The plethora of *Tubeufiaceae* in lakes of the northwestern Yunnan plateau, China

Long-Li Li, Hong-Wei Shen, Dan-Feng Bao, Dhanushka N. Wanasinghe, Yong-Zhong Lu, Yuan Feng and Zong-Long Luo

The diversity of lignicolous freshwater fungi in northwestern Yunnan, China, has been studied for several years in the College of Agriculture and Biological Science, at Dali University. Over the last 5 years, we published two new genera and nine new species of *Tubeufiaceae* from northwestern Yunnan. This study focused on introducing tubeufia-like hyphomycetous fungi found in freshwater lakes in the northwestern Yunnan plateau. Eleven fresh collections of tubeufiaceous taxa were gathered and identified. Among them, a new genus, *Neomanoharachariella*, is introduced to accommodate *Neomanoharachariella aquatica*, which is characterized by a light brown to dark brown color, dicytoseptate, and broadly oval to ellipsoid and well-developed conidiophores.

Two new species, viz., *Neohelicosporium suae* and *Parahelicomyces suae*, one new record, *Helicoma rufum*, and three new collections, namely, *H. rugosum*, *P. hyalosporus*, and *Tubeufia cylindrothecia* are introduced based on morphological evidence and molecular phylogenetic analysis of combined ITS, LSU, tef 1-α, and RPB2 sequence data. Detailed descriptions and illustrations of these species are provided, and a morphological comparison with similar taxa is discussed.

**KEYWORDS**

*Dothideomycetes*, lignicolous freshwater fungi, helicosporous hyphomycetes, morphology, multigene phylogeny

**Introduction**

Lignicolous freshwater fungi are an important group of organisms, involved in nutrient cycling by decaying submerged wood (Hyde et al., 2016a; Shen et al., 2022). Yunnan Province is one of the richest biodiversity hotspots, containing abundant resources of lignicolous freshwater fungi, with more than 281 species reported since 1986 (Shen et al., 2022). Among lignicolous freshwater fungi, *Tubeufiaceae* is one of the most species-rich groups in *Dothideomycetes*. *Tubeufiaceae* was introduced by Boonme et al. (2014) based on molecular phylogenetic analysis to accommodate *Tubeufiaceae*. Liu et al. (2017) treated *Bezierromycetaceae* and *Wiesneriomycetaceae* as accepted families.
in Tubeufiales based on divergence time estimates. To date, Tubeufiales contains three families, viz., Bezerrymycetaceae, Tubeufiaceae, and Wiesneriomyctaceae. The majority of Tubeufiaceae comprised freshwater taxa (Doilom et al., 2017; Lu et al., 2018a;b; Dong et al., 2020; Hongsanan et al., 2020). The family was established by Barr (1979) based on the generic type Tubeufia (Penzig and Saccardo, 1897). In the last decade, several studies of Tubeufiaceae have been published, with many species reported in freshwater habitats; most of them were asexual morphs (Boonmee et al., 2011; Hyde et al., 2016b, 2017; Brahmanage et al., 2017; Luo et al., 2017; Liu et al., 2018; Lu et al., 2018a,b). Lu et al. (2018b) reappraised and provided an updated phylogenetic tree for Tubeufiales which included 13 new genera, and expanded the circumscription of the type family Tubeufiaceae. To date, Tubeufiaceae includes 47 genera. They are widely distributed in tropical, subtropical, and temperate regions (Boonmee et al., 2011, 2014; Luo et al., 2017; Lu et al., 2018b), and most taxa are saprobic on woody substrates in terrestrial and freshwater habitats (Cai et al., 2003; Zhao et al., 2007; Lu et al., 2018b).

Members of Tubeufiaceae are a group of microfungi that are morphologically fascinating (Zhao et al., 2007) and have helicosporous hyphomycetes. Tubeufiaceae has been reported as sexual and asexual morphs. Asexual morphologies are mostly found as helicosporous hyphomycetes, while some are phragmosporous and chlamydosporous conidia (Lu et al., 2018b; Dong et al., 2020). Helicosporous hyphomycetes make up a large part of the order Tubeufiales. They are known to be present in many genera, such as Acanthohelicosporium, Berkleasmium, Chlamydotubeufia, Dematiohelicosporum, Helicangiopsis, Helicodochium, Helicothalminus, Helicoma, Helicomyces, Helicostephanospora, Neohelicosporium, Neoacanthostigma, Neohelicomyces, Neohelicomyces, Parahelicomyces, and Tubeufia (Boonmee et al., 2011, 2014; Brahmanage et al., 2017; Lu et al., 2017a,b,c; 2018a,b; Luo et al., 2017; Liu et al., 2018). Chlamydosporous and phragmosporous hyphomycetes in Tubeufiaceae are reported in Aquaphila, Berkleasmium, Chlamydotubeufia, Dictyospora, Helicoma, Kamalomyces, Neohelicosporium, Tamhinispora, and Tubeufia (Lu et al., 2018b). Their sexual morphs are characterised by superficial ascomata, bitunicate asc, and hyaline to pale brown, elongate, obvoid or oblong, and septate ascospores (Barr, 1986; Kodsueb et al., 2006; Boonmee et al., 2011, 2014; Brahmanage et al., 2017; Lu et al., 2018b).

Helicoma was introduced by Corda (1837) with the type species H. muelleri. It is one of the earliest described helicosporous genus (Morgan, 1892; Linder, 1929; Moore, 1955). Helicoma includes two asexual morphs, one is characterized by conidia pleurogenous, helicoid, becoming loosely coiled in water, conidiogenous cells with denticles, and tooth-like protrusions. Other conidia are acrogenous, helicoid, circinate, tapering toward the apex, truncating at the base, and not becoming loose in water (Lu et al., 2018b). Neohelicosporium was introduced by Lu et al. (2018a) based on phylogenetic and morphological evidence. Currently, 24 species are accepted in the genus, of which 11 species were reported in freshwater habitats. Pseudohelicomyces was established by Lu et al. (2018b) to accommodate five species, viz., Ps. aquaticus, Ps. hyalosporus, Ps. indicus, Ps. paludosus, and Ps. talbotii (type species) based on multi-gene phylogenetic analysis. However, following previous publications, this generic name has an older homonym: Pseudohelicomyces (Valenzuela and Garnica, 2000), and this rendered the Pseudohelicomyces described by Lu et al. illegitimate. Lu et al. (2020) provided a proposal to conserve Pseudohelicomyces (Tubeufiaceae) against Pseudohelicomyces (Hymenogastraceae). Hsieh et al. (2021) established Parahelicomyces to replace Pseudohelicomyces and transferred all species of Pseudohelicomyces to Parahelicomyces. Until recently, nine species are accepted in Parahelicomyces (Lu et al., 2018b; Li et al., 2022; Tian et al., 2022). Tubeufia is the largest genus in Tubeufiaceae and is commonly reported as saprobes on submerged decaying wood in freshwater habitats (Ho et al., 2001; Cai et al., 2002; Liu et al., 2018; Lu et al., 2018b; Jayasiri et al., 2019). Members of Tubeufiaceae are mostly saprobic and widely distributed and are often found on woody substrates in terrestrial and freshwater habitats (Lu et al., 2018b). The southern China areas of Guangdong, Guangxi, Guizhou, Hubei, Yunnan, and other subtropical or tropical regions are very suitable for the growth and distribution of Tubeufiaceae fungi (Cai et al., 2002; Liu et al., 2018; Lu et al., 2018a,b).

During our investigation of freshwater fungi on submerged decaying wood, more than 100 specimens of freshwater hyphomycetes were collected from the lakes in the northwestern Yunnan plateau. This article aims to introduce eleven helicosporous hyphomycetes which were collected from the Luguhu and Shudu lakes. Phylogenetic analyses of combined ITS, LSU, tef 1-α, and RP22 sequence data place them in Helicoma, Neohelicosporium, Parahelicomyces, and Tubeufia. A new genus Neomanoharachariella and three new species, viz., Neomanoharachariella aquatica, Neohelicosporium suae, and Parahelicomyces suae are introduced with morphological and phylogenetic evidence. Helicoma rugosum is newly recorded in freshwater habitats for the first time in China. In addition, we combine Helicoma sp. (HKUCC 9118) as H. rugosum (HKUCC 9118) according to multi-gene phylogeny analysis and morphological evidence. Three known species, namely, Helicoma rugosum, Parahelicomyces hyalosporus, and Tubeufia cylindrothecia, are also accounted. Full descriptions, color photo plates of the species, and an updated phylogenetic tree for Tubeufiaceae are provided. This study provides a case study for lakes as a worthwhile niche area for the further study of hyphomycetous associations and hints that these lakes in the Yunnan plateau may potentially host numerous unknown fungal species.
Materials and methods

Collection, isolation, and morphology

Specimens of submerged decaying wood were collected from the Luguhu and Shuduhu lakes in the northwestern Yunnan province of China and were taken to the laboratory in ziplock plastic bags. The specimens were incubated at room temperature for 1 week in plastic boxes lined with moistened tissue paper. Specimen observations and isolation were performed by following the protocols provided by Liu et al. (2018) and Senanayake et al. (2020). Macromorphological characteristics of samples were observed using an Optec SZ 760 compound stereomicroscope. Temporarily prepared microscope slides were placed under a Nikon ECLIPSE Ni-U compound stereomicroscope for observation and micro-morphological-photography. The morphologies of colonies on native substrates were photographed with a Nikon SMZ1000 stereo zoom microscope. Single spore isolation was performed according to the following steps: the conidia suspension from specimens was transported using a sterilized pipette, placed on potato dextrose agar (PDA), and incubated at room temperature overnight. Germinated conidia were transferred to new PDA/malt extract agar (MEA) (Beijing land bridge technology CO., LTD., China) plates and incubated at room temperature (25°C). The specimens were deposited in the Herbarium of Cryptogams Kunming Institute of Botany, Academia Sinica (KUN-HKAS), Kunming, China. Living cultures were deposited in the China General Microbiological Culture Collection Center (CGMCC), Beijing, China, and the Kunming Institute of Botany Culture Collection Center, Kunming, China (KUNCC). Mycobank numbers were registered (https://www.mycobank.org). New species were established following the recommendations outlined by Chethana et al. (2021).

DNA extraction, PCR amplification, and sequencing

Fungal mycelium was removed from the surfaces of colonies that were grown on PDA or MEA for 4–6 weeks and transferred to a 1.5 ml centrifuge tube. A Trelief TM Plant Genomic DNA Kit (TSP101-50) was used to extract DNA from the ground mycelium according to the manufacturer's instructions. Four gene regions; ITS, LSU, tef 1-α, and RPB2 were amplified using ITS5/ITS4, LR0R/LR5 (Vilgalys and Hester, 1990), 983F/2218R, and RPB2-5F/RPB2-7CR (Liu et al., 1999). The PCR mixture was prepared as follows: 12.5 μl of 2 × Taq Master Mix (Genes and Biotech Co., Ltd), 1 μl of each primer, 1 μl of genomic DNA extract, and 9.5 μl of deionized water. The PCRs of ITS, LSU, tef 1-α, and RPB2 genes were processed as described in Su et al. (2015). PCR amplification was confirmed on 1% agarose electrophoresis gels stained with ethidium bromide. Sequencing was carried out by Tsingke Biological Engineering Technology and Services Co., Ltd (Yunnan, P.R. China).

Sequence alignment

Sequences were assembled using BioEdit. A BLAST search was performed on sequences with high similarity indices to find the closest matches with taxa in Tubeufaccae and in recently published data (Luo et al., 2017; Lu et al., 2018b; Dong et al., 2020). All consensus sequences and the reference sequences were automatically aligned with MAFFT version 7.0 (Kuraku et al., 2013; Katoh et al., 2019). Aligned sequences of each gene region (ITS, LSU, tef 1-α, and RPB2) were combined and manually improved using BioEdit v. 7.0 (Hall, 1999). Ambiguous regions were excluded from the analysis and gaps were treated as missing data.

Phylogenetic analyses

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian tree building criteria. Maximum likelihood (ML) analysis was carried out using RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis, 2006; Stamatakis et al., 2008) on the CIPRES Science Gateway website (Miller et al., 2010; http://www.phylo.org/portal2) and the estimated proportion of invariant sites was determined using the GTR+Γ+I model. Bayesian analyses were performed using MrBayes v. 3.1.2. (Ronquist and Huelsenbeck, 2003). The model of each gene was estimated using MrModeltest 2.3, and the GTR + I + G model was the best-fit model for ITS, LSU, tef 1-α, and RPB2 Bayesian analyses. Posterior probabilities (PP) (Ranala and Yang, 1996) were performed by Markov chain Monte Carlo sampling (BMCMC) in MrBayes v.3.1.2 (Liu et al., 2012). Six simultaneous Markov chains were run for 10 million generations, and trees were sampled every 100th generation (resulting in 100,000 trees). The first 20,000 trees, representing the burn-in phase of the analyses, were discarded and the remaining 80,000 (post-burning) trees were used for calculating PP in the majority rule consensus tree (Cai et al., 2006; Liu et al., 2012). Phylogenetic trees were represented by FigTree v. 1.4.0 and edited in Microsoft Office PowerPoint 2016. Newly-generated sequences in this study were submitted to GenBank, and the strain information used in this paper is provided in Table 1.

Results

Phylogenetic analyses

Phylogenetic analyses of combined ITS, LSU, tef 1-α, and RPB2 sequences comprised a total of 3,316 characters
| Taxa                        | Strain           | GenBank Accession No. |
|----------------------------|------------------|-----------------------|
|                            |                  | ITS | LSU | tef 1-α | RPB2 |
| Acanthohelicospora pinicola³ | MFLUCC 10-0116   | KF301526 | KF301534 | KF301555 | – |
| Acanthohelicospora scopula  | ANM 386          | GQ856141 | GQ850489 | – | – |
| Acanthostigmina multisepatum| ANM 475          | GQ856145 | GQ850492 | – | – |
| Acanthostigmina multisepatum| ANM 665          | GQ856144 | GQ850493 | – | – |
| Acanthotubeufia filiforme³ | ANM 101          | – | – | GQ850495 | – |
| Acanthotubeufia filiforme  | ANM 514          | GQ856146 | GQ850494 | – | – |
| Acanthotubeufia alliicans  | BCC 3463         | DQ341097 | DQ341100 | – | – |
| Acanthotubeufia alliicans  | BCC 3520         | DQ341098 | DQ341102 | – | – |
| Acanthotubeufia alliicans  | BCC 3543         | DQ341106 | DQ341101 | – | – |
| Acanthotubeufia alliicans  | MFLUCC 16-0010   | KX454165 | KX454166 | KX177034 | MF535255 |
| Acanthotubeufia alliicans  | MFLUCC 16-0020   | KX454167 | KX454168 | – | MF535256 |
| Berkleasmium aquaticum³    | MFLUCC 17-0049   | KY790444 | KY790432 | KY792608 | MF535268 |
| Berkleasmium fusiforme³    | MFLUCC 17-1978   | MHS588693 | MHS58820 | MHS50884 | MHS50107 |
| Berkleasmium guangxiense³ | MFLUCC 17-0042   | KY790448 | KY790436 | KY792612 | MF535270 |
| Berkleasmium longiporum³  | MFLUCC 17-1999   | MHS588698 | MHS58825 | MHS50889 | MHS51012 |
| Boerlagiomyces macrospora³| MFLUCC 12-0388   | KU144927 | KU764712 | KU872570 | – |
| Botryosphaeria dothidea    | CBS 115476       | KF66151 | DQ678051 | DQ767637 | DQ677944 |
| Chlamydotubeufia cylindrica³| MFLUCC 16-1130  | MHS587020 | MHS58830 | MHS50893 | MHS51018 |
| Chlamydotubeufia huaiyangplaensis³ | MFLUCC 10-0926 | – | – | – | – |
| Chlamydotubeufia krabeniensis³ | MFLUCC 16-1134 | KHY78767 | KHY78759 | KHY792598 | MF535261 |
| Dematiohelicoma pulchrum    | MUCL 39827       | AY916457 | AY856872 | – | – |
| Dematiohelicomyces helicosporus³ | MFLUCC 16-0213 | KX454169 | KX454170 | KY170355 | MF535258 |
| Dematiohelicomyces helicosporus | MFLUCC 16-0003 | MHS587030 | MHS58831 | MHS50894 | MHS51019 |
| Dematiohelicomyces helicosporus | MFLUCC 16-0007 | MHS587040 | MHS58832 | MHS50895 | MHS51020 |
| Dematiohelicosporus guttulatum³ | MFLUCC 17-2011 | MHS587050 | MHS58833 | MHS50896 | MHS51021 |
| Dematiohelicosporus chiangraiensis³ | MFLUCC 10-0115 | JN865210 | JN865198 | – | – |
| Dictyospora thailandica³   | MFLUCC 16-0001   | KY873627 | KY873622 | KY873286 | MHS51023 |
| Dictyospora thailandica    | MFLUCC 11-0512   | KF301528 | KF301536 | – | – |
| Dictyospora thailandica    | MFLUCC 16-0215   | KY873628 | KY873623 | KY873287 | – |
| Helicangiospora lignicola³ | MFLUCC 11-0378   | KF301523 | KF301531 | KF301552 | – |
| Helicocarctatus aquaticus¹ | MFLUCC 17-1996   | MHS587070 | MHS58835 | MHS50898 | MHS51024 |
| Helicocarctatus thailandicus¹ | MFLUCC 18-0332  | – | ON764311 | MK341685 | – |
| Helicodochium aquaticum    | MFLUCC 16-0008   | MHS587080 | MHS58836 | MHS50899 | MHS51025 |
| Helicodochium aquaticum⁷   | MFLUCC 17-2016   | MHS587090 | MHS58837 | MHS50900 | MHS51026 |
| Helicohyalinum aquaticum   | MFLUCC 16-1131   | KY873625 | KY873620 | KY873284 | MF535257 |
| Helicohyalinum infundibulum³ | MFLUCC 16-1133 | MHS58712 | MHS58840 | MHS50903 | MHS51029 |
| Helicoma ambians           | UAMH 10533       | AY916451 | AY856916 | – | – |
| Helicoma ambians           | UAMH 10534       | AY916450 | AY856869 | – | – |
| Helicoma aquaticum³         | MFLUCC 17-2025   | MHS58713 | MHS58841 | MHS50904 | MHS51030 |
| Helicoma bruneisporum³     | MFLUCC 17-1983   | MHS58714 | MHS58842 | MHS50905 | MHS51031 |
| Helicoma demissi           | NBRC 30667       | AY916455 | AY856897 | – | – |
| Helicoma fusiforme³         | MFLUCC 17-1981   | MHS58715 | – | MHS50906 | – |
| Helicoma guttulatum³       | MFLUCC 16-0022   | KX454171 | KX454172 | MF535254 | MHS51032 |
| Helicoma hongkongense      | MFLUCC 17-2005   | MHS58716 | MHS58843 | MHS50907 | MHS51033 |

(Continued)
TABLE 1 (Continued)

| Taxa                          | Strain     | GenBank Accession No. |
|-------------------------------|------------|-----------------------|
|                               | ITS        | LSU                   | tef 1-α | RPB2       |
| Helicoma khunkornensis       | MFLUCC 10–0119 | JN865203            | JN865191   | KF301559   | –         |
| Helicoma linderi             | NBRC 9207  | AY916454             | AY856895   | –          | –         |
| Helicoma longisporum         | MFLUCC 16–0002 | MHH8717            | MHH58844   | MHH50908   | MHH51034  |
| Helicoma longisporum         | MFLUCC 16–0005 | MHH58718            | –          | MHH50909   | MHH51035  |
| Helicoma longisporum         | MFLUCC 16–0211 | MHH58719            | MHH58845   | MHH50910   | MHH51036  |
| Helicoma longisporum         | MFLUCC 17–1997 | MHH58720            | MHH58846   | MHH50911   | MHH51037  |
| Helicoma miscanathi           | MFLUCC 11–0375 | KF301525            | KF301533   | KF301554   | –         |
| Helicoma muelleri            | CBS 964.69  | AY916453             | AY856877   | –          | –         |
| Helicoma muelleri            | UBC F13877  | AY916452             | AY856917   | –          | –         |
| Helicoma multiseptatum       | GZCC 16–0080 | MHH58721            | MHH58847   | MHH50912   | MHH51038  |
| Helicoma nematosporum        | MFLUCC 16–0001 | MHH58722            | MHH58848   | MHH50913   | MHH51039  |
| Helicoma rubriappendiculatum  | MFLUCC 18–0491 | MHH58723            | MHH58849   | MHH50914   | MHH51040  |
| Helicoma rafum               | MFLUCC 17–1806 | MHH58724            | MHH58850   | MHH50915   | –         |
| Helicoma rafum               | CGMCC 3.2354 | OP184080            | OP184069   | OP186053   | OP186061  |
| Helicoma rugosum             | ANM 196     | GQ856138             | GQ850482   | –          | –         |
| Helicoma rugosum             | ANM 953     | GQ856139             | GQ850483   | –          | –         |
| Helicoma rugosum             | ANM 1169    | –                     | GQ850484   | –          | –         |
| Helicoma rugosum             | JCM 2739    | –                     | AY856888   | –          | –         |
| Helicoma rugosum             | HKUCC 9118  | –                     | AY849966   | –          | –         |
| Helicoma septoconstrictum    | MFLUCC 17–1993 | MHH58725            | MHH58851   | MHH50916   | MHH51041  |
| Helicoma septoconstrictum    | MFLUCC 17–2001 | MHH58726            | MHH58852   | MHH50917   | MHH51042  |
| Helicoma siamensi            | MFLUCC 10–0120 | JN865204            | JN865192   | KF301558   | –         |
| Helicoma tectonica           | MFLUCC 12–0563 | KU144928            | KU764713   | KU872751   | –         |
| Helicoma vaccinii            | CBS 216.90  | AY916486             | AY856879   | –          | –         |
| Helicomyces hyalosporus      | GZCC 16–0070 | MHH58728            | MHH58854   | MHH50919   | MHH51047  |
| Helicomyces hyalosporus      | MFLUCC 17–0051 | MHH58731            | MHH58857   | MHH50922   | MHH51048  |
| Helicomyces torquatus        | MFLUCC 16–0217 | MHH58732            | MHH58858   | MHH50923   | MHH51048  |
| Helicomyces chiayiensis      | BCRC FU30842 | LC316604            | –          | –          | –         |
| Helicomyces colligatus       | MFLUCC 16–1132 | MHH58727            | MHH58853   | MHH50918   | MHH51043  |
| Helicosporium flavidum       | MFLUCC 16–1230 | KY873626            | KY873621   | KY873285   | –         |
| Helicosporium tateosporum    | MFLUCC 16–0226 | KY321324            | KY321327   | KY792601   | MHH51056  |
| Helicosporium vesicarium     | MFLUCC 17–1795 | MHH58739            | MHH58864   | MHH50930   | MHH51055  |
| Helicotrunatum palmigenum    | NBRC 32663  | AY916480             | AY856898   | –          | –         |
| Helicotubefia guangxiensis   | MFLUCC 17–0040 | MHH90018            | MHH90023   | MHH90028   | MHH90033  |
| Helicotubefia hydei          | MFLUCC 17–1980 | MHH90021            | MHH90026   | MHH90031   | MHH90036  |
| Helicotubefia jonesii        | MFLUCC 17–0043 | MHH90020            | MHH90025   | MHH90030   | MHH90035  |
| Kamalomyces thailandicus     | MFLUCC 11–0158 | MFS06883            | MFS06881   | MFS06885   | –         |
| Kamalomyces thailandicus     | MFLUCC 13–0233 | MFS06884            | MFS06882   | MFS06886   | –         |
| Manonarakarhiella tectonia   | MFLUCC 12–0170 | KU144935            | KU784705   | KU872762   | –         |
| Muritulchra aquatica         | DLUCC 0671   | KY320531             | KY320548   | –          | –         |
| Muritulchra aquatica         | KUMCC 15–0245 | KY320533             | KY320550   | KY320563   | MHH51057  |
| Muritulchra aquatica         | KUMCC 15–0276 | KY320534             | KY320551   | KY320564   | MHH51058  |
| Muritulchra aquatica         | MFLUCC 15–0249 | KY320532             | KY320549   | –          | –         |
| Neocanthurigaster fusiforme  | MFLUCC 11–0510 | KF301529            | KF301537   | –          | –         |

(Continued)
| Taxa                        | Strain       | GenBank Accession No. |
|----------------------------|--------------|-----------------------|
|                            |              | ITS                   | LSU       | tef 1-α    | RPB2       |
| Neochlamydotubeufia fusiformis\(^2\) | MFLUCC 16–0016 | MH558740              | MH558865  | MH550931  | MH551059   |
| Neochlamydotubeufia fusiformis\(^2\) | MFLUCC 16–0214 | MH558741              | MH558866  | MH550932  | MH551060   |
| Neochlamydotubeufia khunkornensis\(^2\) | MFLUCC 16–0118 | JN865202              | JN865190  | KF301564  | –           |
| Neochlamydotubeufia khunkornensis | MFLUCC 16–0025 | MH558742              | MH558867  | MH550933  | MH551061   |
| Neohelicoma fagacearum\(^2\)  | MFLUCC 11–0379 | KF301524              | KF301532  | KF301553  | –           |
| Neohelicomycetes aquaticus\(^2\) | KUMCC 15–0470 | KX454173              | KX454174  | –          | MH51067    |
| Neohelicomycetes grandisporus\(^2\) | MFLUCC 16–1106 | KY320530              | KY320547  | –          | MH51068    |
| Neohelicomycetes submersus\(^2\) | MFLUCC 16–0993 | KY320528              | KY320545  | KY320561  | MH51066    |
| Neohelicosporium abuense      | CBS 101688   | AY916470              | AY916085  | –          | –           |
| Neohelicosporium acrogenisporum | MFLUCC 17–2019 | MH558746              | MH558871  | MH550937  | MH51069    |
| Neohelicosporium aquaticum\(^2\) | MFLUCC 17–1519 | MF467916              | MF467929  | MF535242  | MF535272   |
| Neohelicosporium arundinellum | ANM 718      | GQ856140              | GQ850485  | –          | –           |
| Neohelicosporium bambuscola\(^2\) | MFLUCC 21–0156 | OL608157              | OL608146  | OL64517   | OL64523    |
| Neohelicosporium ellipsoides\(^2\) | MFLUCC 16–0229 | MH558748              | MH558873  | MH550939  | MH51071    |
| Neohelicosporium fusiformis\(^2\) | MFLUCC 16–0642 | MG017612              | MG017613  | MG017614  | –           |
| Neohelicosporium grisum       | UAMH 1694    | AY916873              | AY856902  | –          | –           |
| Neohelicosporium guangxianense | GZCC 16–0686 | MH558749              | MH558874  | MH550940  | MH51072    |
| Neohelicosporium guangxianense | MFLUCC 17–1522 | MF467922              | MF467935  | MF535248  | MF535278   |
| Neohelicosporium hyalosporum\(^2\) | GZCC 16–0076  | MF467923              | MF467936  | MF535249  | MF535279   |
| Neohelicosporium irregulare\(^2\) | MFLUCC 17–1796 | MH55875               | MH558877  | MH550943  | MH51075    |
| Neohelicosporium krabense      | MFLUCC 16–0224 | MH558754              | MH558879  | MH550945  | MH51077    |
| Neohelicosporium laxisporum\(^2\) | MFLUCC 17–2027 | MH558755              | MH558880  | MH550946  | MH51078    |
| Neohelicosporium morganii      | CBS 281.54   | MH857331              | MH868874  | –          | –           |
| Neohelicosporium morganii      | CBS 222.58   | AY916469              | AY856880  | –          | –           |
| Neohelicosporium ovoidesporum\(^2\) | GZCC 16–0064 | MH558756              | MH558881  | MH550947  | MH51079    |
| Neohelicosporium panacheum     | CBS 257.59   | MH857857              | –          | –          | –           |
| Neohelicosporium parvisporum   | GZCC 16–0078  | MF467924              | MF467937  | MF535250  | MF535280   |
| Neohelicosporium parvisporum   | MFLUCC 17–1523 | MF467926              | MF467939  | MF535252  | MF535282   |
| Neohelicosporium sp.           | HKUCC 10235  | –                     | AY849942  | –          | –           |
| Neohelicosporium sp.            | CBS 189.95   | AY916472              | AY856882  | –          | –           |
| Neohelicosporium submersum     | MFLUCC 17–2376 | NR_171979             | MN913738  | –          | –           |
| Neohelicosporium sueae\(^2\)   | CGMCC 3.23541 | OP184079              | OP184068  | OP186052  | OP265702   |
| Neohelicosporium taiwanense\(^7\) | BCRC FU30841 | LC316603              | –         | –         | –           |
| Neohelicosporium thailandicum\(^7\) | MFLUCC 16–0221 | MF467928              | MF467941  | MF535253  | MF535283   |
| Neomanoharachariella aquatica\(^7\) | CGMCC 3.23539 | OP184074              | OP184063  | OP186047  | OP186058   |
| Neomanoharachariella aquatica\(^7\) | CGMCC 3.23540 | OP184075              | OP184064  | OP186048  | OP186059   |
| Neotubeufia krahensi\(^2\)     | MFLUCC 16–1125 | MG012031              | MG012024  | MG012010  | MG012017   |
| Parahelicomyces aquaticus\(^2\) | MFLUCC 16–0234 | MH558766              | MH558891  | MH550958  | MH51092    |
| Parahelicomyces changmaicensis\(^2\) | MFLUCC 21–0159 | OL697884              | OL608145  | OL645154  | OL645242   |
| Parahelicomyces hyalosporus    | CBS 283.51   | AY916464              | AY856881  | DA77928   | DA77981    |
| Parahelicomyces hyalosporus    | KUMCC 15–0281 | KY320526              | KY320543  | KY320559  | MH51089    |
| Parahelicomyces hyalosporus    | KUMCC 15–0322 | KY320525              | KY320542  | KY320558  | –           |

(Continued)
| Taxa                                      | Strain               | GenBank Accession No. | ITS       | LSU       | tef 1-α   | RPB2    |
|------------------------------------------|----------------------|-----------------------|-----------|-----------|-----------|---------|
| **Parahelicomyces hyalosporus**          | KUMCC 15–0411        | KY320527              | KY320544  | KY320560  | –         |         |
| **Parahelicomyces hyalosporus**          | KUMCC 15–0430        | KY320524              | KY320541  | KY320557  | –         |         |
| **Parahelicomyces hyalosporus**          | MFLUCC 15–0343       | KY320523              | KY320540  | –         | –         |         |
| **Parahelicomyces hyalosporus**          | CGMCC 3.23353        | OP184073              | OP184062  | OP186046  | OP186057  |         |
| **Parahelicomyces hyalosporus**          | KUNCC 22–12443       | OP184076              | OP184065  | OP186049  | –         |         |
| **Parahelicomyces hyalosporus**          | KUNCC 22–12444       | OP184077              | OP184066  | OP186050  | OP186060  |         |
| **Parahelicomyces indicus**               | CBS 374.93           | AY916477              | AY856885  | –         | –         |         |
| **Parahelicomyces menglunicus**          | KUN HKAS 85795       | MK335914              | –         | MK335916  | –         |         |
| **Parahelicomyces paludosus**            | CBS 120503           | DQ341095              | DQ341103  | –         | –         |         |
| **Parahelicomyces querus**               | MFLUCC 17–0895       | MK347720              | MK347934  | MK360077  | MK434906  |         |
| **Parahelicomyces suae**                 | CGMCC 3.23353        | OP184072              | OP184061  | OP186045  | OP186056  |         |
| **Parahelicomyces suae**                 | CGMCC 3.23358        | OP184081              | OP184070  | OP186054  | –         |         |
| **Parahelicomyces tallouei**             | MUCL 33010           | AY916465              | AY856874  | –         | –         |         |
| **Parahelicomyces talbotii**             | MFLUCC 17–2021       | MH558765              | MH558890  | MH550957  | MH551091  |         |
| **Parahelicomyces yunnanensis**          | CGMCC 3.20429        | MZ092717              | MZ841658  | –         | OM022000  |         |
| **Pleuro helicosporium parvisporum**     | MFLUCC 17–1982       | MH558764              | MH558899  | MH550956  | MH551088  |         |
| **Pseudo helicoon gigantisporum**        | BCC 3550             | AY916467              | AY856904  | –         | –         |         |
| **Pseudo helicoon subglobosum**          | BCRC FU30843         | LC316607              | LC316610  | –         | –         |         |
| **Tamhinspora indica**                   | NFOCC 2924           | KC469282              | KC469283  | –         | –         |         |
| **Tamhinspora ruminocarii**              | NFOCC 4231           | MG263746              | MG263745  | –         | –         |         |
| **Thaxteriellopsis lignicola**           | MFLUCC 10–0123       | JN865207              | JN865195  | KF301562  | –         |         |
| **Thaxteriellopsis lignicola**           | MFLUCC 10–0124       | JN865208              | JN865196  | KF301561  | –         |         |
| ** Tubefusia abundata**                  | ATCC 42524           | AY916458              | AY856911  | –         | –         |         |
| ** Tubefusia aquatica**                  | MFLUCC 16–1249       | KY320522              | KY320539  | KY320556  | MH551142  |         |
| ** Tubefusia aquatica**                  | MFLUCC 17–1794       | MH558770              | MH558895  | MH550962  | MH551096  |         |
| ** Tubefusia bambusicola**               | MFLUCC 17–1803       | MH558771              | MH558896  | MH550963  | MH551097  |         |
| ** Tubefusia brevis**                    | MFLUCC 17–1799       | MH558772              | MH558897  | MH550964  | MH551098  |         |
| ** Tubefusia brunnea**                   | MFLUCC 17–2022       | MH558773              | MH558898  | MH550965  | MH551099  |         |
| ** Tubefusia chiangmaiensis**            | MFLUCC 11–0514       | KF301530              | KF301538  | KF301557  | –         |         |
| ** Tubefusia chiangmaiensis**            | MFLUCC 17–1801       | MH558774              | MH558899  | MH550966  | MH551100  |         |
| ** Tubefusia chlamydospora**             | MFLUCC 16–0223       | MH558775              | MH558900  | MH550967  | MH551011  |         |
| ** Tubefusia cocci**                     | MFLUCC 22–0001       | OM102544              | OL985957  | OM354866  | OM354941  |         |
| ** Tubefusia cylindrothecia**            | MFLUCC 16–1253       | KY320519              | KY320536  | KY320553  | –         |         |
| ** Tubefusia cylindrothecia**            | MFLUCC 16–1283       | KY320518              | KY320535  | KY320552  | MH551143  |         |
| ** Tubefusia cylindrothecia**            | MFLUCC 17–1792       | MH558776              | MH558901  | MH550968  | MH551102  |         |
| ** Tubefusia cylindrothecia**            | MFLUCC 11–0076       | MT627709              | MN913702  | –         | –         |         |
| ** Tubefusia cylindrothecia**            | MFLUCC 10–0919       | MT627710              | MN913701  | –         | –         |         |
| ** Tubefusia cylindrothecia**            | CGMCC 3.23352        | OP184071              | OP184060  | OP186044  | OP186055  |         |
| ** Tubefusia dictyospora**               | MFLUCC 17–1805       | MH558778              | MH558903  | MH550970  | MH55104  |         |
| ** Tubefusia eccentrica**                | GZCC 16–0084         | MH558781              | MH558906  | MH550973  | MH55107  |         |
| ** Tubefusia eccentrica**                | MFLUCC 17–1524       | MH558782              | MH558907  | MH550974  | MH55108  |         |
| ** Tubefusia entadae**                   | MFLU 18–2102         | NR633232              | –         | –         | –         |         |
| ** Tubefusia fanghengensis**             | MFLUCC 17–0047       | MH558783              | MH558908  | MH550975  | MH55109  |         |
| ** Tubefusia filiformis**                | MFLUCC 16–1128       | –                     | KY092407  | KY117028  | MFS35284  |         |

(Continued)
TABLE 1 (Continued)

| Taxa           | Strain       | GenBank Accession No.          |
|----------------|--------------|--------------------------------|
|                | ITS          | LSU                            | tef 1-α               | RPB2               |
| Tubeufia filiformis | MFLUCC 16–1135 | KY092416                       | KY092411              | KY117032           | MF535285          |
| Tubeufia geniculataT | BCRC FU30849   | LC335817                       | –                     | –                  | –                 |
| Tubeufia geniculata | NCYU U2–1B     | LC335816                       | –                     | –                  | –                 |
| Tubeufia guangxiensis | MFLUCC 17–0045 | MG012025                       | MG012018              | –                  | –                 |
| Tubeufia heichianusT | MFLUCC 17–0052 | MJ558785                       | MJ558810              | MJ550978           | MJ551112          |
| Tubeufia hyalospora | MFLUCC 15–1250 | MJ558786                       | MJ558811              | MJ550979           | –                 |
| Tubeufia inaequalis | MFLUCC 17–0053 | MJ558789                       | MJ558814              | MJ550982           | MJ551115          |
| Tubeufia javanica | MFLUCC 12–0545 | JY800034                       | JY800036              | –                  | –                 |
| Tubeufia krabiensis | MFLUCC 16–0228 | MJ558792                       | MJ558917              | MJ550985           | MJ551118          |
| Tubeufia latispora | MFLUCC 16–0219 | KY092417                       | KY092412              | KY117033           | MF535286          |
| Tubeufia laxispora | MFLUCC 16–0232 | KY092413                       | KY092408              | KY117029           | MF535287          |
| Tubeufia laxispora | MFLUCC 17–2023 | MJ558794                       | MJ558919              | MJ550987           | MJ551121          |
| Tubeufia lilliputiae | NBRC 32664     | AY916483                       | AF386899              | –                  | –                 |
| Tubeufia longihelicospora | MFLUCC 16–0753 | MZ835531                       | MZ835655              | MZ67106            | –                 |
| Tubeufia longihelicospora | MFLUCC 21–0151 | OL606156                       | OL606149              | OL64520            | OL64526           |
| Tubeufia longiseta | MFLUCC 15–0188 | KU940133                       | –                     | –                  | –                 |
| Tubeufia machaerinae | MFLUCC 17–0055 | MJ558795                       | MJ558920              | MJ550988           | MJ551122          |
| Tubeufia mackenzieiT | MFLUCC 16–0222 | KY092415                       | KY092410              | KY117031           | MF535288          |
| Tubeufia nigroseptumT | CGMCC 3.20430  | MZ092716                       | MZ093187              | OM022002           | OM022001          |
| Tubeufia parvispora | MFLUCC 17–1992 | MJ558796                       | MJ558921              | MJ550989           | MJ551123          |
| Tubeufia parvispora | MFLUCC 17–2009 | MJ558798                       | MJ558923              | MJ550991           | MJ551125          |
| Tubeufia rooseholicospora | MFLUCC 15–1247 | KX454177                       | KX454178              | –                  | MJ551144          |
| Tubeufia rubraT | GZCC 16–0881 | MZ853187                       | MJ558926              | MJ550994           | MJ551128          |
| Tubeufia sahyadriensisT | NFCCI 4252    | MH033849                       | MH033850              | MH033851          | –                 |
| Tubeufia sessilis | MFLUCC 16–0021 | MJ558803                       | –                     | MJ550996           | MJ551130          |
| Tubeufia symphydylaspora | GZCC 16–0049  | MJ558804                       | MJ558928              | MJ550997           | MJ551131          |
| Tubeufia symphydylaspora | GZCC 16–0051  | MJ558805                       | MJ558929              | MJ550998           | MJ551132          |
| Tubeufia sympodihylospora | MFLUCC 17–0044 | MJ558806                       | MJ558930              | MJ550999           | MJ551133          |
| Tubeufia sympodilaxispora | MFLUCC 17–0048 | MJ558808                       | MJ558932              | MJ551001           | MJ551135          |
| Tubeufia taiwanensis | BCRC FU30844 | LC316605                       | –                     | –                  | –                 |
| Tubeufia tectonaeT | MFLUCC 12–0392 | KU144923                       | KU764706              | KU872763           | –                 |
| Tubeufia tectonae | MFLUCC 16–0235 | MJ558809                       | MJ558833              | MJ551002           | MJ551136          |
| Tubeufia tratensisT | MFLUCC 17–1993 | MJ558811                       | MJ558835              | MJ551004           | MJ551138          |
| Tubeufia xylophila | GZCC 16–0038 | MJ558812                       | MJ558836              | MJ551005           | MJ551139          |
| Tubeufia xylophila | MFLUCC 17–1520 | MJ558813                       | MJ558937              | MJ551006           | MJ551140          |

Ex-type strains are indicated by T after the species name. Newly generated sequences are indicated in bold. The symbol “–” indicates information unavailable.

including gaps, ITS (1–534 bp), LSU (535–1,362 bp), tef 1-α (1,363–2,273 bp), and RPB2 (2,274–3,316 bp) including 217 strains, with Botryosphaeria dothidea (CBS 115476) as the outgroup taxon. RAxML and Bayesian analyses of the combined dataset resulted in phylogenetic reconstructions with largely similar topologies. The result of ML analyses with a final likelihood value of −53,732.520635 is shown in Figure 1. Alignment exhibits 1,618 distinct alignment patterns; the proportion of gaps and completely undetermined characters in this alignment is 27.38%. Gamma distribution shape
Phylogenetic analyses showed that the new isolates were nested in *Tubeufiaceae* with close affinities to four exciting genera, *viz.*, *Helicoma*, *Neohelicosporium*, *Parahelicomyces*, *Tubeufia*, and the new genus *Neomanoharachariella*, forming a distinct clade among the genera of *Tubeufiaceae*. KUNCC 22–12445 and CGMC 3.23543 clusted within *Helicoma*, sister to *Helicom rugosum* (ANM 196, ANM 953, ANM 1169, and JCM 2739) with 97% ML and 0.99 PP support values. Another strain, CGMC 3.23543 nested in *H. rubriappendiculatum* (MFLUCC 18–0491) and *H. rufum* (MFLUCC 17–1806) with 87% ML and 0.99 PP support values. CGMC3.23541 nested in *N. morganii* (CBS 281.54) with strong bootstrap support (100% ML/1.00 PP). CGMC3.23539 and CGMC 3.23540 clusted as a monophyletic clade sister to *Helicocartatus aquaticus* (MFLUCC 17–1996) and *H. tailandicus* (MFLUCC 18–0332). Three new collections (CGMC 3.23535, KUNCC 22–12443, and KUNCC 22–12444) clusted within *Parahelicomyces hyalosporus* (CBS 283.51, MFLUCC 15–0343, KUMCC 15–0430, KUMCC 15–0411, KUMCC 15–0322, and KUMCC 15–0281) with 100% ML and 1.00 PP support. CGMC 3.23534 and CGMC 3.23538 formed a sister lineage to *Parahelicomyces yunnanensis* (CGMC 3.20429) with 90% ML and 1.00 PP support. CGMC 3.23552 clusted with five strains of *Tubeufia cylindrothecia* (MFLUCC 10–0919, MFLUCC 11–0076, MFLUCC 16–1253, MFLUCC 16–1283, and MFLUCC 17–1792) with 100% ML and 1.00 PP support.

**Taxonomy**

**Helicoma rugosum** (C. Booth) Boonmee and K.D. Hyde [as 'rugosa'], Fungal Divers. 68: 266 (2014), Figure 2

*Index Fungorum*: IF 340543; *Facesoffungi number*: FoF 02650

Saprobit on submerged decaying wood in the lake.

**Asexual morph**: Hyphomycetous, helicosporous. Colonies on natural substrate superficial, effuse, discrete, dilute, and light brown to brown. Mycelium composed of partly immersed, partly superficial, septate, pale brown to brown, branched hyphae, with masses of crowded, glistening conidia. Conidiophores 95–151 µm long, 5·4–6·8 µm wide (S = 122.6 × 6 µm, n = 20), macronematous, mononematous, straight to slightly bent, unbranched, septate, cylindrical, erect, pale brown to brown, and smooth-walled. Conidiogenous cells 9–12 µm long, 5–6 µm wide, holoblastic, mono- to polyblastic, integrated, intercalary, cylindrical, with denticles, tiny tooth-like protrusions (0.9–2.6 µm long, 0.5–1.7 µm wide), brown, and smooth-walled. Conidia 60.7–85.5 µm diameter, conidial filament 4–8.5 µm wide (S = 73 × 4.4 µm, n = 20), 216–290 µm long, slightly coiled 1.0–2.5 times, pleurogenous, helicoid, rounded at tip, septate, becoming loosely coiled in water, guttulate, pale brown, and smooth-walled. Sexual morph: not observed.

**Culture characteristics**: Conidia germinating on PDA and germ tubes produced from conidia within 12 h. Colonies growing on PDA, irregular, center umbonate, with a rough surface, wrinkle, edge undulate, reaching 10–15 mm in 2 weeks at 26°C, and pale brown to brown in the PDA medium. Mycelium superficial and partially immersed, branched, septate, hyaline to pale brown, and smooth-walled.

**Material examined**: China, Yunnan Province, Lugubu lake, on submerged decaying wood, 22 October 2021 (Altitude: 2,625 m, 27°42′41″N, 100°46′48″E), Long-Li Li, L-1013 (KUN-HKAS 124608), living culture, KUNCC 22–12445.

*Notes*: *Helicom rugosum* was reported by Boonmee et al. (2014) to combine *Sphaeria helicoma*, *Thaxteriella helicoma*, and *Tubeufia rugosa* based on phylogenetic and morphological evidence. *H. rugosum* (KUNCC 22–12445) resembles *H. rufum*, presenting macronematous, mononematous, unbranched or branched, septate conidiophores, holoblastic, mono- to ployblastic conidiogenous cells, helicoid, and septate conidia. However, *H. rugosum* (KUNCC 22–12445) is distinct from *H. rufum* as it has shorter and narrower conidiophores (95–151 × 5·4–6·8 vs. 110–210 × 7·8–5·3 µm, longer and wider conidia (60.7–85·5 × 4·4–8·8 vs. 35·45 × 4·5–5·5 µm), and shorter conidial filaments (216–290 × 4–5 vs. 240–410 × 4·5–5·5 µm). Furthermore, *H. rufum* produces a reddish brown pigment in the PDA medium in 7 days but *H. rugosum* lacks this characteristic. In the phylogenetic analyses, *H. rugosum* (KUNCC 22–12445) cluster together with *H. rugosum* (ANM 196, ANM 1169, ANM 953, and JCM 2739) and *Helicoma* sp. (HKUCC 9118) with strong support (91% ML and 0.99 PP). In this study, we introduce our new collection with *Helicoma* sp. (HKUCC 9118) as *H. rugosum* because of identical LSU nucleotide sequences and morphological characteristics. Our fresh collection is morphologically similar to *Helicoma* sp. (HKUCC 9118) (Kodsueb et al., 2004) in terms of conidiogenous cells with tiny tooth-like protrusions, denticil, conidiophores brownish-gray, upright, and the same conidia size (61–86 × 4–5 vs. 37–86·4 × 4·6–5·4 µm). Furthermore, both of their morphologies fitting into the generic group *Helicoma*, and the analyses show that they should be the same species.

**Helicoma rufum** Y.Z. Lu, J.C. Kang, and K.D. Hyde, Fungal Divers. 92: 183 (2018), Figure 3

*Index Fungorum*: IF 554843; *Facesoffungi number*: FoF 04718

Saprobit on submerged decaying wood in the lake.

**Asexual morph**: Hyphomycetous, helicosporous. Colonies...
superficial, effuse, gregarious, and brown. Mycelium composed of immersed, partly superficial, hyaline to pale brown, septate, branched hyphae, with masses of crowded, glistening conidia. Conidiophores 136–209 µm long, 6–7 µm wide (± = 173 ± 6.5 µm, n = 30), macronematous, mononematous, cylindrical, erect, straight to slightly bent, mostly unbranched, septate, the lower part brown and the upper part pale yellow, and smooth-walled. Conidiogenous cells 12–14 µm long, 5–7 µm wide, holoblastic, mononematous, integrated, intercalary, cylindrical, with denticles, rising laterally from the lower portion of conidiophores as tiny tooth-like protrusions (2.7–3.9 µm long, 1.5–2.3 µm wide), brown, and smooth-walled. Conidia 57–104 µm diameter, conidial filament 3.4–5.2 µm wide (± = 80.6 ± 4.3 µm, n = 20), 248–327 µm long, solitary, pleurogenous, helicoid, rounded at tip, septate, slightly constricted at septa, loosely coiled 1.5–3.5 times, becoming loosely coiled in water, guttulate, hyaline to pale brown, and smooth-walled. Sexual morph: not observed.

Culture characteristics: Conidia germinating on PDA within 12 h and many germ tubes produced from conidium cells. Colonies growing on PDA, reaching 25 mm, and started producing reddish brown pigment in 3 weeks at 26°C, brown to reddish brown in the PDA medium, irregular, with a
FIGURE 1 (Continued)
FIGURE 1
Phylogram generated from maximum likelihood analysis (RAxML) of Tubeufiaceae based on ITS, LSU, tef-1-α, and RPB2 sequence data. Maximum likelihood bootstrap values equal to or above 75% and Bayesian posterior probabilities (PP) equal to or above 0.95 are given above the nodes. The tree is rooted at Botryosphaeria dothidea CBS 115476. Newly-generated sequences are indicated in red. Ex-type strains are indicated in black/red bold.

flat surface, edge slightly undulate. Mycelium superficial and partially immersed, branched, septate, hyaline to pale brown, and smooth-walled.

Material examined: China, Yunnan Province, Luguhu lake, on submerged decaying wood (Altitude: 2,717 m, 27° 42′41″N, 100° 46′48″E), 21 October 2021, Long-Li Li, L-1032 (KUN-HKAS 124609), living cultures, CGMCC 3.23543 = KUNCC 22–12439.

Notes: Helicoma rufum was introduced by Lu et al. (2018b) on decaying wood in a mountain in Thailand. The new isolate L-1032 collected from freshwater habitats was identified as H. rufum based on the phylogenetic analyses and the morphological features. Our new collection CGMCC 3.23543 clusters in the same clade with H. rufum (MFLUCC 17–1806) except for the conidia diameter (57–104 vs. 35–45 µm long). The nucleotide comparisons show 4 bp, 1 bp, and 2 bp of ITS, LSU, and tef-1-α differences between the new isolate CGMCC 3.23543 and H. rufum (MFLUCC 17–1806). Between H. rubriappendiculatum (MFLUCC 18–0491) and H. rufum (CGMCC 3.23543), there are 4, 2, and 6 bp of ITS, LSU, and tef-1-α differences; compared with H. rubriappendiculatum, H. rufum (CGMCC 3.23543) produces a reddish brown pigment in the PDA medium and presents a longer conidia diameter (57–104 vs. 25–35 µm), lacking the characteristic red appendant near the apex in conidiophores. Thus, we identify the new isolate as H. rufum based on both phylogenetic analyses and morphological characteristics. This is the first report of H. rufum in freshwater habitats and its occurrence in China.
FIGURE 2
Helicoma rugosum (KUN–HKAS 124608). (a,b) Colony on decaying wood. (c–f) Conidiophores with attached conidia. (g,h) Conidiogenous cells. (i–l) Conidia. (n) Germinating conidium. (o,p) Colony on PDA observed from above and below. Scale bars: (c,d) 30 µm, (e) 50 µm, (f) 50 µm, (g,h) 10 µm, and (i–n) 20 µm.
**FIGURE 3**

*Helicoma rufum* (KUN-HKAS 124609). (a,b) Colony rises from mycelium on natural wood substrate. (c–f) Conidiophores with attached conidia. (g,h) Conidiogenous cells. (i–l) Conidia. (m) Germinating conidium. (n,o) Culture on PDA. Scale bars: (c–f) 60 μm, (g,h) 10 μm, and (i–m) 20 μm.
FIGURE 4

*Neohelicosporium suae* (KUN-HKAS 124610, holotype). (a) Colony on decaying wood. (b,c,e) Conidiophores with attached conidia. (d) Conidiophores. (f–h) Conidiogenous cells. (i–l) Conidia. (m) Germinating conidium. (n,o) Colony on PDA observed from above and below. Scale bars: (b,c) 30 μm, (d,e) 20 μm, and (f–m) 10 μm.
Neohelicosporium suae L.L. Li, H.W. Shen and Z.L. Luo, sp. nov.

MycoBank number: MB 845321, Figure 4

Holotype—KUN-HKAS 124610

Etymology—“suae” (Lat.) in memory of the Chinese mycologist Prof. Hong-Yan Su (4 April 1967–3 May 2022).

Saprobi on submerged decaying wood in the lake. Asexual morph: Hyphomycetous, helicosporous. Colonies on substratum superficial, effuse, and white. Mycelium composed of superficial, partly immersed, brown, septate, branched hyphae, with crowded by conidial masses. Conidiophores 52–97 µm long, 4.2–5.1 µm wide (x = 75 × 4.7 µm, n = 20), macronematous, mononematous, erect, cylindrical, unbranched or less branched, 3–6-septate, hyaline to pale brown, and smooth-walled. Conidiogenous cells 15–27 µm long, 3.5–5.1 µm wide (x = 21 × 4.2 µm, n = 20), holoblastic, mono- to polyblastic, cylindrical, truncate at apex after conidial secession. Conidia germinating on PDA within 8 h. Colonies growing on PDA, circular, with a flat surface, edge entire, reaching 28 mm in 3 weeks at room temperature, pale brown to brown in the MEA medium. Mycelium superficial and partially immersed, branched, septate, hyaline to pale brown, and smooth-walled. Sexual morph: not observed.

Culture characteristics: Conidia germinating on PDA within 8 h. Colonies growing on PDA, circular, with a flat surface, edge entire, reaching 28 mm in 3 weeks at room temperature, pale brown to brown in the MEA medium. Mycelium superficial and partially immersed, branched, septate, hyaline to pale brown, and smooth-walled.

Material examined: China, Yunnan Province, Luguhu lake, on submerged decaying wood in the lake (Altitude: 2.242 m, 26°48′29″N, 100°43′4.8″E), 21 October 2021, Long-Li Li, L-1030 (KUN-HKAS 124610, holotype), ex-type cultures, CGMCC 3.23541 = KUNCC 22–12438.

Notes: Neohelicosporium suae is introduced as a new species based on morphological and phylogenetic evidence. In phylogeny, N. suae (CGMCC 3.23541) is a sister to N. morganii with strong bootstrap support (100% ML and 1.00 PP). Based on pairwise nucleotide comparisons, the new strain N. suae (CGMCC3.23541) is different from N. morganii (CBS 281.54) in 9/532 bp (1.69%) of the ITS and 3/804 bp (0.37%) of the LSU. Morphologically, N. suae can be distinguished from N. morganii: the conidiophores of N. suae are unbranched or less branched, the latter are branched and shorter (52–97 µm long, 4.2–5.1 µm wide vs. up to 145 µm long, 5–7 µm wide) (Zhao et al., 2007), and the number of septa is more than 6. The conidiogenous cells of N. suae are 15–27 µm long, swollen, with longer and wider denticles (2–3 × 1.5–2.4 vs. 1–2.5 × 0.5–1.5 µm), terminal, whereas N. morganii displays no swelling. Furthermore, N. suae is distinct from N. morganii, presenting distinguished conidia characteristics in terms of a larger diameter (45–55 × 5–7 vs. 17–23 × 3–4 µm).

Neomanoharachariella L.L. Li, H.W. Shen, and Z.L. Luo, gen. nov.

MycoBank number: MB 845535

Etymology—The generic epithet, neo (Lat., new), refers to the similarity to Manoharachariella.

Saprobi on decaying wood in the lake. Asexual morph: Hyphomycetous, dictyosporous. Colonies on the substratum superficial, effuse, and dark brown. Conidiophores macronematous, mononematous, erect, cylindrical, unbranched, straight or flexuous, paler, and smooth-walled. Conidiogenous cells monoblastic, integrated, terminal, cylindrical, subhyaline to pale brown, and smooth-walled. Conidia holoblastic smooth, shiny, simple, broadly oval to ellipsoid, muriform, tuberculous at the top, white and pale brown when immature, becoming dark to black when mature, and pale yellow at the basal cell and brown at other parts. Sexual morph: not observed.

Type species: Neomanoharachariella aquatica L.L. Li, H.W. Shen, and Z.L. Luo.

Notes: Neomanoharachariella is morphologically similar to Chlamydotubeufia, Dictyospora, and Neochlamydotubeufia, presenting dictyoseptate, broadly oval to ellipsoid, and darkened to black when matured conidia. However, Neomanoharachariella can be distinguished from other chlamydotubeufial genera by well-developed conidiophores. The morphological characteristics allow the assignment of Neomanoharachariella to Tubefiaceae. In phylogeny, it formed a well-separated clade from all other genera of Tubefiaceae (Figure 5). The molecular phylogenetic studies indicate its placement in Tubefiaceae as a genus that is phylogenetically close to the genera, Berkleiasium, Dictyospora, Helicoarctatus, Helicoma, and Helicosporium.

Neomanoharachariella aquatica L.L. Li, H.W. Shen, and Z.L. Luo, sp. nov.

MycoBank number: MB 845536, Figure 5

Holotype—KUN-HKAS 124611

Etymology—“aquatica” referring to the aquatic habitat of this fungus.

Saprobi on decaying woods in the lake. Asexual morph: hyphomycetous, dictyosporous. Colonies on the substratum superficial, effuse, and dark brown. Conidiophores 20–31 µm long, 3.5–4.2 µm wide (x = 25 × 4 µm, n = 20), macronematous, mononematous, erect, cylindrical, unbranched, straight or flexuous, paler, and smooth-walled. Conidiogenous cells monoblastic, integrated, terminal, cylindrical, subhyaline to pale brown and smooth-walled. Conidia 37–61 µm long, 17–32 µm wide (x = 49 × 24 µm, n = 20), muriform 8–10-transversely septate, with 1–4-longitudinal septa, smooth, shiny, simple, broadly oval to ellipsoid, tuberculous at the top, hyaline to pale brown when immature, becoming dark to black when mature, and pale yellow at the basal cell and brown at other parts. Sexual morph: not observed.
Neomanoharachariella aquatica (KUN-HKAS 124611, holotype). (a, b) Colony erect on decaying wood. (c–e) Conidiophores with attached conidia. (f,g) Conidiogenous cells. (h–m) Conidia. (n) Germinating conidium. (o, p) Culture on PDA. Scale bars: (c, e) 25 µm, (f, g) 5 µm, (h–j) 15 µm, and (d, k–m) 20 µm.
Culture characteristics: Conidia germinating on PDA within 12 h. Colonies growing on PDA, circular, with a flat surface, edge entire, reaching 15 mm in 3 weeks at 26°C, and brown to dark brown in the PDA medium. Mycelium superficial and partially immersed, branched, septate, hyaline to pale brown, and smooth-walled.

Material examined: China, Yunnan Province, Shuduhu lake, on submerged decaying wood (Altitude: 3,578 m, 27°54′24″N, 99°57′15″E), 25 August 2020, Zheng-Quan Zhang, L-190 (KUN-HKAS 124611, holotype), ex-type cultures, CGMCC 3.23539 = KUNCC 22–12437; China, Yunnan Province, Shuduhu lake, on submerged decaying wood (Altitude: 3,578 m, 27°54′24″N, 99°57′15″E), 25 August 2020, Zheng-Quan Zhang, L-281 (KUN-HKAS 124612), living cultures, CGMCC 3.23540 = KUNCC 22–12442.

Notes: The new collection can be easily distinguished from other Tubeufiaceae genera by the long oval and dictyosporous conidia with well-developed conidiophores. In the phylogenetic analyses, Neomanoharachariella aquatica shares a sister relationship to Helicoarctatus aquaticus (MFLUCC 17–1996) and H. thailandicus (MFLUCC 18–0332). However, there are great differences in morphology: the asexual morph of H. aquaticus and H. thailandicus are helicosporous, and our new collection is dictyosporous. H. aquaticus and H. thailandicus are characterized by setiform, unbranched, septate conidiophores, holoblastic, mono- to poly-blastic, denticulate conidigenous cells, pleurogenous, helicosporous, holoblastic, multi-septate, guttulate, and hyaline conidia. Based on pairwise nucleotide comparisons, the new strain CGMCC 3.23540 is different from the type species Helicoarctatus aquaticus (MFLUCC 17–1996) in 30/541 bp (5.54%) of the ITS, 24/805 bp (2.98%) of the LSU, 74/875 bp (8.46%) of the tef 1-α, and 154/1045 bp (14.74%) of the RPB2. In addition, Neomanoharachariella aquatica is most similar to the asexual state of Chlamydotubeufia hyaikangplaensis, but the conidia of N. aquatica are shorter (37–61 × 17–32 vs. 50–77 × 39–42) and presenting erect, unbranched, and smooth-walled conidiophores; the phylogenetic analyses also clearly segregate it from C. huaikangplaensis. We therefore identify the newly obtained taxon as Neomanoharachariella aquatica sp. nov.

Parahelicomyces hyalosporus (Y.Z. Lu, J.K. Liu, and K.D. Hyde) S. Y. Hsieh, Goh, and C. H. Kuo, Mycol. Prog. 20(2): 182 (2021) Figure 6

Index Fungorum: IF 554888; Facesoffungi number: FoF 04812
Saprobidic on submerged decaying woods in the lake. Asexual morph: Hyphomycetous, helicosporous. Colonies on wood substrate superficial, effuse, gregarious, and hyaline to white. Mycelium composed of partly immersed, partly superficial, pale brown, septate, anastomosing, reaping, with masses of crowded conidia. Conidiophores 60–142 × 4–5.2 µm wide (X = 101 × 4.6 µm, n = 10), macronematous, mononematous, cylindrical, branched, septate, hyaline to pale brown, and smooth-walled. Conidigenous cells 5–10 × 1–4 µm wide, holoblastic, mono-to poly-blastic, integrated, terminal or intercalary, cylindrical, truncate at apex after conidial secession, hyaline to pale brown, and smooth-walled. Conidia 40–56.7 × 3.5–4.5 µm in diameter, and conidial filaments 3.5–4.5 × 4 µm wide (X = 48 × 4 µm, n = 20), 145–180 × 1.5 µm long, loosely coiled 1–2.5 times, solitary, pleurogenous or acropleurogenous, helicoid, rounded at tip, multi-septate, becoming loosely coiled in water, guttulate, hyaline, and smooth-walled. Sexual morph: not observed.

Culture characteristics: Conidia germinating on PDA within 12 h; many germ tubes produced from conidium cells. Colonies growing on PDA, circular, with umbonate surface, edge dulate, and brown to dark brown in PDA medium, reaching 20 mm in 3 weeks at 26°C, and brown to dark brown in the PDA medium. Mycelium superficial and partially immersed, branched, septate, hyaline to pale brown, and smooth-walled.

Material examined: China, Yunnan Province, Luguhu lake, on submerged decaying wood (Altitude: 2,698 m, 27°41′11″N, 100°48′18″E), 5 March 2021, Zheng-Quan Zhang, L-159 (KUN-HKAS 124603), living cultures, CGMCC 3.23535 = KUNCC 22–12436; China, Yunnan Province, Luguhu lake, on submerged decaying wood (Altitude: 2,734 m, 27°45′18″N, 100°46′42″E), 5 March 2021, Zheng-Quan Zhang, L-315 (KUN-HKAS 124606), living culture, KUNCC 22–12443; China, Yunnan Province, Luguhu lake, on submerged decaying wood (Altitude: 2,794 m, 27°45′02″N, 100°51′02″E), 5 March 2021, Zheng-Quan Zhang, L-326 (KUN-HKAS 124605), living cultures, CGMCC 3.23537 = KUNCC 22–12444.

Notes: Parahelicomyces hyalosporus was first introduced as Pseudohelicomyces hyalosporus by Lu et al. (2018b) based on morphological and phylogenetic evidence. Hsieh et al. (2021) transferred it to Parahelicomyces as the genus Pseudohelicomyces, an older homonynym and illegitimate. In this paper, three newly-obtained isolates were identified as Parahelicomyces hyalosporus, and the morphology characteristics fit well with Parahelicomyces hyalosporus; the conidiophores macronematous, mononematous, branched, septate, conidigenous cells with denticles, holoblastic, mono- to poly-blastic, intercalary or terminal, determinate or sympodial and pleurogenous or acropleurogenous, conidia helicoid, multi-septate, and hyaline to pale brown. Species of the P. hyalosporus are widely found in lakes and streams of freshwater habitats in China and Thailand (Luo et al., 2017; Lu et al., 2018b; Li et al., 2022). Based on pairwise nucleotide comparisons, ITS and LSU are identical between the type species (MFLUCC 15–0343) and P. hyalosporus (CGMCC 3.23535).

Parahelicomyces suae I.L. Li, H.W. Shen, and Z.L. Luo, sp. nov.

Mycobank number: MB 845534, Figure 7
Holotype—KUN-HKAS 124604
Etymology—“suae” (Lat.) in memory of the Chinese mycologist Prof. Hong-Yan Su (4 April 1967–3 May 2022).
Saprobidic on submerged decaying woods in the lake. Asexual morph: Hyphomycetous, helicosporous. Colonies on the wood substratum superficial, effuse, gregarious, and white. Mycelium...
Parahelicomyces hyalosporus (KUN-HKAS 124603). (a) Colony on decaying wood. (b–d) Conidiophores with attached conidia and lateral minute polyblastic denticles. (e,f,i,j) Conidiogenous cells. (g,h,k–p) Conidia. (p,q) Colony on PDA observed from above and below. Scale bars: (b) 50 µm, (c,d) 40 µm, and (e–p) 10 µm.
Parahelicomyces suae (KUN-HKAS 124604, holotype). (a) Colony on decaying wood. (b–d) Conidiophores with attached conidia. (e–h) Conidiogenous cells. (i–m) Conidia. (n) Germinating conidium. (o,p) Colony on MEA observed from above and below. Scale bars: (b) 70 μm, (c) 60 μm, (d) 30 μm, (e–h,n) 10 μm, and (i) 15 μm.
composed of partly immersed, partly superficial, hyaline to pale brown, septate, abundantly branched hyphae, with masses of crowded, glistening conidia. Conidiophores 114.8–173.5 µm long, 3–4 µm wide (\(\bar{x} = 144 \times 3.5 \mu m, n = 20\), macroconidiate, conidial, branched or unbranched, erect, septate, dark brown at base, becoming hyaline toward apex, and smooth-walled. Conidiogenous cells 12–18 µm long, 3–4 µm wide, sympodial, holoblastic, monoblastic, integrated, terminal, cylindrical, truncate at apex after conidial secession, denticles or bladder-like cells, hyaline to pale brown, and smooth-walled. Conidia 29–36 µm diameter, conidial filament 1.8–2.2 µm wide (\(\bar{x} = 32.5 \times 2 \mu m, n = 20\)), 103–121 µm long, coiled 1–3.5 times, solitary, helicoid, rounded at tip, young conidia have indistinct septate, not easily loosely coiled in water, guttulate, hyaline, and smooth-walled. Sexual morph: not observed.

**Culture characteristics:** Conidia germinating on PDA within 12 h and many germ tubes produced from conidium cells. Colonies growing on MEA, reaching 14 mm diameter in 2 weeks at 26°C, circular, with a flat surface, edge entire, and pale brown to brown in the MEA medium. Mycelium superficial and partially immersed, branched, septate, hyaline to pale brown, and smooth. **Material examined:** China, Yunnan Province, Luguhu lake, on submerged decaying wood in the lake. Material examined: China, Yunnan Province, Luguhu lake, on submerged decaying wood in the lake (Altitude: 2,698 m, 27°41′11″N, 100°48′18″E), 3 March 2021, Sha Luan, L-158 (KUN-HKAS 124604, holotype), ex-type cultures, CGMCC 3.23534 = KUNCC 22–12435; China, Yunnan Province, Luguhu lake, on submerged decaying wood in the lake (Altitude: 2,698 m, 27°42′43″N, 100°44′56″E), 3 March 2021, Long-Li Li, L-1038, (KUN-HKAS 124607), living cultures, CGMCC 3.23538 = KUNCC 22–12440.

**Notes:** Parahelicomyces suae is introduced as a new species from Luguhu lake in Yunnan, China. In phylogeny, P. suae constitutes a strongly supported independent lineage basal to P. yunnanensis. Compared with CGMCC 3.20429, there are 5/563 (0.89%), 11/1048 bp (1.05%) base pair differences in the ITS and RPB2 regions between these two species. Morphologically, compared with P. yunnanensis, the conidia of P. suae are shorter (103–121 vs. 104–156 µm). In addition, our isolate conidia are not easily loosely coiled in water, conidiogenous cells with denticulate, and hyaline. Therefore, we identify the isolate as a new species of P. suae.

**Tubefia cylindrothecia** (Seaver) Hohn Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 128: 562 (1919), Figure 8

**Index Funorum:** IF 340543; Facesofungi number: FoF 02650

**Saprobiecic** on decaying wood in the lake. **Asexual morph:** Hyphomycetous, helicosporous. Colonies on the substratum superficial, effuse, gregarious, and white to pale brown. Mycelium composed of partly immersed, partly superficial, hyaline to pale brown, septate, abundantly branched hyphae, with masses of crowded, glistening conidia. Conidiophores 97–200 µm long, 5–6 µm wide (\(\bar{x} = 148 \times 5.5 \mu m, n = 30\), macroconidiate, mononematous, cylindrical, branched or unbranched, erect, flexuous, pale brown to brown, and smooth-walled. Conidiogenous cells 10.4–17 × 4–6 µm (\(\bar{x} = 13.7 \times 5 \mu m, n = 30\), holoblastic, mono- to polyblastic, integrated, intercalary or terminal, cylindrical, repeatedly genulate, truncate at the apex after conidial secession, each with single or several conidia hyaline to pale brown, and smooth-walled. Conidia 41.6–57.8 µm diameter and conidial filament 3.7–4.9 µm wide (\(\bar{x} = 50 \times 4.3 \mu m, n = 30\)), 105–206 µm long, coiled 1.5–3.5 times, solitary, acrogenous or acropleurogenous, helicoid, rounded at tip, becoming loosely coiled in water, guttulate, young Conidia hyaline and pale brown when edged, and smooth-walled. Sexual morph: not observed.

**Culture characteristics:** Conidia germinating on PDA within 12 h. Colonies growing slowly on CMA, reaching 15 mm diameter after 2 weeks at 26°C, effuse, the middle is dark, velvety to hairy, edge undulate, brown to dark brown in the CMA medium, mycelium superficial, effuse, with irregular edge, and hyphae pale yellow to brown.

**Material examined:** China, Yunnan Province, Luguhu lake, on submerged decaying wood (Altitude: 2,734 m, 27°45′18″N, 100°46′42″E), 5 March 2021, Zheng-Quan Zhang, L-157 (KUN-HKAS 124602), living cultures, CGMCC 3.23552 = KUNCC 22–12434.

**Notes:** The asexual morph of Tubefia cylindrothecia was first reported by Luo et al. (2017) and later encountered by Lu et al. (2018b) in freshwater habitats. In this study, the newly obtained collection has longer conidiophores (97–200 vs. 50–81 µm) and shorter conidia (105–206 vs. 256–314 µm) compared with the holotype (Luo et al., 2017). However, their ITS, LSU, tef 1-α, and RPB2 sequence data are identical; we therefore identify it as Tubefia cylindrothecia.

**Discussion**

The modern classification of Tubefiaceae was established by Boonmee et al. (2014), based on phylogenetic analyses and morphology. However, there are still taxonomic confusions in this group, especially in those types with helicosporous assexual morphs; their morphologically-based intergeneric classifications are controversial. Some species have been transferred or are synonymous to other genera of Tubefiaceae, for example, Helicosporm pannosum, Neohelicosporium griseum, and N. morganii have been transferred several times. The asexual state of Neomanoharachariella is dictyosporous conidia. It is a unique tubefiaceous fungus with broadly oblong, elongate, multisepate, muriform conidia, at first pale brown, becoming dark brown, with well-developed conidiophores, and basal cells are hyaline and bulging. These characteristics make it distinct from all related Tubefiaceae genera and is hence
FIGURE 8
Tubeufia cylindrothecia (KUN-HKAS 124602). (a,b) Colony on decaying wood. (c) Conidiophores with attached conidia. (d) Conidiophores. (e–h) Conidiogenous cells. (i–m) Conidia. (n) Germinating conidium. (o,p) Colony on CMA observed from above and below. Scale bars: (c) 70 µm, (d,e) 20 µm, and (f–n) 10 µm.
proposed as a new genus. Phylogenetic analyses based on ITS, LSU, tef 1-α, and tefB2 sequence (Figure 1) also distinguish N. aquatica from other dictyosporous members of Tubeufiaceae. The new genus is related to Helicoarctatus aquaticus (MFLUCC 17–1996) and Helicoarctatus thailandicus (MFLUCC 18–0332) which formed a distinct clade. The phylogenetic analyses also clearly segregated other dictyosporous genera of Tubeufiaceae such as Chlamydotubeufia, Dictyospora, Manoharachariella, and Tamhinispora in well-differentiated monophyletic lineages.

An abundance of lakes is a major feature of the Yunnan plateau. In recent years, lignicolous freshwater fungi were investigated in Yunnan, in nine freshwater lakes on the plateau. These lakes are distributed in high-altitude areas and most of them are depression pools formed by the subsidence of faults, with no water channels connected (Yang et al., 2004; Shen et al., 2022). Because of their unique development, formation, and relative isolation, each lake possesses its own unique species. In this study, we have also examined seven tubeufiaceous species collected from these plateau lakes. Of which, three were introduced as new species and a new genus Neomanoharachariella, while four were identified as existing species based on phylogenetic analyses and morphological characteristics. The nine species were placed in Helicoma, Neohelicosporium, Parahelicomyces, and Tubeufia. This study provides a case study for lakes as a worthwhile niche area of hyphomycetous associations. Parahelicomyces is well studied, and eight species in this genus have sequence data in the GenBank. For the common and confusing genera Helicoma, Neohelicosporium, and Tubeufia, morphological characteristics (conidiophores, conidiogenous cells, and conidia including size and color) and phylogenetic analyses are essential to distinguish them.

In conclusion, some tubeufiaceous species have the potential to produce new structural and active secondary metabolites (Mao et al., 2014; Lu et al., 2018a). Fang et al. (2019) tested and reported that most Tubeufiaceae species have certain antibacterial and anti-tumor activities in vitro. At present, few studies have reported secondary degradation products of Helicoma, Helicomyces, and Helicosporium species. In view of the potential to produce active compounds, and the reports on secondary metabolites of Tubeufiaceae, the prospect of active research is broad, and it is very possible to obtain new compounds with various biological activities from Tubeufiaceae.

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 in the article-supplementary material.

Author contributions

I-LL conducted the experiments, analyzed the data, and wrote the manuscript. D-FB, DW, and Y-ZL revised the manuscript. H-WS planned the experiments and analyzed the data. Z-LL planned and funded the experiments. YF conducted the experiments. 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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