

# Morphology and multi-locus phylogeny reveal three new *Cortinarius* (Cortinariaceae, Agaricales) species from northwestern Yunnan, China

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## Abstract

Yunnan's complex topography and pronounced geographic heterogeneity, together with marked climatic variability, luxuriant vegetation, and the seasonal influx of warm, moisture-laden air masses from the Indian and Pacific Oceans, have created abundant refugial habitats throughout the Quaternary glaciations. These combined abiotic and biotic factors have made the region highly favorable for the survival, diversification, growth, and reproduction of higher fungi. This study reports three new species: *Cortinarius acuticonus*, *C. tricholomopsoides*, and *C. wudihuensis* from the subalpine and alpine forests of northwestern Yunnan, China, identified through morphological investigations and multi-locus phylogenetic analyses. *Cortinarius acuticonus* and *C. tricholomopsoides* are placed in the subgenus *Leprocyebe*. *Cortinarius acuticonus* is distinguished by an acutely conical pileus with dense black, *Strobilomyces*-like scales and a distinct membranous annulus. In contrast, *Cortinarius tricholomopsoides* exhibits large, pale yellow basidiomata and forms associations with *Abies* species. *Cortinarius wudihuensis*, assigned to section *Anomali*, is characterized by small basidiomata with violaceous to brownish tones, an association with *Quercus aquifolioides*, and larger, broadly ellipsoid basidiospores ( $7\text{--}9 \times 5.5\text{--}7 \mu\text{m}$ ). These findings underscore the substantially underestimated diversity of *Cortinarius* in the high-altitude regions of Yunnan and offer important insights into the ecological specialization and evolutionary divergence of Asian *Cortinarius* lineages.

**Key words:** Morphology, novel species, phylogeny, sect. *Anomali*, subg. *Leprocyebe*



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## Introduction

Northwestern Yunnan stands as one of the world's most remarkable biogeographical transition zones, where the eastern escarpment of the Qinghai–Tibet Plateau descends through successive vegetation belts into subtropical valleys incised by the Jinsha, Lancang, and Nujiang river systems (Lu et al. 2026). This tri-river landscape, designated by the United Nations Educational, Scientific and Cultural Organization (UNESCO) as a World Heritage Site, forms a sharply compressed altitudinal gradient exceeding 5,000 m within horizontal distances of

only several tens of kilometers, thereby generating an exceptional diversity of microhabitats (Liu et al. 2024).

*Cortinarius* (Pers.) Gray is the most species-rich genus within Agaricales (Teder-soo and Nara 2010; Soop et al. 2019), and it plays a critical role in forest ecosystems as an ectomycorrhizal symbiont with a global distribution (Bödeker et al. 2014; Martin et al. 2016). Despite its ecological prominence, the taxonomy of the genus has historically been impeded by its immense diversity and morphological complexity (Soop et al. 2019). Traditionally, infrageneric classification relied heavily on macromorphology and chemotaxonomy. Liimatainen et al. (2022a) proposed a refined classification system for the genus *Cortinarius* by integrating genomic analysis with multi-gene phylogenetics. This updated system delineates 11 subgenera: *Cortinarius* subg. *Cortinarius* (Pers.) Gray, *Camphorati* Liimat., Niskanen & Ammirati, *Dermocybe* (Fr.) Trog, *Illumini* Liimat., Niskanen & Kytöv., *Infracti* Niskanen & Liimat., *Iodolentes* Niskanen & Liimat., *Leprocye* M.M. Moser, *Myxacium* (Fr.) Trog, *Orellani* (M.M. Moser) Gasparini, *Paramyxacium* M.M. Moser & E. Horak, and *Telamonina* (Fr.) Trog (Moser 1969; Niskanen and Kytövuori 2008; Liimatainen 2014; Liimatainen et al. 2015, 2017, 2020, 2022a; Niskanen et al. 2016).

In recent decades, the integration of molecular phylogenetics has changed the understanding of *Cortinarius* systematics (Lindahl et al. 2013; Liimatainen 2014; Liimatainen et al. 2015, 2017, 2020, 2022a). The application of DNA barcoding, particularly using the nuclear ribosomal internal transcribed spacer (ITS) region, has revealed extensive cryptic diversity across various infrageneric groups (Lindahl et al. 2013). Recent studies in different geographical regions have demonstrated that many widely distributed names encompass multiple distinct phylogenetic species, many of which remain undescribed (Skrede et al. 2011; Harrower et al. 2015). This is particularly evident in regions such as East Asia, where intensive sampling and molecular analyses continue to uncover a wealth of novel taxa (Liimatainen et al. 2022a; Xie et al. 2025).

During ongoing investigations of fungal diversity in China (Zhou et al. 2022; Zeng et al. 2023; Su et al. 2025; Wang et al. 2025; Li et al. 2025, 2026; Lu et al. 2026; Zhou et al. 2026), two distinct *Cortinarius* populations belonging to subg. *Leprocye* and sect. *Anomali* were collected. Morphological and molecular phylogenetic analyses substantiate that these collections constitute three previously undescribed species. Herein, these three new species of *Cortinarius* are formally described, with illustrations, taxonomic comparisons, and a discussion of their phylogenetic positions within the genus.

## Materials and methods

### Sample collection

Specimens were collected from Laojun Mountain Nature Reserve in Lijiang City and Jinguangsi Nature Reserve in Yongping County, Dali, Yunnan Province. Fresh basidiomata were photographed *in situ* prior to collection; collection details were noted (Rathnayaka et al. 2025); and subsequently, they were transported to the laboratory in plastic collection boxes. All specimens were examined according to the methods described by Zhao et al. (2015) and Yang et al. (2025), with specific procedures detailed below. Macroscopic features of the fresh basidiomata were recorded and described based on *in situ* photographs,

with color codes following Kornerup and Wanscher (1981). The basidiomata were dried in an electric dryer at 40 °C until completely dehydrated for preservation. The specimens were deposited in the Herbarium of Cryptogams of Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS).

### Morphological observation

Microscopic features were examined and photographed using a stereomicroscope (SterEO Discovery.V12, Carl Zeiss Microscopy GmbH, Germany) and a compound microscope (Nikon ECLIPSE 80i, Nikon, Japan) equipped with a Nikon DS-Ri2 digital camera (Nikon, Japan). For microscopic observation, thin sections were prepared by hand using a razor blade and placed on sterile filter paper moistened with water to maintain hydration. Sections were then mounted in 10% KOH and stained with Congo Red when necessary. Microscopic characteristics were recorded, with at least 30 basidiospores and 20 basidia measured for each mature specimen. To observe basidiospore ornamentation, small hymenophoral fragments were taken from dried specimens, mounted on aluminum stubs with double-sided adhesive tape, coated with gold-palladium, and examined under a ZEISS Sigma 300 scanning electron microscope (SEM) at the Kunming Institute of Botany, Chinese Academy of Sciences (Jia et al. 2025). Microstructures were measured using Image Frame Work v.0.9.7 software. Measurements are presented as (a–) b–c (–d), where a denotes the minimum value, d the maximum value, and b–c the 90% confidence interval. The number of basidiospores (*n*), basidiomata (*m*), and specimens (*p*) measured is denoted as [*n/m/p*]. *Q* represents the length-to-width ratio of individual basidiospores, and *Q* (referring to the mean value here) represents the average of these ratios ± standard deviation. Illustrations were created using Adobe Photoshop 2022 (Adobe Systems, USA).

### DNA extraction, PCR amplification, and sequencing

DNA was extracted directly from *Cortinarius* fruiting bodies using a *Trelief*<sup>™</sup> Fungal Genomic DNA Extraction Kit (Tsingke Biotechnology Co., Ltd., Beijing, China). The nuclear ribosomal internal transcribed spacer (ITS) region and the nuclear ribosomal large subunit (nrLSU) were amplified using the universal primer pairs ITS1/ITS4 (White et al. 1990) and LR0R/LR5 (Vilgalys and Hester 1990), respectively. The polymerase chain reaction (PCR) protocol consisted of an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 53 °C for 20 s, and extension at 72 °C for 30 s, with a final extension step at 72 °C for 10 min. PCR products were sequenced by Tsingke Biotechnology Co., Ltd. (Beijing, China).

### Sequence alignment and phylogenetic analyses

Newly generated sequences were verified and assembled using DNAMAN v.9.0.1.116 (Lynnon BioSoft). To construct phylogenetic trees, these sequences were combined with those of closely related species retrieved from GenBank (Tables 1, 2). Multiple sequence alignment was performed using MAFFT v.7 (Katoh and Standley 2013; Katoh et al. 2019) and trimmed with TrimAl v.1.3 (Capella-Gutiérrez et al. 2009), with a gap threshold of 0.5 for both the ITS and

**Table 1.** Names, voucher numbers, countries, references, and corresponding GenBank accession numbers of the taxa used in this study. Names shaded in blue indicate newly described species in this study. All type specimens are highlighted with “T.” “—” indicates missing data.

| Species                         | voucher                  | Locations   | GenBank Accession No. |          | Reference                     |
|---------------------------------|--------------------------|-------------|-----------------------|----------|-------------------------------|
|                                 |                          |             | ITS                   | nrLSU    |                               |
| <i>Cortinarius acuticonus</i> T | KUN-HKAS 151741          | China       | PX765862              | PX765871 | This study                    |
| <i>C. acuticonus</i>            | KUN-HKAS 151743          | China       | PX765863              | PX765872 | This study                    |
| <i>C. acuticonus</i>            | KUN-HKAS 151742          | China       | PX765864              | PX765873 | This study                    |
| <i>C. apius</i> T               | WTU:3460                 | Canada      | MW009182              | —        | Ammirati et al. (2021)        |
| <i>C. atkinsiae</i> T           | TENN:F-071879            | USA         | NR_173275             | —        | Ammirati et al. (2021)        |
| <i>C. atosquamosus</i>          | H:T. Niskanen 12-278     | USA         | MW009183              | —        | Ammirati et al. (2021)        |
| <i>C. aureopigmentatus</i>      | JFA 11940                | Costa Rica  | EF420140              | —        | Ammirati et al. (2007)        |
| <i>C. clandestinus</i>          | WTU:J.F. Ammirati 9286   | USA         | MW009213              | —        | Ammirati et al. (2021)        |
| <i>C. cotoneus</i> T            | S:H. Lindstrom CFP1032   | Sweden      | MW009216              | —        | Ammirati et al. (2021)        |
| <i>C. cf. cotoneus</i>          | HMAS260331               | China       | KX513578              | —        | Bidaud et al. (2021)          |
| <i>C. cf. cotoneus</i>          | ZWL560                   | China       | KX444284              | —        | Bidaud et al. (2021)          |
| <i>C. flavifolius</i> T         | TENN:068695              | USA         | MW009217              | —        | Ammirati et al. (2021)        |
| <i>C. fuscoflavidus</i> T       | WTU:J.F. Ammirati 11644  | USA         | MW009221              | —        | Ammirati et al. (2021)        |
| <i>C. fuscotomentosus</i> T     | DBB00566                 | USA         | MT853246              | —        | Ammirati et al. (2021)        |
| <i>C. griseoaurantinus</i> T    | HMAS 353381              | China       | PQ796783              | PV174519 | Dang et al. (2025)            |
| <i>C. griseoaurantinus</i>      | HMAS 353382              | China       | PQ796784              | PV174520 | Dang et al. (2025)            |
| <i>C. hengduanensis</i> T       | HMAS:250455              | China       | KX513581              | —        | Hong et al. (2024)            |
| <i>C. hengduanensis</i>         | KUN-HKAS 151746          | China       | PX765866              | PX765877 | This study                    |
| <i>C. hengduanensis</i>         | KUN-HKAS 151747          | China       | PX765865              | PX765876 | This study                    |
| <i>C. hughesiae</i> T           | TENN:J.F. Ammirati 13086 | USA         | MW009224              | —        | Ammirati et al. (2021)        |
| <i>C. jimenezianus</i> T        | JA:CUSSTA9402            | Spain       | NR_186956             | —        | Bidaud et al. (2021)          |
| <i>C. leproleptopus</i> T       | PC:R. Henry 84.109       | France      | MW009226              | —        | Ammirati et al. (2021)        |
| <i>C. loringii</i> T            | WTU:SCL6030              | USA         | MW009227              | —        | Ammirati et al. (2021)        |
| <i>C. lutescens</i> T           | NYS:f1781                | USA         | MW009228              | —        | Ammirati et al. (2021)        |
| <i>C. melanotus</i> T           | S:H. Lindstrom CFP1101   | France      | NR_172988             | —        | Ammirati et al. (2021)        |
| <i>C. nigrosquamosus</i>        | HMJAU 58929              | China       | PZ274249              | —        | Xie (2022)                    |
| <i>C. nigrosquamosus</i>        | HMJAU 49111              | China       | PZ274250              | —        | Xie (2022)                    |
| <i>C. olivaceosquamosus</i> T   | H:T. Niskanen 10-105     | Canada      | MW009231              | —        | Ammirati et al. (2021)        |
| <i>C. parkeri</i> T             | ADP000-502-1 (WTU)       | USA         | JN976987              | —        | Ammirati et al. (2012)        |
| <i>C. pescolanensis</i> T       | MCVE:29054               | Italy       | NR_153070             | —        | Picillo and Marchionni (2016) |
| <i>C. phrygianus</i> T          | S:H. Lindstrom CFP774    | Sweden      | MW009234              | —        | Ammirati et al. (2021)        |
| <i>C. selinolens</i> T          | MPU:1116858              | France      | NR_184930             | —        | Bidaud et al. (2021)          |
| <i>C. squamivenetoideus</i> T   | H:T. Niskanen 11-005     | USA         | MW009239              | —        | Ammirati et al. (2021)        |
| <i>C. squamivenetus</i> T       | H:6001874                | Finland     | NR_131864             | —        | Liimatainen (2014)            |
| <i>C. subcotoneus</i> T         | PML 2143                 | France      | MW010122              | —        | Bidaud et al. (2021)          |
| <i>C. subleproleptopus</i> T    | H:T. Niskanen 12-344     | USA         | MW009241              | —        | Ammirati et al. (2021)        |
| <i>C. tricholomopsoides</i> T   | KUN-HKAS 151739          | China       | PX765860              | PX765874 | This study                    |
| <i>C. tricholomopsoides</i>     | KUN-HKAS 151740          | China       | PX765861              | PX765875 | This study                    |
| <i>C. veneto—occidentalis</i> T | H:T. Niskanen 11-051     | USA         | MW009243              | —        | Ammirati et al. (2021)        |
| <i>C. venetus</i> T             | S:H. Lindstrom CFP112    | Sweden      | MW009250              | —        | Ammirati et al. (2021)        |
| <i>C. cf. venetus</i>           | 2M06                     | Japan       | LC373240              | —        | Bidaud et al. (2021)          |
| <i>C. cf. venetus</i>           | HMAS:274611              | China       | KX513584              | —        | Bidaud et al. (2021)          |
| <i>C. cf. venetus</i>           | HMAS:268596              | China       | KX513586              | —        | Bidaud et al. (2021)          |
| <i>C. veronicae</i> T           | PDD 68468                | New Zealand | NR_157917             | —        | Bidaud et al. (2021)          |
| <i>C. veronicoides</i>          | MEL2120747               | Australia   | GQ890324              | —        | Danks et al. (2010)           |
| <i>C. viridans</i> T            | MPU:1116859              | Cyprus      | NR_184931             | —        | Bidaud et al. (2021)          |
| <i>C. yadingensis</i> T         | HMAS:254819              | China       | OR538892              | —        | Hong et al. (2024)            |

**Table 2.** Names, voucher numbers, countries, references, and corresponding GenBank accession numbers of the taxa used in this study. Names shaded in blue indicate newly described species in this study. All type specimens are highlighted with “T.” “—” indicates missing data.

| Taxa                            | voucher       | Locations   | GenBank Accession No. |          | Sequence origin                  |
|---------------------------------|---------------|-------------|-----------------------|----------|----------------------------------|
|                                 |               |             | ITS                   | nrLSU    |                                  |
| <i>Cortinarius adrianae</i>     | UCH C05272    | Panama      | OP265184              | —        | Liimatainen et al. (2022b)       |
| <i>C. albidipes</i> T           | NYS-F-000129  | USA         | MZ580485              | —        | Dima et al. (2021)               |
| <i>C. albidovellaneus</i> T     | MICH10313     | USA         | MZ580483              | —        | Dima et al. (2021)               |
| <i>C. albocyaneoides</i> T      | HMJAU 48664   | China       | ON254420              | OR105105 | Xie et al. (2025)                |
| <i>C. albocyaneus</i>           | HMJAU 44500   | China       | ON254434              | OR105121 | Xie et al. (2025)                |
| <i>C. albocyaneus</i> T         | CFP1177       | Sweden      | KX302206              | —        | Dima et al. (2016)               |
| <i>C. albomalus</i> T           | H7000816      | Canada      | MZ568645              | —        | Liimatainen and Niskanen (2021)  |
| <i>C. anocorium</i> T           | H7068022      | USA         | MZ568646              | —        | Liimatainen and Niskanen (2021)  |
| <i>C. anomalobrunneus</i> T     | UCH AC653     | Panama      | OP265185              | —        | Liimatainen et al. (2022b)       |
| <i>C. anomalodelicatus</i> T    | JFA8146       | USA         | MZ580480              | —        | Dima et al. (2021)               |
| <i>C. anomalomontanus</i> T     | JFA9919       | USA         | MZ580478              | —        | Dima et al. (2021)               |
| <i>C. anomalopacificus</i> T    | DBB11745      | USA         | MZ663774              | —        | Dima et al. (2021)               |
| <i>C. anomalovelatus</i> T      | JFA13109      | USA         | FJ717605              | FJ717605 | Harrower et al. (2011)           |
| <i>C. anomalus</i> T            | CFP1154       | Sweden      | KX302224              | —        | Dima et al. (2016)               |
| <i>C. azureovelatus</i>         | HMJAU 48656   | China       | ON254406              | OR105092 | Xie et al. (2025)                |
| <i>C. azureovelatus</i>         | LE315531      | Russia      | MN308204              | —        | Brandrud et al. (2019)           |
| <i>C. barlowensis</i> T         | JFA13140      | USA         | FJ717554              | FJ717554 | Harrower et al. (2011)           |
| <i>C. brevissimus</i> T         | NYS-F-000541  | USA         | MZ580467              | —        | Dima et al. (2021)               |
| <i>C. bolaris</i> T             | CFP1008       | Sweden      | KX302233              | —        | Dima et al. (2016)               |
| <i>C. bolaris</i>               | TUB 0118524   | Germany     | AY669596              | AY669596 | Garnica et al. (2005)            |
| <i>C. caeruleoanomalus</i> T    | JFA13084      | USA         | MZ663780              | —        | Dima et al. (2021)               |
| <i>C. caesiifolius</i> T        | MICH10326     | USA         | MZ580462              | —        | Dima et al. (2021)               |
| <i>C. campanianomalus</i>       | HMJAU 48693   | China       | ON254474              | OR105160 | Xie et al. (2025)                |
| <i>C. campanianomalus</i> T     | HMJAU 48748   | China       | ON254479              | OR105165 | Xie et al. (2025)                |
| <i>C. caninus</i>               | HMJAU 44258   | China       | ON254441              | OR105129 | Xie et al. (2025)                |
| <i>C. caninus</i> T             | CFP627        | Sweden      | KX302250              | —        | Dima et al. (2016)               |
| <i>C. cinnamomeolilacinus</i> T | TCWH 007      | China       | OQ913384              | —        | Xie et al. (2025)                |
| <i>C. cinnamomeolilacinus</i>   | Li 161015-10  | China       | OQ913385              | —        | Xie et al. (2025)                |
| <i>C. clackamasensis</i> T      | JFA11616      | USA         | MZ580452              | —        | Dima et al. (2021)               |
| <i>C. clintonianus</i> T        | NYS-F-000786  | USA         | MZ580450              | —        | Dima et al. (2021)               |
| <i>C. deceptivus</i> T          | MICH10343     | USA         | MZ663788              | —        | Dima et al. (2021)               |
| <i>C. durifoliorum</i> T        | PDD101829     | New Zealand | KJ635210              | MW263597 | Soop et al. (2018)               |
| <i>C. epsomiensis</i>           | HMJAU 44242   | China       | ON254422              | OR105107 | Xie et al. (2025)                |
| <i>C. epsomiensis</i> T         | K(M)74963     | UK          | MK010952              | —        | Liimatainen and Ainsworth (2018) |
| <i>C. harvardensis</i> T        | NL-5415       | USA         | MZ663789              | —        | Dima et al. (2021)               |
| <i>C. jonimitchelliae</i> T     | HL03-339      | Sweden      | KX302253              | —        | Dima et al. (2016)               |
| <i>C. kranabetteri</i>          | HMJAU 48644   | China       | ON254398              | OR105086 | Xie et al. (2025)                |
| <i>C. kranabetteri</i> T        | TN11-287      | USA         | MZ580449              | —        | Dima et al. (2021)               |
| <i>C. latiodistributus</i> T    | DB6139        | Sweden      | MZ663791              | —        | Dima et al. (2021)               |
| <i>C. lepidopus</i>             | HMAS 271997   | China       | ON254483              | OR105169 | Xie et al. (2025)                |
| <i>C. lepidopus</i>             | HMAS 272035   | China       | ON254484              | OR105170 | Xie et al. (2025)                |
| <i>C. lividomalvaceus</i> T     | JMT-15102001  | France      | KY315416              | —        | Zhang et al. (2023)              |
| <i>C. luteoperonatus</i>        | JMB2011112610 | France      | KY315415              | —        | Zhang et al. (2023)              |
| <i>C. microalbocyaneus</i>      | HMJAU 48649   | China       | ON254461              | OR105147 | Xie et al. (2025)                |
| <i>C. microalbocyaneus</i> T    | HMJAU 48706   | China       | ON254462              | OR105148 | Xie et al. (2025)                |
| <i>C. modestus</i> T            | NYS-F-001966  | USA         | MZ580446              | —        | Dima et al. (2021)               |
| <i>C. neocaninus</i> T          | HMJAU 48691   | China       | ON254453              | OR105140 | Xie et al. (2025)                |

| Taxa                                  | voucher         | Locations   | GenBank Accession No. |          | Sequence origin            |
|---------------------------------------|-----------------|-------------|-----------------------|----------|----------------------------|
|                                       |                 |             | ITS                   | nrLSU    |                            |
| <i>C. neocaninus</i>                  | HMJAU 48690     | China       | ON254455              | OR105141 | Xie et al. (2025)          |
| <i>C. nettieae</i> <b>T</b>           | JFA9613         | USA         | MZ580442              | —        | Dima et al. (2021)         |
| <i>C. ochraceodiscus</i> <b>T</b>     | DJM2195         | USA         | MZ663795              | —        | Dima et al. (2021)         |
| <i>C. parvulosquamulosus</i> <b>T</b> | UCH AC371       | Panama      | OP339753              | —        | Liimatainen et al. (2022b) |
| <i>C. pelerinii</i> <b>T</b>          | XC2012-21       | France      | MH784627              | —        | Dima et al. (2021)         |
| <i>C. perrotensis</i> <b>T</b>        | TENN071126      | Canada      | KX897405              | —        | Dima et al. (2021)         |
| <i>C. perrotensis</i>                 | HMJAU 48662     | China       | OR140843              | OR140846 | Xie et al. (2025)          |
| <i>C. perrugatus</i>                  | 771             | Italy       | JF907864              | —        | Osmundson et al. (2013)    |
| <i>C. perviolaceus</i> <b>T</b>       | FLAS-F32992     | USA         | MZ580438              | —        | Dima et al. (2021)         |
| <i>C. qilianensis</i> <b>T</b>        | HMJAU 44508     | China       | ON254416              | OR105102 | Xie et al. (2025)          |
| <i>C. qilianensis</i>                 | HMJAU 44509     | China       | ON254417              | OR105103 | Xie et al. (2025)          |
| <i>C. rarus</i> <b>T</b>              | DBB04712        | USA         | MZ663800              | —        | Dima et al. (2021)         |
| <i>C. rattinoides</i> <b>T</b>        | PDD88283        | New Zealand | JX000375              | JX000406 | Soop et al. (2018)         |
| <i>C. robustianomalus</i> <b>T</b>    | HMAS 254763     | China       | ON254459              | OR105145 | Xie et al. (2025)          |
| <i>C. robustianomalus</i>             | HMAS 254764     | China       | ON254460              | OR105146 | Xie et al. (2025)          |
| <i>C. rufolilacinus</i> <b>T</b>      | HMJAU 48739     | China       | ON254456              | OR105142 | Xie et al. (2025)          |
| <i>C. rufolilacinus</i>               | HMJAU 48745     | China       | ON254457              | OR105143 | Xie et al. (2025)          |
| <i>C. sclerophyllum</i> <b>T</b>      | HO-A20430A6     | Australia   | AY669637              | AY669637 | Garnica et al. (2005)      |
| <i>C. sericeolazulinus</i> <b>T</b>   | JFA12053        | Costa Rica  | EF420146              | —        | Ammirati et al. (2007)     |
| <i>C. subalbocyaneus</i>              | HMJAU 44282     | China       | ON254424              | OR105111 | Xie et al. (2025)          |
| <i>C. subalbocyaneus</i> <b>T</b>     | HMJAU 48659     | China       | ON254425              | OR105112 | Xie et al. (2025)          |
| <i>C. subanomalus</i>                 | HMAS 277626     | China       | ON254488              | OR105174 | Xie et al. (2025)          |
| <i>C. subanomalus</i> <b>T</b>        | HMJAU 48752     | China       | ON254489              | OR105175 | Xie et al. (2025)          |
| <i>C. subclackamasensis</i>           | HMAS 291362     | China       | ON254394              | OR105082 | Xie et al. (2025)          |
| <i>C. subclackamasensis</i>           | HMAS 281433     | China       | ON254395              | OR105083 | Xie et al. (2025)          |
| <i>C. suecicolor</i> <b>T</b>         | PDD74698        | New Zealand | JX000360              | JX000391 | Soop et al. (2018)         |
| <i>C. tabularis</i>                   | HMJAU 44248     | China       | ON254468              | OR105154 | Xie et al. (2025)          |
| <i>C. tabularis</i> <b>T</b>          | CFP949          | Sweden      | KX302275              | —        | Dima et al. (2016)         |
| <i>C. tetonensis</i> <b>T</b>         | JFA10350        | USA         | MZ580436              | —        | Dima et al. (2021)         |
| <i>C. tropicus</i> <b>T</b>           | tcqushi006      | China       | OQ913379              | —        | Xie et al. (2025)          |
| <i>C. tropicus</i>                    | Li 150728-56    | China       | OQ913380              | —        | Xie et al. (2025)          |
| <i>C. vernalianomalus</i> <b>T</b>    | HMJAU 48770     | China       | ON254487              | OR105173 | Xie et al. (2025)          |
| <i>C. violaceobrunneus</i>            | UCH AC41        | Panama      | OP265182              | —        | Liimatainen et al. (2022b) |
| <i>C. wudihuensis</i>                 | KUN-HKAS 151737 | China       | PZ274244              | PZ274247 | This study                 |
| <i>C. wudihuensis</i> <b>T</b>        | KUN-HKAS 151738 | China       | PZ274245              | PZ274248 | This study                 |
| <i>C. xizangensis</i>                 | HMAS 275210     | China       | ON254495              | OR105177 | Xie et al. (2025)          |
| <i>C. xizangensis</i> <b>T</b>        | HMAS 274227     | China       | ON254496              | —        | Xie et al. (2025)          |

nrLSU regions. The trimmed sequences were concatenated into a combined dataset using Sequence Matrix v.1.8 (Vaidya et al. 2011).

To construct the phylogenetic tree based on the dataset of subg. *Leprocyebe*, maximum likelihood (ML) analysis was conducted using RAXML-HPC2 v.8.2.12 (Miller et al. 2010) under the GTRCAT model with 1,000 rapid bootstrap replicates. For Bayesian inference (BI), the optimal evolutionary models were determined using MrModeltest v.2.3 (Nylander et al. 2004) based on the Akaike information criterion (AIC). The GTR+I+G and GTR models were selected for the ITS and nrLSU regions, respectively. BI was performed using MrBayes v.3.2 with four simultaneous Markov chains running for 1,240,000 generations, sampling every 100 generations. The first 25% of trees were discarded as burn-in. Convergence was assumed when the standard deviation of split frequencies fell below 0.01 and the effective sample size (ESS) exceeded 200. The final

phylogenetic trees were visualized using FigTree v.1.4.4 (Rambaut 2018) and refined in Adobe Illustrator CC 2018 (Adobe, USA).

To construct the phylogenetic tree based on the dataset of sect. *Anomali*, ML analysis was conducted using RAxML-HPC2 v.8.2.12 (Miller et al. 2010) under the GTRCAT model with 1,000 rapid bootstrap replicates. For BI, the optimal evolutionary models were determined using MrModeltest v.2.3 (Nylander et al. 2004) based on the AIC. The HKY+I+G and GTR+I+G models were selected for the ITS and nrLSU regions, respectively. BI was performed using MrBayes v.3.2 (Ronquist et al. 2012) with four simultaneous Markov chains running for 2,610,000 generations, sampling every 100 generations. The first 25% of trees were discarded as burn-in. Convergence was assumed when the standard deviation of split frequencies fell below 0.01, and the ESS exceeded 200. The final phylogenetic tree was visualized using FigTree v.1.4.4 and refined in Adobe Illustrator CC 2018 (Adobe, USA).

## Results

### Molecular analyses

In Fig. 1 and Table 1, the concatenated dataset comprised 56 sequences (47 ITS and nine nrLSU) representing 37 taxa (47 vouchers), including 42 publicly available sequences and 14 newly generated sequences. *Cortinarius veronicoides* (MEL2120747) and *C. veronicae* (PDD 68468) were designated as outgroup taxa following Hong et al. (2024). The aligned matrix comprised 1,508 aligned nucleotide positions (ITS: 1–660; nrLSU: 661–1,508). GenBank accession numbers for all sequences are listed in Table 1. ML and BI analyses yielded congruent topologies; the ML tree was selected for phylogenetic representation (Fig. 1). Phylogenetic analyses provided robust support for the taxonomic independence of *Cortinarius tricholomopsoides* and *C. acuticonus*. Both taxa formed statistically well-supported monophyletic clades within subg. *Leprocye*.

In Fig. 2 and Table 2, the concatenated dataset comprised 120 sequences (84 ITS, 36 nrLSU) representing 63 taxa (84 vouchers), including 116 publicly available sequences and four newly generated sequences. Following the study by Xie et al. (2025), *Cortinarius bolaris* (CFP1008) and *C. bolaris* (TUB 0118524) were designated as outgroup taxa. The aligned matrix comprised 1,505 aligned nucleotide positions (ITS: 1–613; nrLSU: 614–1,505). GenBank accession numbers for all sequences are listed in Table 2. ML and BI analyses yielded congruent topologies; therefore, the ML tree was selected for phylogenetic representation (Fig. 2). Phylogenetic analyses provided robust support for the taxonomic independence of *Cortinarius wudihuensis*. This taxon formed a statistically well-supported monophyletic clade within sect. *Anomali*.

### Taxonomy

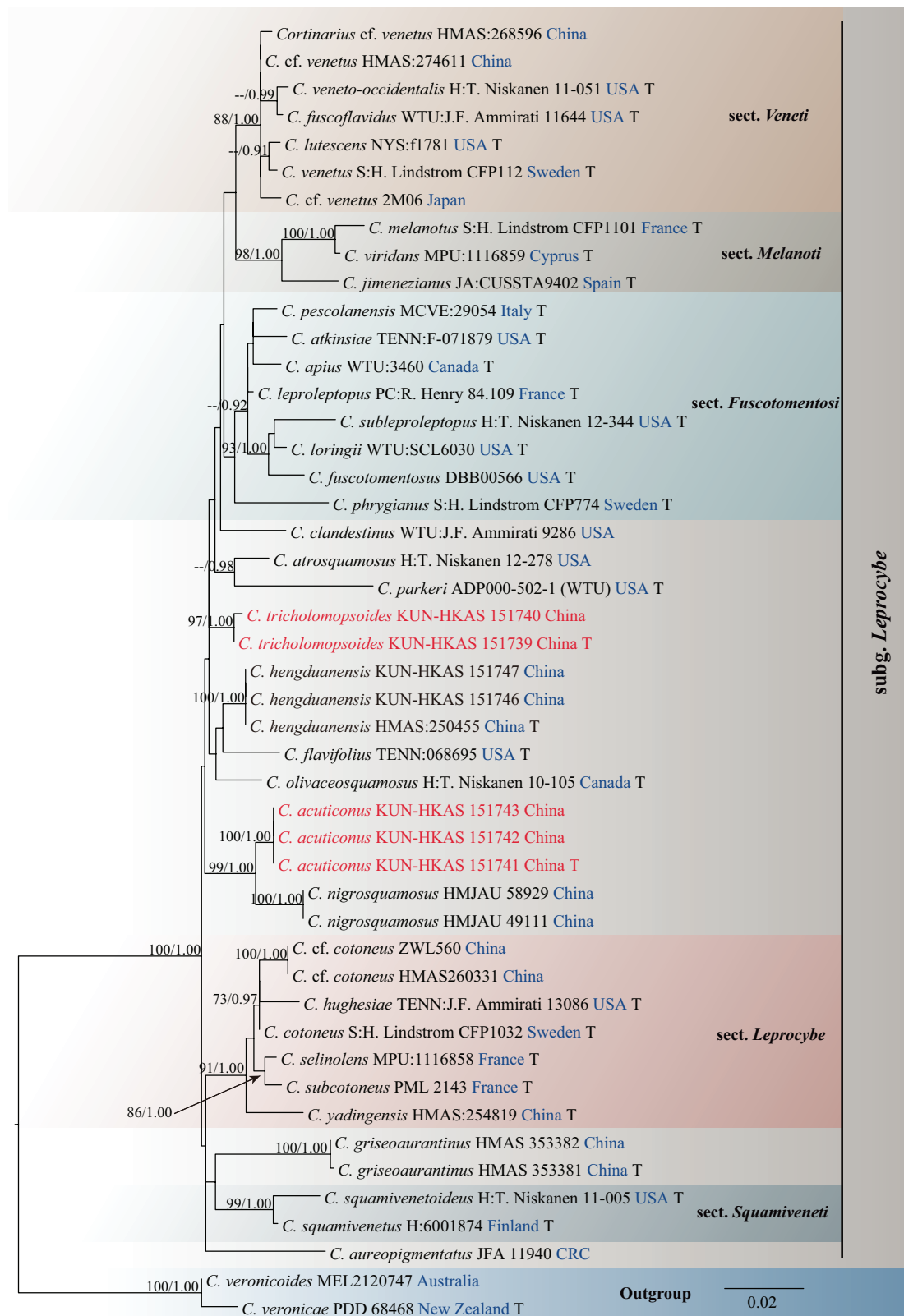
***Cortinarius acuticonus* Y.W. Yang, Y. Zhang & Q. Zhao, sp. nov.**

Index Fungorum: IF905217

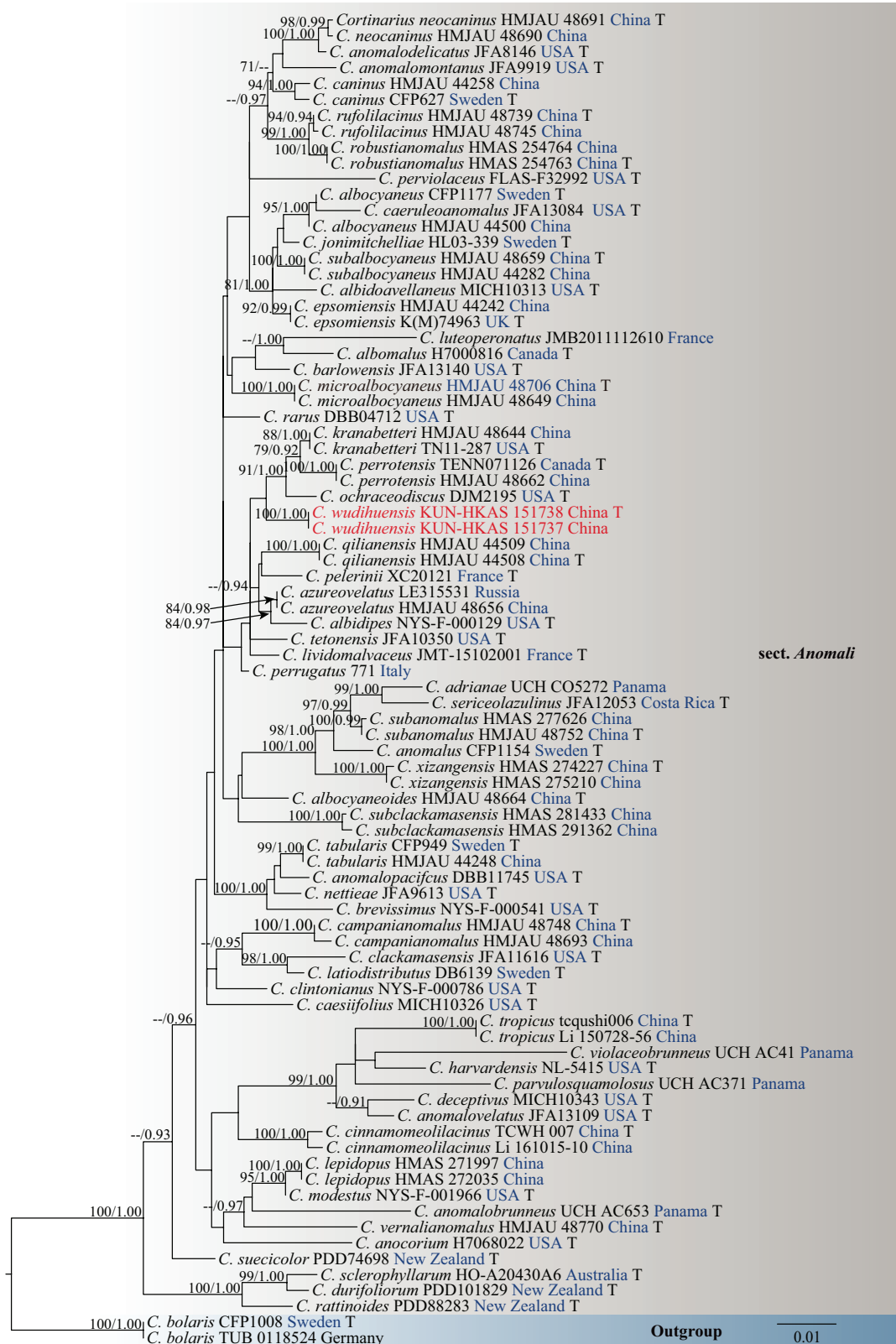
Fig. 3

**Chinese name.** 细锥鳞丝膜菌 (xi zhui lin si mo jun).

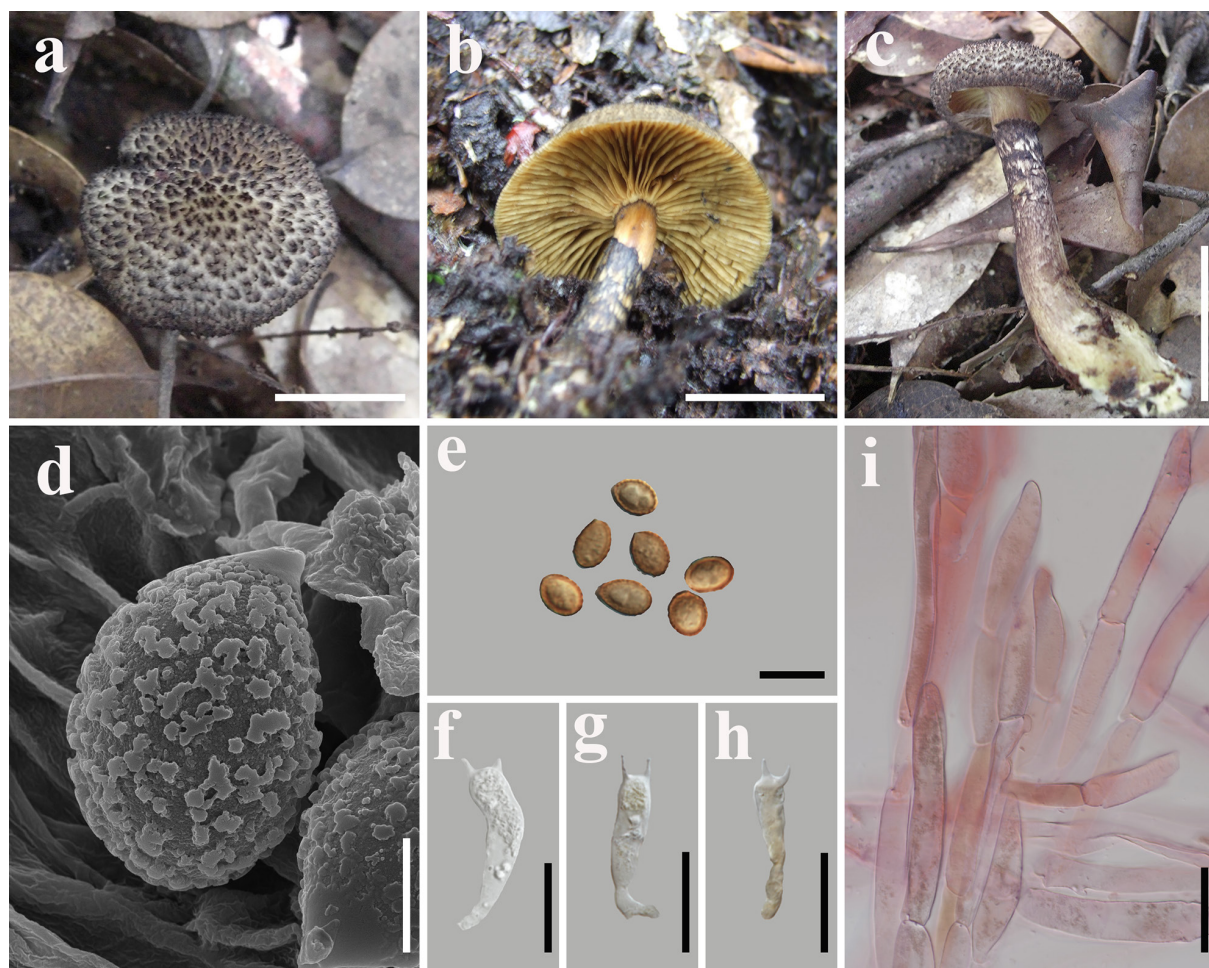
**Etymology.** “*acuticonus*” refers to the acutely conical shape of the pileus.



**Figure 1.** Phylogenetic tree of *Cortinarius* subgenus *Leprocye* generated from the concatenated nrITS and nrLSU dataset using maximum likelihood (ML) and Bayesian inference (BI) analyses. The dataset comprises 56 sequences representing 37 taxa, with *Cortinarius veronicoides* (MEL2120747) and *C. veronicae* (PDD 68468) designated as outgroup taxa following Hong et al. (2024). Maximum likelihood bootstrap (ML-BP)  $\geq 70\%$  and Bayesian posterior probabilities (BI-PP)  $\geq 0.90$  are indicated above the nodes. “-” indicates that the support value was less than the respective threshold. The specimen vouchers and country are indicated after the species names. New samples collected in this study are indicated in red. “T” indicates type specimens.



**Figure 2.** Phylogenetic tree of *Cortinarius* sect. *Anomali* generated from the concatenated nrITS and nrLSU dataset using maximum likelihood (ML) and Bayesian inference (BI) analyses. The dataset comprises 120 sequences representing 63 taxa, with *Cortinarius bolaris* (CFP1008) and *C. bolaris* (TUB 0118524) designated as outgroup taxa following Xie et al. (2025). Maximum likelihood bootstrap (ML-BP)  $\geq 70\%$  and Bayesian posterior probabilities (BI-PP)  $\geq 0.90$  are indicated above the nodes. “-” indicates that the support value was less than the respective threshold. The specimen vouchers and country are indicated after the species names. New samples collected in this study are indicated in red. “T” indicates type specimens.



**Figure 3.** *Cortinarius acuticonus*. **a–c.** Basidiomata (**a, c.** KUN-HKAS 151741, holotype; **b.** KUN-HKAS 151742); **d.** Scanning electron micrograph of basidiospore; **e.** Basidiospores; **f–h.** Basidia; **i.** Epicutis. Scale bars: 1 cm (**a, b**); 2 cm (**c**); 2 µm (**d**); 10 µm (**e**); 20 µm (**f–i**).

**Holotype.** CHINA • Yunnan Province: Dali, Yongping County, Jinguangsi Nature Reserve at 25.321450°N, 99.886342°E, alt. 2449 m, in *Castanopsis* spp. forest, 8 Jul. 2009, JGS-15-03 (KUN-HKAS 151741).

**Diagnosis.** *Cortinarius acuticonus* differs from *C. nigrosquamosus* by its acutely conical pileus entirely lacking olive tinges, covered with much finer and more densely arranged black, *Strobilomyces*-like scales, a distinct membranous annulus on the stipe, and broadly ellipsoid to ellipsoid basidiospores (6–8.5 × 4.5–6.5 µm). Molecularly, it is distinguished by 13 significant base-pair differences in the sequence alignment.

**Macrostructures.** **Basidiomata** medium-sized. **Pileus** 2–4 cm diam., initially acutely conical, becoming hemispherical to applanate with age; surface reddish brown (8E4) at the disc, fading to reddish grey (7B2) towards the margin, entirely covered with black (G1) scales resembling *Strobilomyces*. **Context** 2–6 mm thick, brown (7E5). **Lamellae** adnexed, 3–5 mm broad, moderately crowded, unequal, greyish yellow (4C5) to yellowish brown (5D6); edge undulating. **Stipe** 40–70 × 5–10 mm, clavate, base slightly bulbous; surface pale yellow (4A3) at the apex, brown (6C5) to brownish orange (6E4) in the middle, becoming paler downwards, covered with black (G1) fibrils, with a membranous annulus; longitudinally striate. **Basal mycelium** yellowish white (2A2), distinctive.

**Microstructures.** *Basidiospores* [90/3/3] (6–) 6.5–8 (–8.5) × (4.5–) 5–6 (–6.5) µm [ $Q = (1.05–) 1.15–1.47 (–1.55), Q = 1.3 \pm 0.1$ ], broadly ellipsoid to ellipsoid, cinnamon in 10% KOH, light orange-brown, and distinctly verrucose. *Basidia* 20–38 × 5.5–9 µm, clavate, thin-walled, mostly subhyaline, 4-spored, colorless or with yellowish contents. *Lamella trama* hyphae 4.5–6.5 µm diam., smooth, colorless. *Lamella edges* heterogeneous, with sterile cells, 17–23.5 × 5–7 µm, clavate, subhyaline. *Pleurocystidia* absent. *Pileipellis* duplex: epicutis well developed, hyphae interwoven, with some ascending fascicles, 5.5–14.5 µm diam., cylindrical, colorless or with greyish-black pigment; Hypodermium composed of uniform, moniliform, tightly interwoven, hyaline cells, hyphae 7–21 µm diam. *Stipe hyphae* 7.5–13 µm diam., colorless, smooth. *Clamp connections* present.

**Habitat.** Scattered or gregarious on the ground in *Castanopsis orthacantha* forest.

**Distribution.** Known from the western Yunnan Province, China.

**Additional material examined.** CHINA • Yunnan Province: Dali, Yongping County, Jinguangsi Nature Reserve at 25.351003°N, 99.860261°E, alt. 2490 m, in *Castanopsis orthacantha* forest, 8 Sep. 2009, JGS-27-11 (KUN-HKAS 151742); CHINA • Yunnan Province: Dali, Yongping County, Jinguangsi Nature Reserve at 25.321450°N, 99.886342°E, alt. 2449 m, in *Castanopsis orthacantha* forest, 5 Aug. 2009, JGS-18-17 (KUN-HKAS 151743).

**Notes.** *Cortinarius acuticonus* is a striking species that is easily recognized in the field, characterized by an acutely conical pileus densely covered with black, *Strobilomyces*-like scales, a distinct membranous annulus on the stipe, and broadly ellipsoid to ellipsoid basidiospores (6–8.5 × 4.5–6.5 µm). Morphologically, it can be easily confused with *C. nigrosquamosus*. The latter is another dark-scaled species previously recorded in Shangri-La Pudacuo National Park and discussed in recent comprehensive studies of the genus *Cortinarius* in China (Xie 2022). However, *C. acuticonus* can be distinguished from *C. nigrosquamosus* by the absence of an olive tinge on its pileus surface. Additionally, the scales on the pileus of *C. acuticonus* are finer and more densely arranged than those of *C. nigrosquamosus*. At the molecular level, sequence alignment between *C. acuticonus* and *C. nigrosquamosus* reveals 13 significant base-pair differences, providing strong evidence for recognizing *C. acuticonus* as a distinct species. Furthermore, the collection sites for *C. acuticonus* have an average elevation of 2460 m, which is lower than the 3500 m for *C. nigrosquamosus*. This altitudinal difference may be a contributing factor to the morphological and molecular divergences observed between the two species.

***Cortinarius tricholomopsoides* Y.W. Yang, Y. Zhang & Q. Zhao, sp. nov.**

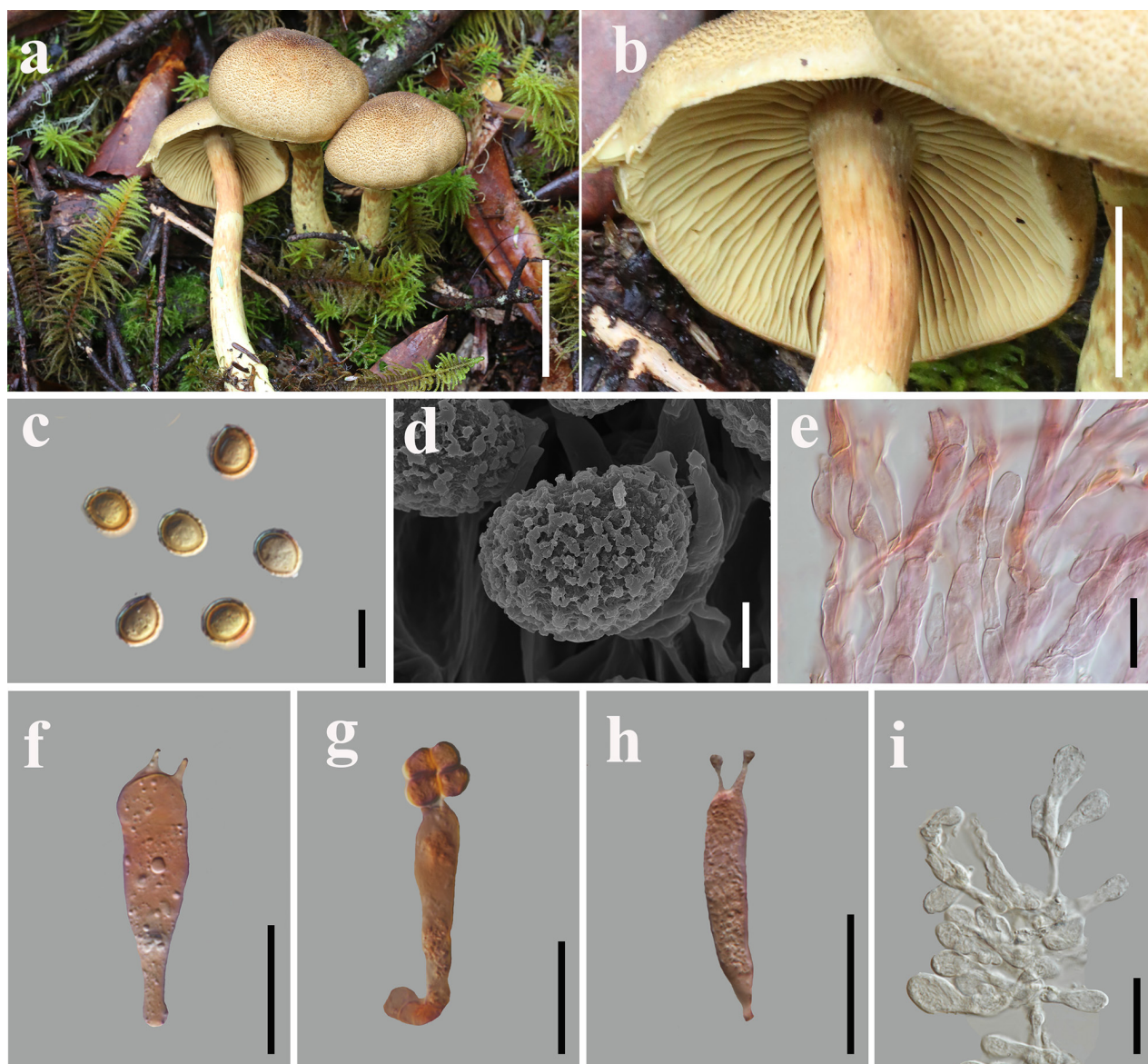
Index Fungorum: IF905218

Fig. 4

**Chinese name.** 拟口蘑丝膜菌 (ni kou mo si mo jun).

**Etymology.** “*tricholomopsoides*” refers to the resemblance of this new species to the genus *Tricholomopsoides*.

**Holotype.** CHINA • Yunnan Province: Lijiang City, Laojunshan Nature Reserve, at 26.631426°N, 99.719085°E, alt. 3960 m, in *Abies* forest, 26 Jul. 2018, LJ1334 (KUN-HKAS 151739).



**Figure 4.** *Cortinarius tricholomopsoides*. **a, b.** Basidiomata (**a.** KUN-HKAS 151739, holotype; **b.** KUN-HKAS 151740); **c.** Basidiospores; **d.** Scanning electron micrograph of basidiospore; **e.** Epicutis; **f–h.** Basidia; **i.** Lamella edges. Scale bars: 5 cm (**a**); 2 cm (**b**); 10 µm (**c**); 2 µm (**d**); 20 µm (**e–i**).

**Diagnosis.** *Cortinarius tricholomopsoides* is macromorphologically reminiscent of the European species *C. cotoneus* due to its tomentose to squamulose pileal surface but can be distinctively separated by its pale yellow to light brown pileal coloration entirely lacking olivaceous pigments throughout the basidiocarp, the presence of greyish-orange squamules on the stipe surface, and its negligible odor, slightly smaller, narrower basidiospores ( $7\text{--}9 \times 6\text{--}7.5\text{ }\mu\text{m}$ ).

**Macrostructures.** **Basidioma** large-sized. **Pileus** 5–10 cm diam., initially hemispherical, becoming applanate; surface initially pastel yellow (3A4), becoming light brown (7D5), covered with light-brown (7D5) squamules, dense at the disc, sparse towards the margin; context 1–4 mm thick, yellowish white (1A2). **Lamellae adnexed**, 5–7 mm broad, moderately crowded, unequal, greyish yellow (1B3); edge entire. **Stipe** 80–120 × 8–20 mm, cylindrical, tapering upwards; surface greyish yellow (2B3), covered with greyish orange (5B6)

fibrillose squamules, with a cortinate annular zone, longitudinally striate. **Basal mycelium** white (A1). **Odor** not distinctive.

**Microstructures.** **Basidiospores** [60/2/2] (7–) 7.5–9 (–9.5) × (6–) 6.5–7.5 (–8) µm [ $Q = (1.04–) 1.08–1.4 (–1.51)$ ,  $Q = 1.24 \pm 0.09$ ], subglobose to ellipsoid, cinnamon in 10% KOH, light brownish yellow, and distinctly verrucose. **Basidia** 26.5–46.5 × 5.5–10.5 µm, clavate, thin-walled, mostly subhyaline, 4-spored. **Lamella edges** heterogeneous, with sterile cells, 16–26 × 5.5–8.5 µm, clavate, subhyaline, thin-walled. **Lamella trama**, colorless or with yellowish contents, hyphae 4.5–6.5 µm diam. **Pleurocystidia** absent. **Pileipellis** duplex: epicutis well developed, hyphae interwoven, with some ascending fascicles, 4.5–12 µm diam., cylindrical, colorless or with yellowish contents; hypocutis composed of cylindrical, strongly interwoven, colorless or with yellowish contents, hyphae 5.5–9 µm diam. **Stipe hyphae** 8.5–12.5 µm diam., colorless, smooth. **Clamp connections** present.

**Habitat.** Scattered or gregarious on the ground in the *Abies* forest.

**Distribution.** Known from the Northwestern Yunnan Province, China.

**Additional material examined.** CHINA • Yunnan Province: Lijiang City, Laojunshan Nature Reserve, at 26.631426°N, 99.719085°E, alt. 3960 m, in *Abies* forest, 27 Aug. 2018 LJ1727 (KUN-HKAS 151740).

**Notes.** *Cortinarius tricholomopsoides* is morphologically reminiscent of *C. cotoneus*, both species characterized by tomentose to squamulose pileal surfaces. However, *C. cotoneus* displays characteristic olivaceous to brownish-olivaceous pigmentation throughout the basidiocarp and produces a pronounced raphanoid odor (Bidaud et al. 2021). Conversely, *C. tricholomopsoides* has pale yellow to light brown pileal coloration with grayish-orange squamulation on the stipe surface while exhibiting negligible olfactory characteristics. Additionally, the stipe of *C. cotoneus* is typically clavate to bulbous, whereas *C. tricholomopsoides* has a cylindrical stipe that tapers upward. Microscopically, *C. cotoneus* generally possesses slightly larger and broader basidiospores (typically 8–9.5 × 7–8 µm) compared to those of *C. tricholomopsoides* (7–9 × 6–7.5 µm).

### ***Cortinarius wudihuensis* Y.W. Yang, Y. Zhang & Q. Zhao, sp. nov.**

Index Fungorum: IF905440

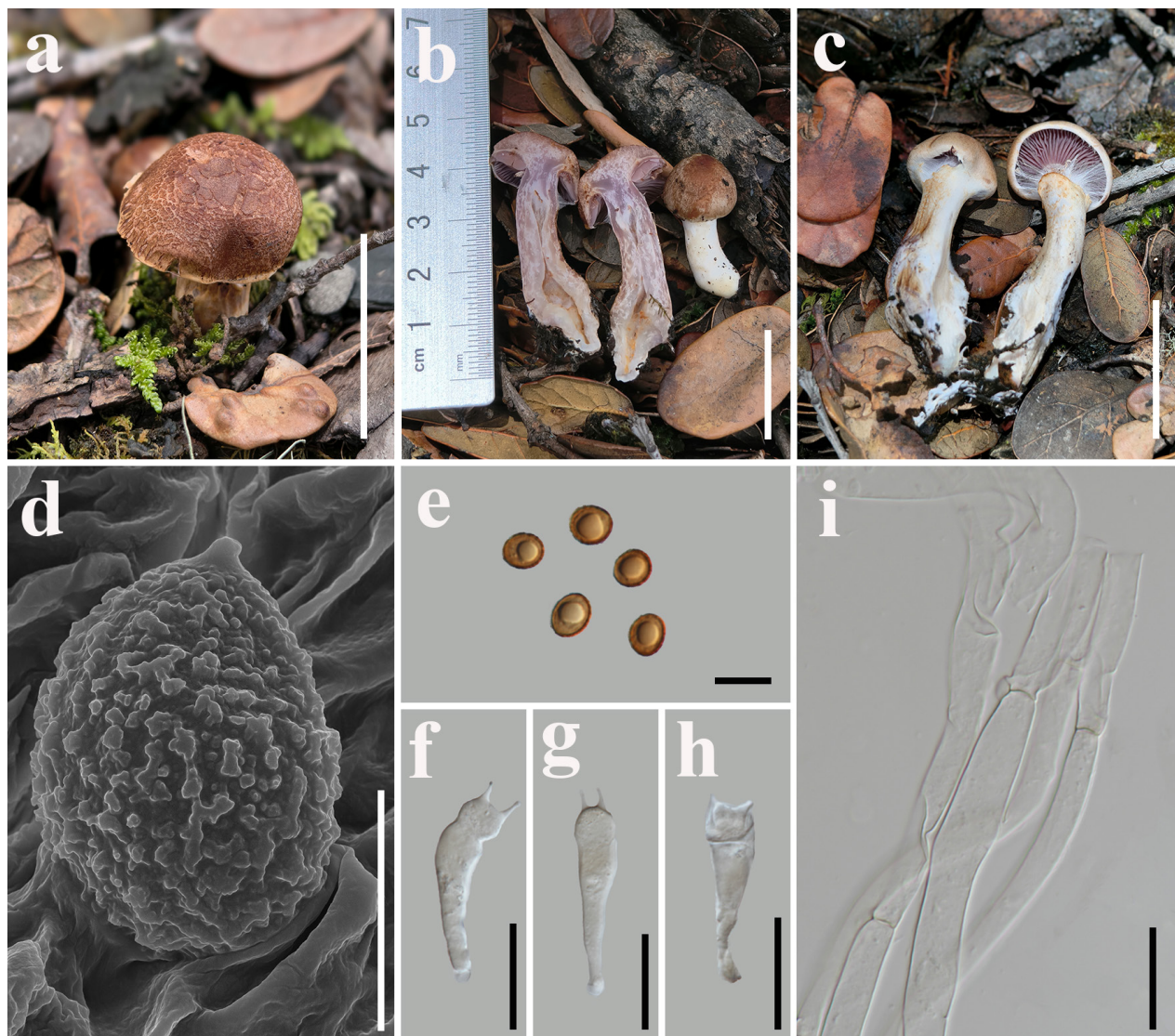
Fig. 5

**Chinese name.** 无底湖丝膜菌 (wu di hu si mo jun).

**Etymology.** “*wudihuensis*” refers to the type locality, Wudi Lake, a famous lake in Shangri-La City, China.

**Holotype.** CHINA • Yunnan Province: Shangri-La City, Potatso National Park, Wudi Lake at 28.249444°N, 99.977709°E, alt. 3850.3 m, in *Quercus aquifolioides* forest, 8 Aug. 2025, Zyue-121 (KUN-HKAS 151738).

**Diagnosis.** *Cortinarius wudihuensis* is macromorphologically most similar to *C. microalbocyaneus*, described from Northeast China, due to its small- to medium-sized basidiomata and a shared color transition from violaceous to brownish tones. However, *C. wudihuensis* can be distinctively distinguished by its slightly larger basidiospores (7–9 × 5.5–7 µm), a brown pileus covered with white fibrils that tends to crack with age, and a stipe featuring a distinct brown ring-like zone.



**Figure 5.** *Cortinarius wudihuensis*. **a, b.** Basidiomata (**a, b.** KUN-HKAS 151738, holotype; **c.** KUN-HKAS 151737); **d.** Scanning electron micrograph of basidiospore; **e.** Basidiospores; **f–h.** Basidia; **i.** Universal veil hyphae. Scale bars: 2 cm (**a–c**); 5  $\mu\text{m}$  (**d**); 10  $\mu\text{m}$  (**e**); 20  $\mu\text{m}$  (**f–i**).

**Macrostructures.** *Basidioma* small- to medium-sized. *Pileus* 1–3 cm diam., initially hemispherical, becoming applanate; surface initially brown (7D7) covered with white (A1) fibrillose, becoming light brown (7D6), covered with light brown (7D6) squamules, surface prone to cracking; context 1–6 mm thick, marbled with dull violet (15D4) and pale violet (15A3). *Lamellae* **adnexed**, 2–4 mm broad, moderately crowded, unequal, dull violet (15D4) to pasted violet (15A4); edge entire. *Stipe* 20–50  $\times$  7–12 mm, slightly thickened at the base, surface white, upper part with greyish violet (15E6) tinges, a brown (7C4) ring-like zone at the middle to upper part, internal part somewhat hollow. *Basal mycelium* white (A1). *Universal veil* white. *Odor* not distinctive.

**Microstructures.** *Basidiospores* [60/2/2] (6–) 7–9  $\times$  (5–) 5.5–7 (–7.5)  $\mu\text{m}$  [ $Q = (1.01\text{--}) 1.06\text{--}1.37$  (–1.43),  $Q = 1.21 \pm 0.1$ ], subglobose to ellipsoid, cinnamon in 10% KOH, reddish brown, and distinctly verrucose. *Basidia* 28.5–44  $\times$  6.5–12  $\mu\text{m}$ , clavate, thin-walled, mostly subhyaline, 4-spored. *Lamella edges* heterogeneous, with sterile cells, 21–29  $\times$  7–8  $\mu\text{m}$ , densely arranged, clavate,

subhyaline, thin-walled. **Lamella trama**, colorless, hyphae 3–4.5 µm diam. **Pleurocystidia** absent. **Pileipellis** duplex: epicutis thinly to moderately developed, hyphae interwoven, yellowish to yellowish brown hyphae, 3.5–5.5 µm wide, smooth to slightly encrusted; hypocutis well developed, hyphae 5–7 µm wide, hyaline or slightly yellowish brown. **Stipe hyphae** 4–5.5 µm diam., colorless, smooth. **Veil hyphae**, 6–9.5 µm diam. **Clamp connections** present.

**Habitat.** Scattered or gregarious on the ground in the *Quercus aquifolioides* forest.

**Distribution.** Known from the Northwestern Yunnan Province, China.

**Additional material examined.** CHINA • Yunnan Province: Shangri-La City, Potatso National Park, Wudi Lake at 28.249436°N, 99.977669°E, alt. 3867.4 m, in *Quercus aquifolioides* forest, 8 Aug. 2025, XDY-107 (KUN-HKAS 151737).

**Notes.** *Cortinarius wudihuensis* is characterized by its small to medium-sized basidiomata, a brown pileus covered with white fibrils that tends to crack with age, and a stipe featuring a distinct brown ring-like zone. Morphologically, it is most similar to *C. microalbocyaneus*, described from Northeast China (Xie et al. 2025). Both species share small basidiospores and a similar color transition from violaceous to brownish tones. However, *C. wudihuensis* can be distinguished by its slightly larger basidiospores (7–9 × 5.5–7 µm vs. 6.8–7.2 × 5.8–6.2 µm in *C. microalbocyaneus*) and its specific habitat in Shangri-La, potentially associated with *Quercus aquifolioides*. Phylogenetically, it belongs to sect. *Anomali*, where many small-sized species show high morphological convergence.

## Discussion

The morphological characteristics of *Cortinarius* subg. *Leprocycbe* have historically been regarded as relatively stable and distinct (Fries 1838). In classical morphological taxonomy, species delimitation within subg. *Leprocycbe* has primarily depended on a suite of diagnostic characters, including dry, non-hygrophanous pilei with tomentose to squamulose surfaces, subglobose to broadly ellipsoid verrucose basidiospores, and the presence of fluorescent pigments observable under ultraviolet light (Ammirati et al. 2021; Bidaud et al. 2021). However, reliance on isolated characters is frequently inadequate for delineating discrete species, as these traits may demonstrate intraspecific variation or represent convergent evolution among phylogenetically distant lineages. For instance, *C. venetus* from Europe, *C. veneto-occidentalis* from North America, and *C. hengduanensis* from China all share similar olive tones despite their geographic separation (Ammirati et al. 2021; Bidaud et al. 2021). The absence of olive tones in *C. tricholomopsoides* is particularly noteworthy (Ammirati et al. 2021). Although green or olive fluorescence attributed to leprocybin compounds has been traditionally regarded as a diagnostic characteristic for subgenus classification, the identification of *C. acuticonus* contributes to accumulating phylogenetic evidence indicating that olive phenotypic expression is not ubiquitous within this taxonomic subgenus. Recent taxonomic revisions in North America and Europe have established significant continental endemism within subg. *Leprocycbe* (Bidaud et al. 2021). The present phylogenetic analyses corroborate this biogeographical framework, demonstrating that the examined taxa represent phylogenetically divergent lineages relative to their European and American congeners. Ecologically, the newly described species exhibit specialized mycorrhizal

partnerships: *C. tricholomopsoides* demonstrates an obligate association with *Abies* spp., while *C. acuticonus* maintains exclusive symbiotic relationships with *Castanopsis* spp. These host-fungus associations differ substantially from the ecological requirements documented for European representatives of subg. *Leprocyebe*, which typically form mycorrhizal associations with *Fagus* or *Quercus* in temperate deciduous forests (Ammirati et al. 2021; Bidaud et al. 2021).

Similar severe taxonomic challenges are also evident in *Cortinarius* sect. *Anomali*. Although this section is species-rich and widely distributed, most known species were originally described from Europe and North America, and its species diversity in Asia has long been severely underestimated (Xie et al. 2025). The introduction of molecular phylogenetics has revealed extremely high cryptic diversity within this section and corrected many historical morphological misidentifications; for example, the widely reported *C. anomalus* has not actually been found in China, with many specimens turning out to be *C. subclackamasensis* or other species (Dima et al. 2016, 2021; Xie et al. 2025). Correctly identifying species in sect. *Anomali* faces significant challenges, primarily because macro- and micromorphological characteristics overlap extensively across species (Dima et al. 2016, 2021; Xie et al. 2025). Species in this section generally possess violaceous to blue tinges in early stages, which often fade to grayish brown or brown upon maturity (Dima et al. 2021). Furthermore, unlike European species that typically have a whitish universal veil, the veil color of Chinese species is highly variable (Dima et al. 2016, 2021). Within this complex taxonomic context, basidioma size and microscopic features serve as key clues for differentiating *Anomali* species. *Cortinarius wudihuensis*, newly described in this study, belongs to this section. Although it closely resembles *C. microalbocyaneus* in its small basidiomata and the color transition from violaceous to brownish tones, molecular evidence indicates that *C. wudihuensis* constitutes a completely independent phylogenetic lineage (Xie et al. 2025).

The identification of *C. acuticonus*, *C. tricholomopsoides*, and *C. wudihuensis* in subalpine forests of northwestern Yunnan highlights the severely underestimated diversity of *Cortinarius* in the province's alpine regions. In recent years, 36 new species of *Cortinarius* have been discovered in this region, including two species belonging to subg. *Leprocyebe* and 11 species belonging to sect. *Anomali* (Zhang et al. 2023; Zhou et al. 2023; Hong et al. 2024; Jia et al. 2025; Wang et al. 2025; Xie et al. 2025; Yang et al. 2025; Li et al. 2026; Zhou et al. 2026). It is worth noting that while the concatenated dataset yielded highly resolved and statistically robust topologies for the new taxa, a limitation of this study lies in the incomplete coverage of nrLSU sequences for several reference species retrieved from public databases. Due to the historical reliance on ITS as the primary fungal barcode (Horak 1987; Shao and Xiang 1997; Liimatainen 2014; Liimatainen et al. 2015, 2017, 2020, 2022a), many earlier collections and type descriptions lack complementary nrLSU data, resulting in missing data zones within the multi-gene matrix. Although maximum likelihood and Bayesian inference frameworks are mathematically resilient to such partial missing data, future systematic revisions would significantly benefit from expanding the sequencing coverage of protein-coding loci and complete ribosomal arrays across all historical type materials to further stabilize the deeper evolutionary branches within subg. *Leprocyebe* and sect. *Anomali*. In contrast to the comprehensive taxonomic documentation of subg. *Leprocyebe* in North America and Europe, only six species have previously been

reported from China, namely *C. cotoneus*, *C. hengduanensis*, *C. griseoaurantinus*, *C. nigrosquamosus*, *C. yadingensis*, and *C. venetus* (Keissler and Hohwag 1937; Horak 1987; Shao and Xiang 1997; Xie 2022; Hong et al. 2024; Dang et al. 2025). The taxonomic descriptions of *C. tricholomopsoides* and *C. acuticonus*, in conjunction with the recently described *C. hengduanensis*, *C. griseoaurantinus*, and *C. yadingensis*, substantially contribute to addressing the considerable knowledge deficiency concerning Asian representatives of this subgenus (Keissler and Hohwag 1937; Horak 1987; Shao and Xiang 1997; Hong et al. 2024; Dang et al. 2025). In China, 26 species of sect. *Anomali* have been previously reported. The current discovery of *C. wudihuensis* confirms that the species diversity of this section remains incompletely understood (Xie et al. 2025).

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

No AI tools were used in the preparation of this manuscript.

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### Author contributions

Methodology: Yi-Wen Yang; formal analysis: Yi-Wen Yang; investigation: Qi Zhao and Ying Zhang; resources: Qi Zhao and Ying Zhang; data curation: Yi-Wen Yang, Qi Zhao, and Ying Zhang; writing—original draft preparation: Yi-Wen Yang; writing—review and editing: Qi Zhao and Ying Zhang; funding acquisition: Qi Zhao and Ying Zhang.

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### Data availability

All of the data that support the findings of this study are available in the main text.