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Enlargement of the knowledge of *Cortinarius* section *Anomali* (Agaricales, Basidiomycota): introducing three new species from China

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Cortinarius is a globally distributed agaricoid genus that has been well studied in Europe and America with over 1,000 described species. However, as part of an ongoing effort to investigate the diversity of *Cortinarius* section *Anomali* in China, the resource investigation and classification research are still limited, and the species diversity has not been clarified by far. During the re-examination of the Chinese *Cortinarius* specimens, *C. cinnamomeolilacinus*, *C. subclackamasensis*, and *C. tropicus*, belonging to the sect. *Anomali*, were described in China as new to science based on morphological examination and phylogenetic analysis. The three new species are described and illustrated in detail according to the Chinese materials. The phylogenetic analysis based on internal transcribed spacer sequences confirmed the placement of the three species in the *Cortinarius* species are discussed.

KEYWORDS

fungi diversity, morphology, new taxa, phylogeny, taxonomy

1 Introduction

Cortinarius (Pers.) Gray, established based on *Cortinarius violaceus* (L.) Gray, is the largest genus of Agaricales with a worldwide distribution (Clements and Shear, 1931; Garnica et al., 2016; Varga et al., 2019). It is mainly marked by a fugacious veil enveloping the basidiocarp and a cortina, which initially covers the lamellae, but later vanishes in expanding basidiocarps (Stensrud et al., 2014). Macroscopically, members of this genus are highly variable, with their basidiocarps, lamellae, and basidiospores varying considerably in size, shape, or color (Peintner et al., 2004; Frøslev et al., 2006; Niskanen et al., 2009; Niskanen et al., 2013; Liimatainen et al., 2014; Liimatainen et al., 2015; Niskanen et al.,

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2016). Cortinarius species are widely reported in temperate and subtropical forests and form mycorrhizal associations with ectotrophic trees, such as plants of the Cistaceae, Fagaceae, Malvaceae, Nothofagaceae, Pinaceae, and Salicaceae families (Singer, 1986; Frøslev et al., 2006; Soop et al., 2018). With the advances in taxonomy and molecular biology techniques, increases have been detected in the number of species in the genus *Cortinarius*. To date, more than 5,000 scientific names in the genus have been published as listed in the Index Fungorum (http://www.indexfungorum.org/Names/names.asp, 2023), and about 2,000 species are estimated in the Dictionary of Fungi, 10th edition (Ammirati et al., 2007; Kirk et al., 2008; Brandrud et al., 2014).

Owing to the considerable morphological variations in this genus, the subdivision of *Cortinarius* into subgeneric units has caused some problems (Peintner et al., 2004). Morphologically, *Cortinarius* has been divided into several different subgenera and infrageneric sections by various taxonomists, which results in taxonomic chaos and indicates that morphology alone is insufficient for recognizing natural units in this group of fungi (Garnica et al., 2005; Garnica et al., 2009). In recent research, phylogenetic analyses of the genus have contributed to the delimitation of taxonomic entities within the genus (Peintner et al., 2003; Suarez-Santiago et al., 2009; Dima et al., 2016; Dima et al., 2021).

Cortinarius sect. Anomali Konrad & Maubl., a species-rich group, is established based on Cortinarius anomalus (Fr.) Fr. It is characterized by a telamonioid/sericeocyboid appearance, often with yellowish to brownish universal veil remnants on the stipe, typically young bluish lamellae, and subglobose to broadly ellipsoid or rarely ellipsoid, verrucose spores (Dima et al., 2016; Dima et al., 2021). Anomali was originally placed by Brandrud et al. (1989) as a section of subgenus Telamonia Melot but not belong to the subgenus Telamonia s. str. based on later phylogenetic data (Høiland and Holst-Jensen, 2000; Peintner et al., 2004; Garnica et al., 2005; Niskanen et al., 2009). Later, many species were added or transferred to sect. Anomali, causing confusions in the classification of sect. Anomali. No consensus on the content or placement of this section have been reached to date (Bidaud et al., 1992; Bidaud et al., 1994; Consiglio et al., 2005; Consiglio et al., 2006; Consiglio, 2012; Dima et al., 2016). For instances, C. spilomeus (Fr.) Fr. and C. bolaris (Pers.) Fr. have been included in the section, and sometimes have been separated in another sect. Spilomei (Moënne-Locc. & Reumaux) Consiglio, D. Antonini & M. Antonini (Dima et al., 2016). Some phylogenetic studies show that sect. Anomali is a monophyletic group in the genus Cortinarius, without any traditional subgenera (Dima et al., 2016; Dima et al., 2021). The classification of sect. Anomali has been studied previously and systematically in Europe and North America, but rarely in Asia and Africa (Kauffman, 1905; Murrill, 1946; Dima et al., 2016; Ammirati et al., 2017). In China, about 163 Cortinarius species, including dozens of new species, have been described in the past 10 years, with only three species belonging to the sect. Anomali (Wei and Yao, 2013; Xie et al., 2019; Luo and Bau, 2021; Xie et al., 2021; Xie, 2022). On this basis, more taxa of the genus are waiting to be discovered in China.

In this study, we conducted taxonomic and phylogenetic studies of *Cortinarius* sect. *Anomali* in China. Three new species were found during the intensive fieldwork and are described here based on their morphological and ecological characteristics, as well as phylogenetic evidence.

2 Materials and methods

2.1 Morphological studies

All specimens have been deposited in the National Institute of Occupational Health and Poison Control, Chinese Center for Disease Control (NIOHP, China CDC). Macro-morphological descriptions were based on field notes and dried specimens. Microscopic features were examined and described in 5% KOH, Congo Red, or Melzer's reagent and observed under a Nikon Eclipse 80i microscope (Nikon, Tokyo, Japan) with a magnification of up to ×1,000. Thirty basidiospores were measured per collection (excluding apiculus and ornamentation), and the averages (av. X) and quotients (av. Q = L/B) were calculated. Color terms are cited from Anonymous (1969) as well as Kornerup and Wanscher (1978).

2.2 DNA extraction and sequencing

A Phire[®] Plant Direct PCR Kit (Finnzymes Oy, Finland) was used to obtain PCR products from dried specimens, according to the manufacturer's instructions and as described previously by Li et al. (2015), with some modifications. The following primer pairs were used to amplify the internal transcribed spacer (ITS): ITS5 (5'-GGA AGT AAA AGT CGT AAC AAG G-3') and ITS4 (5'-TCC TCC GCT TAT TGATAT GC-3') (White et al., 1990). The PCR procedure was as follows: initial denaturation at 98 °C for 5 min, followed by 35 cycles at 98 °C for 5 s, 58 °C for 5 s, and 72 °C for 5 s, and a final extension of 72 °C for 10 min. The PCR products were purified and sequenced by Sangon Biotech, China. The newly generated sequences from this study have been deposited in GenBank and are listed in Table 1.

2.3 Phylogenetic analysis

New sequences generated in this study and additional sequences retrieved from GenBank (Table 1) were aligned using BioEdit 7.0.5.3 (Hall, 1999) and ClustalX 1.83 (Thompson et al., 1997), followed by manual adjustments. Sequences of *Cortinarius bolaris* (sect. *Bolares*) were used as outgroups (Hughes et al., 2009; Dima et al., 2021). The maximum likelihood (ML) and Bayesian inference (BI) methods were used for the phylogenetic analysis. The best-fit model was selected by ModelFinder (Kalyaanamoorthy et al., 2017), adopting Akaike information criterion (AIC). The ML analysis was

TABLE 1 Taxa information and GenBank accession numbers of the sequences used in this study.

Species	Specimen no.	Locality	Section	ITS no.
Cortinarius albidipes	WTU: JFA12420	Colorado, US	Anomali	MZ580486
C. albidipes	NYS-F-000129 (holotype)	New York, US	Anomali	MZ580485
C. albidipes	MQ18-CMMF001826	Québec, Canada	Anomali	MN750945
C. albidipes	HRL0614	Québec, Canada	Anomali	KJ705108
C. albidipes	CNV98	New Hampshire, US	Anomali	MT345274
C. albidoavellaneus	MICH10313 (holotype)	Michigan, US	Anomali	MZ580483
C. albocyaneus	CFP1482	Italy	Anomali	KX302202
C. albocyaneus	CFP1177 (epitype)	Sweden	Anomali	KX302206
C. albocyaneus	NYS-F-000864 (holotype)	New York, US	Anomali	MZ580482
C. albomalus	iNAT59505932	New Jersey, US	Anomali	MW305253
C. albomalus	H7000816 (holotype)	Ontario, Canada	Anomali	MZ568645
C. albomalus	HRL2777	Ontario, Canada	Anomali	MN751632
C. anocorium	H7068022 (holotype)	Florida, US	Anomali	MZ568646
C. anomalodelicatus	TN11-241	Alaska, US	Anomali	MZ580481
C. anomalodelicatus	JFA8146 (holotype)	Colorado, US	Anomali	MZ580480
C. anomalomontanus	JFA9919 (holotype)	Wyoming, US	Anomali	MZ580478
C. anomalomontanus	JFA9973	Wyoming, US	Anomali	MZ580479
C. anomalopacificus	JFA11887	California, US	Anomali	MZ580471
C. anomalopacificus	DBB11745 (holotype)	California, US	Anomali	MZ663774
C. anomalopacificus	DBB27748	California, US	Anomali	MZ663775
C. anomalopacificus	TN12-271	California, US	Anomali	MZ663776
C. anomalopacificus	TN12-301	California, US	Anomali	MZ663777
C. anomalopacificus	TN12-093	California, US	Anomali	MZ580473
C. anomalopacificus	TN12-074	California, US	Anomali	MZ580469
C. anomalopacificus	TN12-253	California, US	Anomali	MZ580468
C. anomalopacificus	TN12-091	California, US	Anomali	MZ580472
C. anomalopacificus	TN12-161	California, US	Anomali	MZ580474
C. anomalopacificus	TN12-164	California, US	Anomali	MZ580475
C. anomalovelatus	JFA13109 (holotype)	Washington, US	Anomali	FJ717605
C. anomalovelatus	DBB23800	Oregon, US	Anomali	MZ663776
C. anomalovelatus	PK4741	British Columbia, Canada	Anomali	FJ039655
C. anomalovelatus	JFA13109 (holotype)	Washington, US	Anomali	KJ019014
C. anomalus	NL-5414	Massachusetts, US	Anomali	MZ663777
C. anomalus	CNV9	New Hampshire, US	Anomali	MT345186
C. anomalus	MQ18-HL1492-QFB30079	Québec, Canada	Anomali	MN750971
C. anomalus	TENN067720	North Carolina, US	Anomali	MZ663778
C. anomalus	TENN067730	North Carolina, US	Anomali	MZ663779
C. anomalus	CFP1154 (neotype)	Sweden	Anomali	KX302224
C. barlowensis	TN07-366	Washington, US	Anomali	KJ019015

Species	Specimen no.	Locality	Section	ITS no.
C. barlowensis	MN	British Columbia, Canada	Anomali	FJ157009
C. barlowensis	JFA13140 (holotype)	Washington, US	Anomali	FJ717554
C. bolaris	3861	Québec, Canada	Bolares	KJ705110
C. bolaris	CFP1008 (neotype)	Sweden	Bolares	KX302233
C. bolaris	TENN61650	Tennessee, US	Bolares	FJ596851
C. brevissimus	Cort H2QY2	New York, US	Anomali	JX030219
C. brevissimus	NYS-F-000541 (holotype)	New York, US	Anomali	MZ580467
C. caeruleoanomalus	JFA13084 (holotype)	Tennessee, US	Anomali	MZ663780
C. caeruleoanomalus	TENN068383	North Carolina, US	Anomali	KY744156
C. caesiellus	MICH10325 (holotype)	Michigan, US	Anomali	MZ580484
C. caesiifolius	SAT13-298-15	Oregon, US	Anomali	MZ048733
C. caesiifolius	MICH10326 (holotype)	Washington, US	Anomali	MZ580462
C. caesiifolius	TN12-136	California, US	Anomali	MZ580465
C. caesiifolius	TN07-489	Washington, US	Anomali	MZ580466
C. caesiifolius	DBB37600	Minnesota, US	Anomali	MZ663781
C. caesiifolius	JMB10-20-2007-15	Washington, US	Anomali	FJ717517
C. caesiifolius	TN12-066	California, US	Anomali	MZ580463
C. caesiifolius	TN12-136	California, US	Anomali	MZ580465
C. caesiifolius	TN12-118	California, US	Anomali	MZ580464
C. camphoratus	EH23	British Columbia, Canada	Camphorati	FJ717505
C. caninus	JFA7985	Ontario, Canada	Anomali	MZ580454
C. caninus	NS18	California, US	Anomali	MZ663782
C. caninus	JFA10347	Wyoming, US	Anomali	MZ580459
C. caninus	JFA9425	Wyoming, US	Anomali	MZ580461
C. caninus	JFA12434	Wyoming, US	Anomali	MZ580456
C. caninus	JFA9470	Wyoming, US	Anomali	MZ580457
C. caninus	JFA10348	Wyoming, US	Anomali	MZ580460
C. caninus	JFA8009	Minnesota, US	Anomali	MZ580455
C. caninus	JFA9920	Wyoming, US	Anomali	MZ580458
C. caninus	CFP627 (epitype)	Sweden	Anomali	KX302250
C. caninus	TH4Cc	British Columbia, Canada	Anomali	KF753582
C. cinnamomeolilacinus	Li 140805-18	Yunnan, China	Anomali	OQ913389*
C. cinnamomeolilacinus	tcmb 005	Yunnan, China	Anomali	OQ913388*
C. cinnamomeolilacinus	TCWH 007 (holotype)	Yunnan, China	Anomali	OQ913384*
C. cinnamomeolilacinus	LLLJ 20170805-002	Yunnan, China	Anomali	OQ913386*
C. cinnamomeolilacinus	WX 20170922065	Yunnan, China	Anomali	OQ913392*
C. cinnamomeolilacinus	LYWF015	Yunnan, China	Anomali	OQ913387*
C. cinnamomeolilacinus	Li 180825-21	Yunnan, China	Anomali	OQ913390*
C. cinnamomeolilacinus	YNLF20220814-155	Yunnan, China	Anomali	OQ913393*

Species	Specimen no.	Locality	Section	ITS no.
C. cinnamomeolilacinus	Li 130908-29	Yunnan, China	Anomali	OQ913391*
C. cinnamomeolilacinus	Li 161015-10	Guizhou, China	Anomali	OQ913385*
C. clackamasensis	JFA11616 (holotype)	Oregon, US	Anomali	MZ580452
C. clackamasensis	OSC114858	Oregon, US	Anomali	EU669315
C. clackamasensis	TN11-451	Washington, US	Anomali	MZ580453
C. clackamasensis	OSC109672	Oregon, US	Anomali	EU652360
C. clintonianus	DBB21645	British Columbia, Canada	Anomali	MZ663783
C. clintonianus	JFA8329	Ontario, Canada	Anomali	MZ580451
C. clintonianus	MIN896348	Minnesota, US	Anomali	MZ663784
C. clintonianus	NYS-F-000786 (holotype)	New York, US	Anomali	MZ580450
C. clintonianus	MQ18-CMMF002618	Québec, Canada	Anomali	MN751121
C. clintonianus	136C	Michigan, US	Anomali	FJ769528
C. clintonianus	SDL13	British Columbia, Canada	Anomali	KM403009
C. deceptivus	iNAT56430786	New York, US	Anomali	MT939445
C. deceptivus	NL-5180	New York, US	Anomali	MZ663785
C. deceptivus	WTU-F-69333	New Hampshire, US	Anomali	MZ663786
C. deceptivus	WTU-F-69313	Massachusetts, US	Anomali	MZ663787
C. deceptivus	MICH10343 (syntype)	New York, US	Anomali	MZ663788
C. durifoliorum	PDD101829 (holotype)	New Zealand	Anomali	KJ635210
C. dysodes	PDD70499 (holotype)	New Zealand	Camphorati	GU233340
C. epsomiensis	K(M)74963 (holotype)	UK	Anomali	MK010952
C. epsomiensis	TN06-165	Finland	Anomali	KX302258
C. eunomalus	PDD94040 (holotype)	New Zealand	incertae sedis	JQ287690
C. ferrusinus	JB8106 13 (holotype)	Spain	Spilomei	KY657254
C. harvardensis	NL-5415 (holotype)	Massachusetts, US	Anomali	MZ663789
C. harvardensis	MQ18-HL1449-QFB30070	Québec, Canada	Anomali	MN751560
C. harvardensis	MQ17058-QFB29566	Québec, Canada	Anomali	MN751559
C. harvardensis	clone ads9.e	Nova Scotia, Canada	Anomali	MK131480
C. holophaeus	UBC-F17161	British Columbia, Canada	Anomali	GQ159904
C. holophaeus	UBC-F17157	British Columbia, Canada	Anomali	GQ159900
C. huddartensis	DBB12118 (holotype)	California, US	Anomali	MZ663790
C. huddartensis	src174	California, US	Anomali	DQ974719
C. ionomataius	PDD89089 (holotype)	New Zealand	incertae sedis	GU222303
C. jonimitchelliae	HL03-339 (holotype)	Sweden	Anomali	KX302253
C. kranabetteri	TN11-287 (holotype)	Alberta, Canada	Anomali	MZ580449
C. kranabetteri	UBC-F16436	British Columbia, Canada	Anomali	FJ039657
C. kranabetteri	UBC-F16435	British Columbia, Canada	Anomali	FJ039656
C. latiodistributus	JFA13487	Washington, US	Anomali	MZ663793
C. latiodistributus	YM187	Japan	Anomali	AB848436

Species	Specimen no.	Locality	Section	ITS no.
C. latiodistributus	OSC115143	Washington, US	Anomali	EU652359
C. latiodistributus	DB6359	Norway	Anomali	MZ663792
C. latiodistributus	TN02-490	Finland	Anomali	MZ580448
C. latiodistributus	SMIA46	British Columbia, Canada	Anomali	FJ039658
C. latiodistributus	OSC114595	Washington, US	Anomali	EU837213
C. latiodistributus	DB6139 (holotype)	Sweden	Anomali	MZ663791_
C. latiodistributus	SMI16	British Columbia, Canada	Anomali	FJ157134
C. lepidopus	DB6253	Hungary	Anomali	MZ663794
C. lepidopus	170817-24	Heilongjiang, China	Anomali	OQ913382*
C. lepidopus	170817-29	Heilongjiang, China	Anomali	OQ913383*
C. lividomalvaceus	JMT-15102001 (holotype)	France	Anomali	KY315416
C. modestus	TN10-035	Québec, Canada	Anomali	MZ580447
C. modestus	MQ17140-QFB29648	Québec, Canada	Anomali	MN751561
C. modestus	NYS-F-001966 (holotype)	New York, US	Anomali	MZ580446
C. modestus	MQ17272-QFB29780	Québec, Canada	Anomali	MN751565
C. modestus	MQ18-HL0629-QFB30005	Québec, Canada	Anomali	MN751564
C. modestus	2313-QFB25737	Québec, Canada	Anomali	KJ705109
C. nettieae	JFA9613 (holotype)	Washington, US	Anomali	MZ580442
C. nettieae	JFA8747	Oregon, US	Anomali	MZ580443
C. nettieae	TN09-167	Oregon, US	Anomali	MZ580444
C. nettieae	TN09-176	Oregon, US	Anomali	MZ580445
C. nettieae	DAVFP27503	British Columbia, Canada	Anomali	EU821675
C. ochraceodiscus	DJM2195 (holotype)	Minnesota, US	Anomali	MZ663795
C. ochraceodiscus	DJM2194	Minnesota, US	Anomali	MZ663796
C. pelerinii	XC2012-21 (holotype)	France	Anomali	MH784627
C. perrotensis	TENN071126 (holotype)	Québec, Canada	Anomali	KX897405
C. perviolaceus	FN05_2	New York, US	Anomali	KU878589
C. perviolaceus	HBK-M11-2	Tennessee, US	Anomali	MG982536
C. perviolaceus	FLAS-F61753	Florida, US	Anomali	MH281882
C. perviolaceus	JFA9132	Florida, US	Anomali	MZ580441
C. perviolaceus	JFA9124	Florida, US	Anomali	MZ580439
C. perviolaceus	FLAS-F32992 (holotype)	Florida, US	Anomali	MZ580438
C. perviolaceus	JFA13070	Tennessee, US	Anomali	MZ663799
C. perviolaceus	JFA9128	Florida, US	Anomali	MZ580440
C. perviolaceus	3Bart56R	New Hampshire, US	Anomali	HQ022110
C. perviolaceus	NL-5173	Massachusetts, US	Anomali	MZ663798
C. perviolaceus	FLAS-F61648	Florida, US	Anomali	MH212024
C. perviolaceus	WU-Myc 44566	Georgia, US	Anomali	MZ663797
C. perviolaceus	FLAS-MES-2177	Florida, US	Anomali	MT415970

Species	Specimen no.	Locality	Section	ITS no.
C. putorius	TN12-230	California, US	Camphorati	KR011123
C. rarus	JLF8707	Oregon, US	Anomali	MW341328
C. rarus	JLF8771	Oregon, US	Anomali	MW341331
C. rarus	JLF3304	California, US	Anomali	MF135162
C. rarus	ADP-140531-1	Washington, US	Anomali	MZ663801
C. rarus	DBB04712 (holotype)	California, US	Anomali	MZ663800
C. rattinoides	PDD88283 (holotype)	New Zealand	Anomali	JX000375
C. sclerophyllarum	HO-A20430A6 (paratype)	Australia	Anomali	AY669637
C. sericeolazulinus	JFA12053 (holotype)	Costa Rica	Anomali	EF420146
C. spilomeus	CFP1137 (neotype)	Sweden	Spilomei	KX302267
C. spilomeus	SMI297	British Columbia, Canada	Spilomei	FJ039659
C. subclackamasensis	BJMTG20170830-34	Beijing, China	Anomali	OQ913395*
C. subclackamasensis	20190822-11	Hebei, China	Anomali	OQ913396*
C. subclackamasensis	Li 170818-16 (holotype)	Heilongjiang, China	Anomali	OQ913394*
C. subclackamasensis	Li 170818-01	Heilongjiang, China	Anomali	OQ913397*
C. subclackamasensis	YJ4	China	Anomali	OM867684
C. subclackamasensis	HBAU15437	China	Anomali	MW862347
C. subclackamasensis	HBAU15679	China	Anomali	MZ145077
C. subclackamasensis	HBAU15672	China	Anomali	MZ145076
C. subclackamasensis	110116MFBPC490	China	Anomali	MW554249
C. suecicolor	PDD74698 (holotype)	New Zealand	Anomali	JX000360
C. tabularis	CFP949 (epitype)	Sweden	Anomali	KX302275
C. tabularis	IK98-1190	Finland	Anomali	KX302269
C. tabularis	TN11-219	Alaska, US	Anomali	MZ580437
C. tasmacamphoratus	HO A20606A0	Tasmania, Australia	Camphorati	AY669633
C. tasmacamphoratus	BH2055F	Tasmania, Australia	Camphorati	JF960672
C. tetonensis	ME12-B10	Alaska, US	Anomali	JX436875
C. tetonensis	ME12-B4	Alaska, US	Anomali	JX436874
C. tetonensis	ME12-D3	Alaska, US	Anomali	JX436876
C. tetonensis	JFA10350 (holotype)	Wyoming, US	Anomali	MZ580436
C. tetonensis	JFA10349	Wyoming, US	Anomali	U56024
C. tetonensis	36_N343	Svalbard, Norway	Anomali	HQ445618
C. tristis s. Garnica	TUB011917	Chile	Anomali	AY669648
C. tropicus	Li 150728-63	Yunnan, China	Anomali	OQ913381*
C. tropicus	tcqushi006 (holotype)	Yunnan, China	Anomali	OQ913379*
C. tropicus	Li 150728-56	Yunnan, China	Anomali	OQ913380*
Cortinarius aff. nettiae	MQ17280-QFB29788	Québec, Canada	Anomali	MN750925
Cortinarius aff. nettiae	MQ17300-QFB29808	Québec, Canada	Anomali	MN750926
Cortinarius LHJ sp. 1	SC20170921-025	Guizhou, China	Anomali	OQ920005*

Species	Specimen no.	Locality	Section	ITS no.
Cortinarius LHJ sp. 2	190527-01	Tibet, China	Anomali	OQ920004*
Cortinarius LHJ sp. 3	170805-35	Yunnan, China	Anomali	OQ920003*
Cortinarius sp.	Pj3-mOTU024	Japan	Anomali	LC260432
Cortinarius sp. 1	7-70M6	California, US	Anomali	JQ393041
Cortinarius sp. 2	YM73	Japan	Anomali	LC175532
Cortinarius sp. 3	GO-2010-171	Mexico	Anomali	KC152091
Cortinarius sp. 4	F18506	British Columbia, Canada	Anomali	FJ157104
Cortinarius sp. 5	TN10-141	Québec, Canada	Anomali	MZ821030
Cortinarius sp. 6	OUC97234	British Columbia, Canada	Anomali	DQ097877
Cortinarius sp. 6	HRL1598-QFB32934	Québec, Canada	Anomali	MW845268
Cortinarius sp. 7	YM1162	Japan	Anomali	LC175062
Cortinarius sp. 8	OUC97199	British Columbia, Canada	Anomali	DQ093855
Cortinarius sp. 9	JLP2431	Oregon, US	Anomali	DQ377379
Cortinarius sp. 10	QFB28611	Québec, Canada	Anomali	MN992356
Cortinarius sp. 11	Pdmt24	Japan	Anomali	AB251830
Cortinarius sp. 12	HV_D8	Alaska, US	Anomali	JX630733
Cortinarius sp. 12	ME12-D2	Alaska, US	Anomali	JX436862
Cortinarius sp. 12	MEN-JG-096	Svalbard, Norway	Anomali	JF304376
Cortinarius sp. 13	Russell iNaturalist 8602253	Indiana, US	Anomali	MZ710565
Cortinarius sp. 13	YM873	Japan	Anomali	AB848465
Cortinarius sp. 15	MQ21-HRL2477-QFB32937	Québec, Canada	Anomali	MW845269
Cortinarius sp. 15	PERTH06437109	Australia	Anomali	MG553013
Cortinarius sp. 16	PDD10596	New Zealand	Anomali	MH101576
Cortinarius sp. 17	NVE433	Colombia	Anomali	KF937326
Cortinarius sp. 17	NVE219	Colombia	Anomali	KF937328
Cortinarius sp. 18	PERTH06659462	Australia	Anomali	MG553083
Cortinarius sp. 19	BH3573F	Tasmania, Australia	Camphorati	JF960738
Cortinarius sp. 20	SWUBC741	British Columbia, Canada	Spilomei	DQ481671
Cortinarius sp. 20	WUBC747	British Columbia, Canada	Spilomei	DQ481752
Cortinarius sp. 21	PDD:107722	New Zealand	incertae sedis	KT875175

New species are in bold. Newly generated sequences are marked with asterisk (*).

carried out using RAxML 8.2.12 (Stamatakis, 2006; Silvestro and Michalak, 2012), and the BI tree reconstruction was reconstructed using MrBayes 3.2.5 (Ronquist et al., 2012). Four Markov chains were run for two runs from random starting trees for 10 million generations, and the trees were sampled every 1,000 generations. The burn-in was set to discard 25% of the trees. A majority rule consensus tree of all remaining trees was calculated. The sequence alignment was deposited at TreeBase (submission ID: 30414). Branches that received bootstrap supports for ML and Bayesian posterior probabilities (BPP) greater than or equal to 75% (ML) and 0.95 (BPP) were considered significantly supported.

3 Results

3.1 Phylogeny

The ITS dataset comprised 229 fungal collections representing approximately 81 taxa of the genus *Cortinarius*. ModelFinder suggested that GTR + I + G was the best-fit model of nucleotide evolution for BI. The Bayesian analysis resulted in a concordant topology with an average standard deviation of split frequencies of 0.005575. The ML and BI analyses resulted in nearly identical topologies, and thus only the ML tree is presented with the bootstrap supports for ML and BPP when they were greater than or equal to 50% and 0.90, respectively.

Our phylogeny, which is inferred from ITS sequences (Figure 1), is similar to those of Dima et al (Dima et al., 2016; Dima et al., 2021). The phylogenetic analysis showed five sections, and each section formed separate monophyletic lineages with strong statistical support. Section *Anomali* formed a distinct highly supported clade (ML = 99 and BPP = 1) and was separated from other sections. Three new species, namely, *C. cinnamomeolilacinus* (ML = 98 and BPP = 1),

C. subclackamasensis (ML = 86 and BPP = 0.99), and *C. tropicus* (ML = 100 and BPP = 1), nested within the sect. *Anomali* clade, and formed an independent lineage with high statistical supports, respectively. It is worth noting that collections of *C. cinnamomeolilacinus* had genetic distances in our phylogeny. However, there were only four base pair differences between them, which were below 1.5% nucleotide differences in the ITS regions. Morphologically, there were no obvious differences of these *C. cinnamomeolilacinus* collections.



FIGURE 1

Maximum likelihood (ML) tree illustrating the phylogeny of *Cortinarius* section *Anomali* based on ITS sequences. Branches are labeled with ML bootstrap > 50% and Bayesian posterior probabilities (BPP) > 0.90, respectively. New species are highlighted in bold.

3.2 Taxonomy

Cortinarius cinnamomeolilacinus Q.Y. Zhang, Jing Si & Hai J.

Li, sp. nov. Figure 2.

MycoBank: 848613

Diagnosis. — This species is characterized by its small basidiomata, more or less hygrophanous, lilac pileal surface with cinnamon buff to brownish cinnamon center, and pale gray to whitish toward margin, subglobose to broadly ellipsoid basidiospores (7–8.5 × 5.8–6.8 μ m); it is gregarious on ground dominant with Fagaceae or Pinaceae.

Type. — China, Yunnan Province, Baoshan, Tengchong, Wuhe Town, Lushan, Alt: 1989 m, N: 24°54′06.98″, E: 98°36′30.37″, on ground dominant with Fagaceae, 8 August 2016, TCWH 007 (holotype), and GenBank accession number for ITS: OQ913384.

Etymology. — *cinnamomeolilacinus* refers to its more or less lilac pileal surface with a cinnamon center.

Habitat and distribution. — Scattered or gregarious on ground dominant with Fagaceae or Pinaceae. Currently, it is only found in tropical Guizhou and Yunnan (nine collections) in summer and autumn.

Macrostructures. — Basidiomata small. Pileus 15-52 mm in diam., hemispheric when young, then convex to plano-convex, some with a low umbo, margin narrowly when young, surface smooth to finely felty, color evenly pale silvery gray to lilac [15A(2 - 4)], the disc slightly more brownish, cinnamon buff, cinnamon to brownish cinnamon [5B(4-5)], pale gray to whitish (1A1-1B1) toward margin, even to rugulose, hygrophanous. Lamellae adnate with decurrent tooth to slightly adnexed, close, violet (16A4-16A5) when young, then grayish violet [16B4-16C5], pale silvery gray to pale drab gray (16B2-16D2), finally pale brown to cinnamon [6D(4 - 8)]. Stipe 30- to 70- mm long, apex 4-6 mm in diam., and base 5 - 10 mm in diam., usually clavate to cylindrical, even or slightly bulbous at base, fragile, shiny, covered with white fibrillose, apex



FIGURE 2

Basidiomata and microscopic structures of *Cortinarius cinnamomeolilacinus*. (A-G) Basidiomata (A, B) TCWH007; (C, D) Li 180825-21; (E) LLLJ20170805-002; (F) tcmb005; (G) 180825-21), (H) Basidiospores, (I-J) Basidia and basidioles, (K) Pileipellis, (L) Hypodermium of pileipellis, and (M) Context hyphae.

violet [16A(4-5)] when young, later pale brownish (6B2–6D2), other part pale silvery gray [15A(2-3)], pale white veil (1A2) usually sparse, forming yellow [3A(3-4)] floccose-girdles on the stipe, often becoming pale yellow [4B(3-5)], sometimes indistinct, basal mycelium white (1A1). Context in pileus solid, firm, sometimes hollow in stipe, pale silvery gray [16B4-16C5] when fresh, finally pale brown to cinnamon in age [6D(4-8)]. Odor and taste of context strongly fungoid.

Microstructures. — Basidiospores [150/5/5] (6.8–) 7–8.5 (–8.8) × (5.5–) 5.8–6.8 (–7) μm, av. 7.7 × 6.1 μm, Q = 1.22-1.29, av. Q = 1.26, subglobose to broadly ellipsoid, buff to cinnamon-buff, coarsely verrucose, non-dextrinoid. Basidia 4-spored, 29-33 × 6-7 μm, clavate, colorless, or yellowish. Lamella trama hyphae smooth, parallel, 5- to 12- μm wide. Lamellae edge fertile, with some small clavate sterile cells. Pileipellis duplex: Epicutis thin to ± well developed, hyphae ± cylindrical, moderately to strongly interwoven, 5- to 8- μm wide, hyaline or yellowish, smooth to encrusted; hypocutis ± cellular or hyphae more interwoven and radially arranged, cylindrical to enlarged, hyaline to yellowish, smooth to encrusted, (3.5) 4–18 (20) μm wide. Clamp connections present.

Remarks. — Cortinarius albomalus Liimat. & Niskanen and C. cinnamomeolilacinus have similar basidiomata. However, C. albomalus has smaller basidiospores $(6.5-7.5 \times 5.5-6 \text{ }\mu\text{m})$ and is distributed in North America (Dima et al., 2021; Liimatainen and Niskanen, 2021). Cortinarius pastoralis Soop, H. Lindstr., Dima, Niskanen, Liimat. & Kytöv. and C. cinnamomeolilacinus share pale buff or brownish pilei, but C. pastoralis has larger basidiospores $(8.5-9 \times 7-8 \mu m; Dima et al., 2016)$. Cortinarius albocyaneus Fr. is similar to C. cinnamomeolilacinus with grayish ochraceous to whitish pilei, but C. albocyaneus has larger basidiomata (40-70 mm) and basidiospores $(8.5-9.0 \times 6.0-7.5 \,\mu\text{m})$, is found in Europe, and is common in northeastern North America (Dima et al., 2021). Cortinarius anomalovelatus Ammirati, Berbee, E. Harrower, Liimat. & Niskanen has gravish-to-white basidiomata and subglobose to broadly ellipsoid basidiospores, which are similar to those of C. cinnamomeolilacinus, but C. anomalovelatus has a heavier universal veil and a gravish-blue to violet pileal surface, and is usually found in western North America (Dima et al., 2021).

Additional specimens (paratypes) examined. — China, Guizhou Province, Liupanshui, Lingshan Temple, on ground of Fagaceae, Alt: 1929 m, N: 26°37'35.94", E: 104°48'54.95", October 15, 2016, Li 161015-10; Yunnan Province, Baoshan, Longling County, Longjiang Town, Laohuangtian, on ground dominant with Fagaceae, Alt: 1773 m, N: 24°41'31.01", E: 98°42'55.24", 5 August 2017, LLLJ 20170805-002; Longyang District, Wafang Town, Dapingdi, on ground of Pinus yunnanensis, Alt: 1921.9 m, N: 25° 21'35.82", E: 99°4'45.73", 6 August 2018, LYWF015; Tengchong, Mangbang Town, Hongdoushu, on ground dominant with Fagaceae, Alt: 1772 m, N: 24°54′52″, E: 98°37′59″, 8 August 2018, tcmb 005; Menglian Town, Xiamenglian Village, on ground of mixed forests composed of Fagaceae and P. yunnanensis, 5 August 2014, Li 140805-18; Chuxiong Yi Autonomous Prefecture, Zixi Mountain, near King Baotou, on ground of mixed forest composed of Fagaceae and P. yunnanensis, Alt: 1926 m, N: 25°1' 3", E: 101°24'7", 25 August 2018, Li 180825-21; Yuxi, Huaning County, on ground dominant with Fagaceae, 8 September 2013, Li 130908-29; Zhaotong, Weixin County, Miaogou Town, Zhashigou Village, on ground dominant with Fagaceae, Alt: 1450 m, N: 27°47′ 6″, E: 104°49′18″, 22 September 2017, WX 20170922065.

Cortinarius subclackamasensis Q.Y. Zhang, Jing Si & Hai J. Li, sp. nov. Figure 3.

MycoBank: 848614

Diagnosis. — This species notably has small- to medium-sized basidiomata, buff-yellow and plano-convex pilei, ellipsoid to oblong ellipsoid basidiospores (9.5–10.8 × 5.8–6.8 µm); it is gregarious on ground of *Salix* or other deciduous trees and distributed in temperate China.

Type. — China, Heilongjiang Province, Huzhong, Huzhong Forest Farm, near Dongfanghong Line 31, on ground of *Salix*, 18 August 2017, Li 170818-16 (holotype), GenBank accession number for ITS: OQ913394.

Etymology. — *Subclackamasensis* refers to its morphological similarity to *C. clackamasensis.*

Habitat and distribution. — Scattered or gregarious on ground of *Salix* or other deciduous trees. Currently, it is found in Northeast and North China in summer.

Macrostructures. - Basidiomata small to medium sized. Pileus 30-60 mm in diam., hemispheric to subhemispheric when young, becoming plano-convex, then depressed at center and wrinkled, margin sharp sometimes waves; surface moist to hygrophanous when young, with fibrous veil remnants; buff yellow (4A4), to light honey yellow (4/5B4), somewhat lighter olivaceous buff (4C4) at margin, finely radially striate with age. Lamellae adnexedemarginate, moderately crowded to crowded, vinaceous (9F6) or peach (6A6) when young, somewhat darkening on manipulation, edge even, somewhat lighter. Stipe 40- to 60- mm long, 5- to 10mm thick above, qual to somewhat clavate, white, and cream with age. Universal veil usually sparse, thin, and somewhat glossy, cream (4A2/3) to light yellow (4A4), flocculose or forming a week girdle on the stipe. Context rather thick, especially in pileus center, brittle, weakly light honey yellow (4/5B4) with age. Odor and taste of context strongly fungoid.

Microstructures. — Basidiospores [90/3/3] 9.5–10.8 (–11) × (5.5–) 5.8–6.8 μ m, av. 9.9 × 6.3 μ m, Q = 1.56–1.60, av. Q = 1.59, ellipsoid to oblong ellipsoid, weekly to moderately, but distinctly verrucose, indextrinoid to weakly dextrinoid. Basidia 4-spored, 22–25 × 8–11 μ m, clavate, colorless or yellowish. Lamella trama hyphae smooth, parallel, 4- to 12- μ m wide. Lamellae edge fertile, with some small clavate sterile cells. Pileipellis duplex: Epicutis about 27- to 32 - μ m thick, hyphae (6–) 11- to 16- μ m wide, in upper part loosely entangled; hypocutis distinct well-developed, colorless or yellowish, irregular, interwoven, with some intracellular pigments, 18–28.5 μ m in diam. Clamp connections present.

Remarks. — Phylogenetically, *C. latiodistributus* Dima, Ammirati, Niskanen, Kytöv., Liimat. & Brandrud, *C. clackamasensis* Ammirati, Liimat., Niskanen & Dima, and *Cortinarius* sp. 12 are closely related to *C. subclackamasensis*. *Cortinarius latiodistributus* has violet to pallid brown pilei, and shorter basidiospores (7–9.5 µm). *Cortinarius clackamasensis* has wider basidiospores (9–11 × 6.5–7.5 µm, av. 9.7 × 6.5 µm, Q =1.4–1.5), grows on the ground under mixed conifers composed of



(D) Basidiospores, (E) Hymenium in trama, (F) One basidium, (G) Epicutis of pileipellis, (H) Hypodermium of pileipellis, and (I) Context hyphae

Picea, Pinus, and Abies, and is distributed in the US (Dima et al., 2021). Similar to C. subclackamasensis, C. clintonianus Peck, and C. anomalopacificus Bojantchev, Liimat., Niskanen, Dima & Ammirati have yellowish and plano-convex basidiomata. However, the basidiospores in C. clintonianus and C. anomalopacificus are shorter (6.7-8.1 × 5.6-6.3 µm vs. 6.5-7 × 5-6 µm; Dima et al., 2021).

Additional specimens (paratypes) examined. — China, Beijing, Mentougou District, Xiaolongmen National Forest Park, 30 August 2017, BJMTG20170830-34; Hebei Province, Baoding, Fuping County, Dongxiaguan Town, Zhujiaying Village, Tianshengqiao, 22 August 2019, 20190822-11; Heilongjiang Province, Huzhong, Huzhong forest farm, near Dongfanghong Line 31, on ground of Salix, 18 August 2017, Li 170818-01 and Li 170818-02.

Cortinarius tropicus Q.Y. Zhang, Jing Si & Hai J. Li, sp. nov. Figure 4.

MycoBank: 848616

Diagnosis. — This species notably has small basidiomata, violet to dark violet pileal surface with fibrillose disc and nearly glabrous, cream to pale violet margin, subglobose to broadly ellipsoid basidiospores (6-8 \times 5-6 μ m); it is scattered or gregarious on ground dominant with Fagaceae.

Type. — China, Yunnan Province, Baoshan, Tengchong, Qushi Town, Qingqiao Village, Alt: 1490 m, N: 25°17′17″, E: 98°35′26″, on ground dominant with Fagaceae, 6 August 2016, tcqushi 006 (holotype), GenBank accession number for ITS: OQ913379.

Etymology. - tropicus refers to its tropical distribution in Southwest China.

Habitat and distribution. - Scattered or gregarious on ground dominant with Fagaceae. Currently, it is only found in tropical Yunnan (three collections) in summer.

Macrostructures. - Basidiomata small. Pileus 20-45 mm in diam., hemispheric to subhemispheric when young, becoming obtusely conical, conico-convex, broadly umbonate, pale brown [5D(4-5)] at center and gradually paler toward margin when young, violet (17B8) to dark violet (17F8) when mature, disc gravish violet (15E5) to dark violet (17F8), margin cream (4A2/3) to pale violet [16A(2-3)], fibrillose at disc and nearly glabrous near margin, somewhat hygrophanous, margin decurved. Lamellae adnexed-emarginate, subclose, purplish to pale violet lilac [16D (4-6)], finally ± pale brown to cinnamon (16D3-16E3). Stipe 50- to 80- mm long, apex 3 to 5 mm in diam., base 5-10 mm in diam., enlarged, narrowly clavate, surface grayish (16B2) with dark violet [16F(3–4)] streaks or silvery violet (16A3) on upper half and watery brownish below, veil usually sparse, forming floccose-girdles on the stipe, often at first brownish (6B2-6C2) then becoming pale yellow [4A(2-3)], sometimes indistinct, and basal mycelium whitish. Context in pileus solid, firm, violet to silvery violet [16C(4-6)] when fresh, finally pale brown to cinnamon (16D4-16F4) in age. Odor and taste of context strongly fungoid.

Microstructures. — Basidiospores [90/3/3] $6-8 \times 5-6 \mu m$, av. $7.4 \times 5.9 \ \mu m$, Q = 1.21 - 1.29, av. Q = 1.25, subglobose to broadly



Basidiomata and microscopic structures of *Cortinarius tropicus*. (A-E) Basidiomata (tcqushi 006, Holotype), (F) Basidiospores, (G-H) Basidia and basidioles, (I) Epicutis of pileipellis, (J) Hypodermium of pileipellis, and (K) Context hyphae.

ellipsoid, buff to cinnamon-buff, coarsely verrucose, non-dextrinoid to slightly dextrinoid. Basidia 4-spored, $30-42 \times 7-11 \mu$ m, clavate, colorless or yellowish. Lamella trama hyphae hyaline, smooth, parallel, 5- to 13- μ m wide. Pileipellis duplex: Epicutis well developed, hyaline or yellow to ochraceous, smooth, cylindrical, radially arranged, ± interwoven, $4-10 \mu$ m wide; hypocutis distinct, colorless or yellowish, smooth to slightly encrusted, cylindrical to enlarged, radially oriented, ± interwoven, (4)6- to 15(17)- μ m wide. Clamp connections present.

Remarks. — *Cortinarius perviolaceus* Murrill is easily confused with *C. tropicus* because of its violet pilei, but *C. perviolaceus* has smaller basidiomata (8–22 mm vs. 20–45 mm) and wider basidiospores (6–6.5 µm vs. 5–6 µm; Dima et al., 2021). *Cortinarius anomalus* has similar pilei with blue tinge when young and larger basidiospores (8–9 × 6–7 µm; Dima et al., 2016). *Cortinarius anomalovelatus, C. deceptivus* Kauffman, and *C. harvardensis* L. Nagy, Dima & Ammirati formed a sister group with *C. tropicus*. Compared with the new species, *C. anomalovelatus* has wider basidiospores (6.3–7 µm vs. 5–6 µm), *C. deceptivus* produces larger basidiospores (7.8–9.3 × 6–7.4 µm), and *C. harvardensis* has bluish to violet pileus, lamellae, and stipe, and slightly bigger basidiospores (7.5 –8.5 × 5.5–6.5 µm; Dima et al., 2021).

Additional specimens (paratypes) examined. - CHINA. Yunnan Province, Dehong Dai and Jingpo Autonomous Prefecture, Mang City, Jiangdong Town, Daxinzhai, Alt: 1619 m, N: 24°27′54″, E: 98°18′56″, on ground dominant with Fagaceae, 28 July 2015, Li 150728-56 and Li 150728-63.

4 Discussion

Cortinarius, the largest agaric genus worldwide, contains important ectomycorrhizal fungi, among which sect. *Anomali* represents a monophyletic, species-rich group of this genus (Dima et al., 2016; Garnica et al., 2016; Soop et al., 2019; Dima et al., 2021; Liimatainen and Niskanen, 2021; Xie, 2022). Species recognition based on morphology is difficult in *Cortinarius* lineages due to overlapping characteristics and variations within species. Notably, the basidiospore size helps identify some species when used in correlation with other characteristics (Frøslev et al., 2006; Niskanen et al., 2013; Liimatainen et al., 2014; Liimatainen et al., 2015; Niskanen et al., 2016).

According to our phylogenetic analysis, sect. *Anomali* indicated a widely distributed lineage of *Cortinarius* in both the northern and southern Hemispheres. Furthermore, certain patterns of distribution correlated with ecology and plant hosts. *Cortinarius albocyaneus* exhibited regional patterns of distribution with conifers in northern Michigan and northern Europe. Several species, including

Cortinarius brevissimus Peck, C. caeruleoanomalus Dima, Matheny, K. Hughes & Ammirati, C. deceptivus, C. harvardensis, C. modestus Rob. Henry, C. perrotensis A. Paul, Matheny & Lebeuf, and C. perviolaceus, occurred in hardwood, mixed hardwood conifer, and/ or conifer forests in eastern North America. Cortinarius rarus Bojantchev, Ammirati, Parker, Liimat., Niskanen & Dima displayed regional patterns of distribution associated with mountain conifer forests (Dima et al., 2016; Dima et al., 2021).

Current studies related to this genus have indicated significant regional variations. Classical European species were examined and typified by Dima et al. (2016) before species from other parts of the world were studied. In sect. Anomali, more than 50 binomials were introduced in the last century, mainly from Europe, with fewer from elsewhere, but only about 20% of these names have been in general use (Dima et al., 2021). China is geographically located in East Asia and has a land area comparable with that of the entire Europe, various climate types ranging from the temperate to the tropical climate, as well as a complex and diverse habitat, which provides an ideal place for the survival of Cortinarius species. However, the resource investigation and taxonomic research on Cortinarius have not yet been extensively carried out in China. Currently, there have been reports of a total of 163 taxa of the genus in China, with only three species in the sect. Anomali, viz. C. caninus (Fr.) Fr., C. albocyaneus, and C. tabularis (Fr.) Fr. Therefore, the collection of more samples from China and exploration of multigene phylogeny are urgently needed to systematically elucidate the diversity of Cortinarius s.l.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/nuccore/OQ913379,OQ913380,OQ913381,OQ913382,OQ913383,OQ913384,OQ913385,OQ913386,OQ913387,OQ913388,OQ913389,OQ913390,OQ913391,OQ913392,OQ913393,OQ913394,OQ913395,OQ913396,OQ913397,OQ920003,OQ920004,OQ920005.

Author contributions

Q-YZ, CJ, H-MZ, Z-YM, Y-ZZ, J-QL, JS, and H-JL designed the research and contributed to data analysis and interpretation. Q-YZ, CJ, H-MZ and Z-YM prepared the samples and drafted the manuscript. Y-ZZ, J-QL, Z-YM, JS, and H-JL conducted the molecular experiments and analyzed the data. JS and H-JL discussed the results and edited the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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