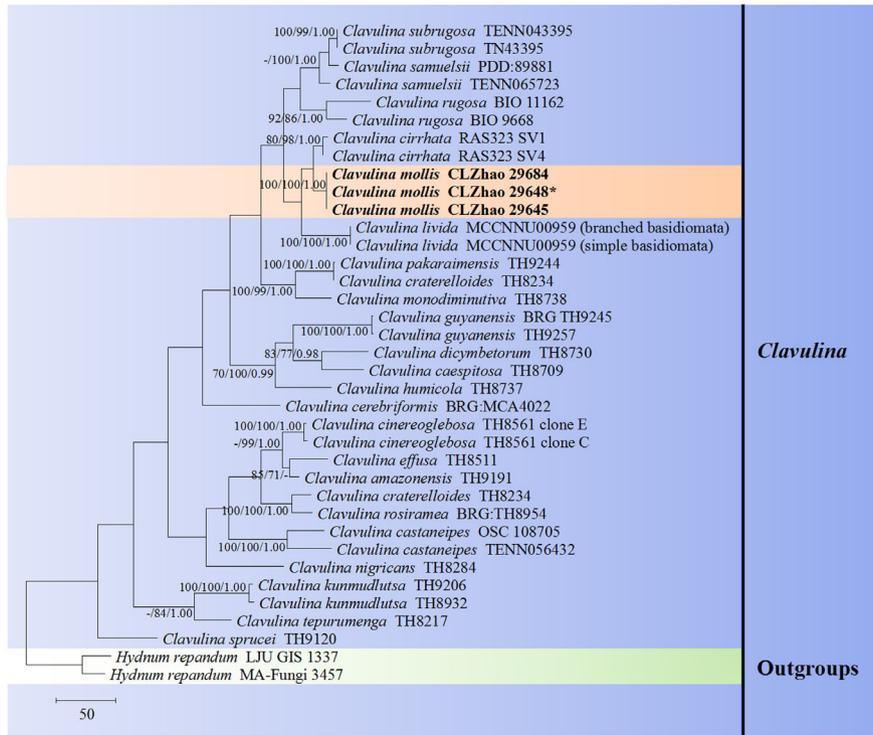


**FIGURE 1** | Maximum parsimony strict consensus tree illustrating the phylogeny of the new species and related species of the family *Hydnaceae* within the order *Cantharellales* based on ITS + nLSU + mtSSU sequences. Branches are labeled with maximum likelihood bootstrap values equal to or above 70%, parsimony bootstrap values equal to or above 70% and Bayesian posterior probabilities equal to or above 0.95. The new species is in bold.

analyses (ML, MP, and BI) showed identical topologies. Four Markov chains were run for 2 runs from random starting trees, each for 2 million generations. The dataset had an aligned length of 2677 characters (ITS = 875, LSU = 1221, mtSSU = 581), of which 562 characters are constant, 595 are variable and parsimony uninformative, and 1520 are parsimony informative. Maximum parsimony analysis yielded 2 equally parsimonious trees (TL = 7027, CI = 0.5234, HI = 0.4766, RI = 0.8100, RC = 0.4240). The best model for the ITS + nLSU + mtSSU dataset, estimated and applied in the Bayesian analysis, was GTR + I + G. Both Bayesian analysis and ML analysis resulted in a similar topology to MP analysis, with an average standard deviation of split frequencies = 0.008949 (BI), and the effective sample size (ESS) across the two runs is double the average ESS (avg ESS) = 214.14. The phylogram depicts an overall topology of the family *Hydnaceae* within the order *Cantharellales*, with the 13 known genera, viz. *Bergerella* Diederich & Lawrey, *Bryoclavula* H. Masumoto & Y. Degawa, *Bulbillia* Diederich, Flakus & Etayo, *Burgella* Diederich & Lawrey, *Cantharellus*, *Clavulina*, *Craterellus*, *Hydnum*, *Minimedusa* Weresub & P. M. LeClair, *Multiclavula* R. H. Petersen, *Neoburgoa* Diederich, E. Zimm. & Lawrey, *Rogersiomyces* J.L. Crane &

Schokn., and *Sistotrema* Fr., in which the new species *Clavulina mollis* is grouped into the genus *Clavulina*.

The aligned dataset encompassed 37 specimens representing 25 taxa, including the new species *Clavulina mollis*, and the outgroup taxa *Hydnum repandum* L. and *H. repandum* L. were retrieved from GenBank in ITS analysis following the previous study (Figure 2; He et al. 2016). The trees from the three analyses (ML, MP, and BI) showed identical topologies. Four Markov chains were run for 2 runs from random starting trees, each for 0.5 million generations. The dataset had an aligned length of 794 characters, of which 278 characters are constant, 126 are variable and parsimony uninformative, and 390 are parsimony informative. Maximum Parsimony analysis yielded 2 equally parsimonious trees (TL = 1742, CI = 0.4816, HI = 0.5184, RI = 0.5741, RC = 0.2765). The best model for ITS dataset, estimated and applied in the Bayesian analysis, was HKY + G. Both Bayesian analysis and ML analysis resulted in a similar topology to MP analysis, with an average standard deviation of split frequencies = 0.009052 (BI), and the effective sample size (ESS) across the two runs is double the average ESS (avg ESS) = 214.28. The phylogeny (Figure 2) based on ITS data shows



**FIGURE 2** | Maximum parsimony strict consensus tree illustrating the phylogeny of the new species and related species of *Clavulina* based on ITS sequences. Branches are labeled with maximum likelihood bootstrap values equal to or above 70%, parsimony bootstrap values equal to or above 70% and Bayesian posterior probabilities equal to or above 0.95, respectively. The new species is in bold.



**FIGURE 3** | Basidiomata of *Clavulina mollis* (holotype, CLZhao 29 648): (a) basidiomata on the ground. (b) Macroscopic characteristics of hymenophore. Bars: d = 1 cm, b = 1 mm.

that the new species *Clavulina mollis* clustered into the *Clavulina* clade and formed a strongly supported group with *C. cirrhata* (Berk.) Corner and *C. livida*.

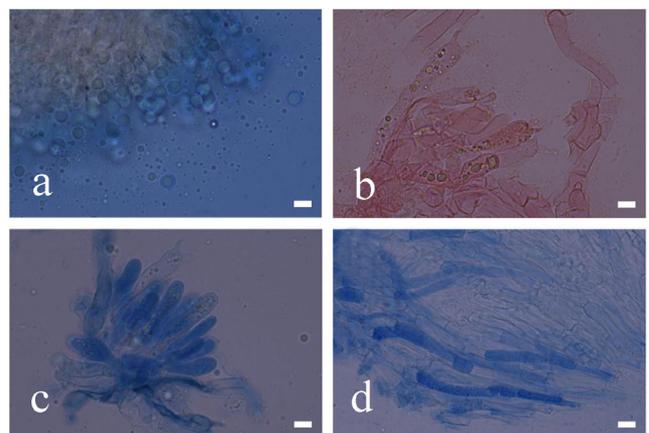
### 3.2 | Taxonomy

***Clavulina mollis*** Y.L. Deng & C.L. Zhao, **sp. nov.** Figures 3 and 4, 5.

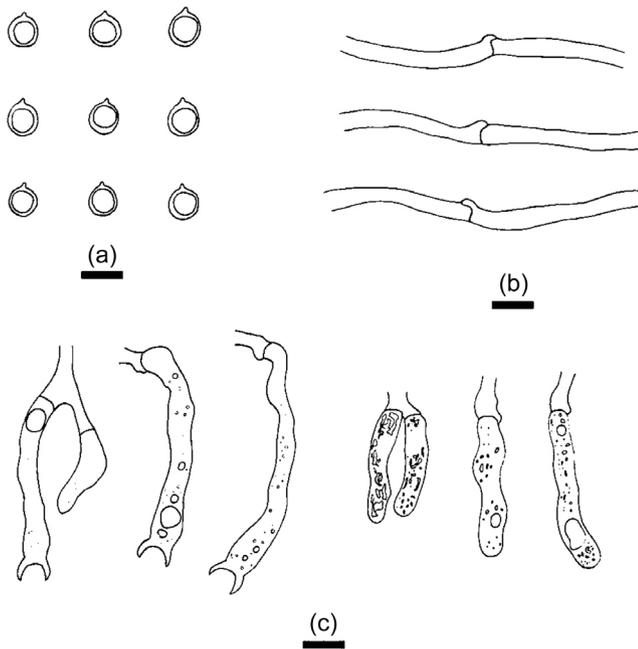
**Mycobank:** MB 852 411

**Etymology:** *mollis* (Lat.): referring to the soft basidiomata of the type specimens.

**Holotype:** China, Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates: 26°69' N, 104°03' E, altitude 2500 m asl., on the ground, leg. C.L. Zhao, 13 July 2023, CLZhao 29 648 (SWFC).



**FIGURE 4** | Sections of hymenium of *Clavulina mollis* (holotype, CLZhao 29 648): (a) basidiospores. (b) Basidia. (c) Basidioles. (d) Tramal hyphae. Bars: a–d = 10 µm.



**FIGURE 5** | Microscopic structures of *Clavulina mollis* (holotype, CLZhao 29 648): (a) Basidiospores. (b) Tramal hyphae. (c) Basidia and basidioles. Bars: a–c = 10  $\mu$ m.

**Description:** *Basidiomata* coralloid, mollis, gregarious in caespitose clusters, clusters 2–4 cm tall, 2–4 mm wide across branches. Individual basidioma up to 3.8 cm tall, up to 2 cm wide across branches, branching two to five times, polychotomous toward apices and irregularly dichotomous to polychotomous at the base, branches nearly clavate to subterete and somewhat flattened with age, branch tips sharply acuminate or cristate when young, becoming blunt with age. *Stipes* subclavate, immature to flattened with age, pale white to cream when fresh, grayish cream to smoky when drying. Hymenium amphigenous, creamy white to slightly smoky, flattened as the hymenium thickened with maturity.

*Hyphal system* monomitic; generative hyphae bearing clamp connections, thin-walled, colorless, 3.5–6.5  $\mu$ m in diameter. *Basidia* subclavate to subcylindrical, 37–55.5  $\times$  6–8  $\mu$ m, with two sterigmata, 5–7  $\mu$ m long, cornute; basidioles abundant, in shape similar to basidia, but slightly smaller. *Basidiospores* subglobose, colorless, thin-walled, smooth, with one large oleiferous guttule, IKI–, CB–, 7–8.5  $\times$  6–8  $\mu$ m, L = 7.88  $\mu$ m, W = 7.17  $\mu$ m, Q = 1.07–1.09 ( $n = 90/3$ ).

**Material examined:** China, Yunnan Province, Zhaotong, Wumengshan National Nature Reserve, GPS coordinates: 26°69' N, 104°03' E, altitude 2500 m asl., on the ground, leg. C.L. Zhao, 13 July 2023, CLZhao 29 645 (SWFC); Dehong, Yingjiang County, Tongbiguan Provincial Nature Reserve, GPS coordinates: 24°71' N, 97°94' E, altitude 1500 m asl., on the ground, leg. C.L. Zhao, 17 July 2023, CLZhao 29 684 (SWFC).

### 3.3 | Key to Known *Clavulina* Species in China

- 1 Tramal hyphae with brown walls.....2
- 1 Tramal hyphae with colorless walls.....6
- 2 Tramal hyphae without clamp connections.....*C. castaneipes*
- 2 Tramal hyphae with abundant clamp connections.....3

- 3 Basidiomata simple or sparsely branched.....4
- 3 Basidiomata repeatedly branched.....5
- 4 Hymenium light pink to light violet..... *C. purpurascens*
- 4 Hymenium light brownish gray to pale gray..... *C. curva*
- 5 Branches subterete to flattened.....*C. lilaceorosea*
- 5 Branches regularly branched two to four times...*C. yunnanensis*
- 6 Basidiomata simple or sparsely branched.....7
- 6 Basidiomata often with plentiful branches... 18
- 7 Basidiomata light bluish gray or gray to dark grayish violet...8
- 7 Basidiomata white to cream white or pale brown.....9
- 8 Basidiospores >10  $\mu$ m long..... *C. livida*
- 8 Basidiospores <10  $\mu$ m long..... *C. griseoviolacea*
- 9 Basidiospores <6.5  $\mu$ m long..... *C. minor*
- 9 Basidiospores >6.5  $\mu$ m long.....10
- 10 Basidiomata surface with rufescent tomentum or spines...11
- 10 Basidiomata surface smooth.....13
- 11 Basidiomata rufescent tomentose only at the base...*C. bessonii*
- 11 Basidiomata (almost) completely covered with spines or tomentum... 12
- 12 Basidiomata surface with spines; cystidia absent.... *C. spina*
- 12 Basidiomata surface with tomentum; cystidia present... *C. tomentosa*
- 13 Basidiomata smooth.....14
- 13 Basidiomata rugulose.....15
- 14 Context pale yellow..... *C. hainanensis*
- 14 Context pale red.....*C. pallidorosea*
- 15 Basidiomata not changing color when bruised..... *C. rugosa*
- 15 Basidiomata changes color when bruised... 16
- 16 Basidiomata turning pinkish then dark brown to black when dry.....*C. tropica*
- 16 Basidiomata white or dirty white when fresh.....17
- 17 Basidiomata cream white to light grayish orange when dry.....*C. chengdeensis*
- 17 Basidiomata changes orange to brownish orange when dry... *C. pallida*
- 18 Basidiomata bright yellow..... *C. flava*
- 18 Basidiomata white or gray or brown... 19
- 19 Branch tips blunt..... *C. cinerea*
- 19 Branch tips acuminate.....20
- 20 Branch tips cristate..... *C. coralloides*
- 20 Branch tips acute.....21
- 21 Stipe white to light brown or brown... *C. baiyunensis*
- 21 Stipe white or greyish white.....22
- 22 Basidiospores <6  $\mu$ m wide.....*C. eburnea*
- 22 Basidiospores >6  $\mu$ m wide.....23
- 23 Basidiomata lilac-white, lilac to orange-brown..... *C. thindii*
- 23 Basidiomata cream to smoke... *C. mollis*

## 4 | Discussion

The increasing use of molecular technologies has led to the continuous discovery and documentation of clavarioid-coralloid fungi worldwide (Cao et al. 2021; Deng et al. 2024; Swenie et al. 2025). In addition, global studies have explored the diversity, ecology, and systematics of clavarioid-coralloid fungi, with variations in focus among the taxa studied (Dai 2012; Hibbett 2016; Tibpromma et al. 2017; Wijayawardene et al. 2020; Cui et al. 2025).

A significant advance has been made in understanding the phylogenetic relationships among clavarioid-coralloid fungi through analyses based on morphology and multi-locus DNA sequence data (He et al. 2024; Liu et al. 2024). Previous studies indicated that clavarioid-coralloid fungi, including *Clavulina*, were highly diverse and distributed worldwide (Corner 1950). According to recent phylogenetic studies, the family *Hydnaceae* includes thirteen well-supported clades representing *Cantharellus*, *Craterellus*, *Hydnum*, *Sistotrema* sensu stricto, *Clavulina-Membranomyces*, *Bulbillia*, *Burgella-Sistotrema*, *Rogersiomyces*, *Multiclavula*, *Neoburgoa*, *Bryoclavula-Bergerella*, *Minimedusa*, and *Burgoa-Sistotrema*. The genus *Clavulina* belongs in the *Clavulina-Membranomyces* clade (González et al. 2016; Cao et al. 2021; Gao et al. 2024). In our phylogenetic analyses, DNA sequence data from three loci (ITS, nLSU, and mtSSU) revealed that the specimens studied represent a distinct, previously undescribed clade within *Clavulina*. The result shows that *Clavulina mollis* grouped with *C. cirrhata* and *C. livida*. However, morphologically, *C. cirrhata* is distinct from *C. mollis* by having ochraceous and white basidiomata, and develops a pale orange hymenium (Uehling et al. 2012b). The species *C. livida* differs from *C. mollis* by its puritan gray to glaucous gray colored basidiomata, larger basidia measuring  $51.5\text{--}76.7 \times 7.0\text{--}12.3 \mu\text{m}$ , and larger basidiospores ( $11.6\text{--}12.9 \times 10.7\text{--}12.5 \mu\text{m}$ ; He et al. 2016).

Morphologically, *Clavulina alba* Meiras-Ottoni, *C. crystallifera* Meiras-Ottoni, *C. cystidiata* Meiras-Ottoni, *C. simplex* Meiras-Ottoni, *C. studerae* Meiras-Ottoni, and *C. terminalis* Meiras-Ottoni are similar to the new species *C. mollis* by sharing generative hyphae with clamp connections. However, *C. alba* differs in its white to pale yellow basidiomata and longer, subglobose to broadly ellipsoid basidiospores ( $8\text{--}10 \times 6\text{--}8 \mu\text{m}$ ; De Meiras-Ottoni and Gibertoni 2023). The species *C. crystallifera* is separated from *C. mollis* by its light brown to dark brown basidiomata, longer basidia ( $50\text{--}65 \times 5\text{--}6 \mu\text{m}$ ), and larger, subglobose to ellipsoid basidiospores ( $7\text{--}10 \times 5\text{--}8.5 \mu\text{m}$ ; De Meiras-Ottoni and Gibertoni 2023). The taxon *C. cystidiata* is distinct from *C. mollis* by having longer basidia ( $35\text{--}57 \times 5\text{--}6 \mu\text{m}$ ; De Meiras-Ottoni and Gibertoni 2023). The species *C. simplex* can be distinguished by its longer, subglobose to broadly ellipsoid basidiospores ( $7\text{--}10 \times 5\text{--}7 \mu\text{m}$ ; De Meiras-Ottoni and Gibertoni 2023). The taxon *C. studerae* is separated from *C. mollis* by having larger basidia ( $40\text{--}60 \times 5\text{--}6 \mu\text{m}$ ) and longer, subglobose to broadly ellipsoid basidiospores ( $6.5\text{--}10 \times 5\text{--}8 \mu\text{m}$ ; De Meiras-Ottoni and Gibertoni 2023). The species *C. terminalis* is distinct from *C. mollis* by its narrower basidia ( $30\text{--}50 \times 5 \mu\text{m}$ ) and smaller, globose to subglobose basidiospores ( $6\text{--}8 \times 5\text{--}7 \mu\text{m}$ ; De Meiras-Ottoni and Gibertoni 2023). Furthermore, the taxon *C. amazonensis* Corner and *C. incrustata* Wartchow are similar to *C. mollis* by having subglobose basidiospores; however, *C. amazonensis* is separated from *C. mollis* by having dull brownish orange basidiomata, larger

basidia ( $46\text{--}74 \times 4.9\text{--}7.4 \mu\text{m}$ ), and smaller basidiospores ( $6\text{--}7.5 \times 5\text{--}7 \mu\text{m}$ ; Henkel et al. 2011). *Clavulina incrustata* is separated from *C. mollis* by its pale vinaceous basidiomata and amphigenous hymenium (De Meiras-Ottoni and Gibertoni 2023). Moreover, *Clavulina ossea* is similar to *C. mollis* by having generative hyphae with clamp connections and subglobose basidiospores, but *C. ossea* differs in its robust, fleshy, and pale lilac basidiomata when fresh, resembling bones when dry and smaller cylindrical basidia ( $21\text{--}44 \times 5\text{--}6 \mu\text{m}$ ; Tibpromma et al. 2017).

Clavarioid-coralloid fungi are an extensively studied group of basidiomycetes in ecological and biogeographical research. Among them, species of the order *Cantharellales* are particularly important and are widely distributed in forest ecosystems (2019a, 2019b, 2022; Hyde et al. 2024; Swenie et al. 2025). With the application of molecular phylogeny, we believe more species of fungi will be reported in the oriental realm, since clavarioid-coralloid fungi are a cosmopolitan group and they are abundant in Asia (Cui et al. 2025; Yang et al. 2025). The present study provides a detailed morphological description and phylogenetic analysis of a new fungal species, contributing to the knowledge of fungal diversity in Asia.

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## Disclosure

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

## Conflicts of Interest

The authors declare no conflicts of interest.

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