

Species diversity and taxonomy of *Scytinostroma* sensu stricto (Russulales, Basidiomycota) with descriptions of four new species from China

Yue Li^{1*}, Wei-Qi Xu^{1*}, Shi-Liang Liu², Ning Yang³, Shuang-Hui He¹

1 School of Ecology and Nature Conservation, Beijing Forestry University, Beijing 100083, China

2 State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China

3 Beijing Municipal Research Institute of Eco-Environmental Protection, Beijing 100037, China

Corresponding author: Shuang-Hui He (heshuanghui@bjfu.edu.cn)

Abstract

Scytinostroma is species-rich genus in Peniophoraceae, Russulales and has been shown to be polyphyletic. In this study, we performed phylogenetic analyses on the core clade of *Scytinostroma* based on concatenated ITS1-5.8S-ITS2-nrLSU sequence data. Fifteen lineages including four new species from China, *Scytinostroma beijingensis*, *S. boidinii*, *S. subduriusculum*, and *S. subrenisporum*, were recognized. The genus *Michenera* was nested within the *Scytinostroma* s.s. clade in the phylogenetic tree of Peniophoraceae. Sequences of *S. portentosum* (type species) and *S. hemidichophyticum* from Europe formed a strongly supported lineage sister to the *S. portentosum* sample from Canada. It is supposed that the European “*S. portentosum*” is *S. hemidichophyticum*, and the former species is restricted in distribution to North America. *Scytinostroma duriusculum* is supposed to be a species complex. Samples from Sri Lanka (the type locality) formed a lineage sister to those from China, Thailand and Vietnam (described herein as *S. subduriusculum*) and two samples from France that might represent an undescribed species. The four new species are described and illustrated, and an identification key to all the 14 *Scytinostroma* s.s. species worldwide is provided. Until now, seven species of *Scytinostroma* s.s. have been found in China. Our results increased the knowledge of species diversity and taxonomy of corticioid fungi in China.

Key words: corticioid fungi, Peniophoraceae, phylogeny, white rot, wood-decaying fungi



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Introduction

The genus *Scytinostroma* Donk sensu lato (Peniophoraceae, Russulales), typified by *S. portentosum* (Berk. & M.A. Curtis) Donk, is characterized by resupinate, effused basidiomes with a smooth to tuberculate hymenophore, a dimictic hyphal system with dextrinoid and cyanophilous skeletal hyphae, presence of gloeocystidia in most species, and subglobose to ellipsoid, variably amyloid or inamyloid, smooth basidiospores (Bernicchia and Gorjón 2010; Liu et al. 2018; Stalpers et al. 2021). It is a widely distributed genus with 42 species level names in Index Fungorum (<http://www.indexfungorum.org>, accessed on 1 January 2023). Morphologically, *Scytinostroma* can be easily distinguished

* These two authors contributed equally to this work.

from other genera of Peniophoraceae by having a dimitic hyphal system and smooth basidiospores. It is similar to *Vararia* P. Karst., which usually differs in having typical dichohyphae (Bernicchia and Gorjón 2010). Liu et al. (2018) demonstrated that *Michenera* Berk. & M.A. Curtis belonged to Peniophoraceae and was closely related to *Scytinostroma*. The two genera are similar in some aspects, such as the texture of basidiome, a dimitic hyphal system, presence of gloeocystidia, but species of *Michenera* have larger basidia and larger, inamyloid, thick-walled basidiospores. Based on morphology, Stalpers et al. (2021) transferred the two species of *Michenera* to *Scytinostroma* and treated the former genus as a synonym of the latter.

Larsson and Larsson (2003) and Miller et al. (2006) showed that five species of *Scytinostroma*, *S. galactinum* (Fr.) Donk, *S. jacksonii* Boidin, *S. ochroleucum* Donk, *S. odoratum* (Fr.) Donk and *S. portentosum* (type species), occurred on five distinct branches that are distantly separated in Peniophoraceae. Leal-Dutra et al. (2018) built the genus *Baltazaria* Leal-Dutra, Dentinger & G.W. Griff. for *S. galactinum* and other three species, *S. neogalactinum* Boidin & Lanq., *S. eurasiatricogalactinum* Boidin & Lanq. and *Parapterulicum octopodites* Corner. Our preliminary phylogenetic analyses showed that some specimens recently collected from China clustered with *S. portentosum* (type species) and several other species, which represented the core clade of *Scytinostroma*. In order to understand the species diversity within this clade, we carried out phylogenetic analyses of Peniophoraceae based on concatenated ITS1-5.8S-ITS2-nrLSU sequence data, focusing on samples of *Scytinostroma* s.s. worldwide. Fifteen species-level lineages were recognized in the phylogenetic tree. Among them, four lineages are new and here described and illustrated as *S. beijingensis*, *S. boidinii*, *S. subduriusculum*, and *S. subrenisporum* spp. nov.

Materials and methods

Specimen collection

In situ photos of specimens were taken with a Canon camera EOS 70D (Canon Corporation, Japan). Specimens were dried with a portable dryer, labelled, and then stored in a freezer at minus 40 °C for two weeks to kill the insects and their eggs before proceeding with morphological and molecular studies. Voucher specimens are deposited at the herbarium of Beijing Forestry University, Beijing, China (BJFC).

Morphological studies

Thin, freehand sections were made from dried basidiomes and mounted in 2% (weight/volume) aqueous potassium hydroxide (KOH) and 1% (w/v) aqueous phloxine. Amyloidity and dextrinoidity of hyphae and basidiospores were checked in Melzer's reagent (IKI). Cyanophily of hyphal and basidiospore walls were observed in 1% (w/v) cotton blue in 60% (w/v) lactic acid (CB). Microscopic examinations were carried out with a Nikon Eclipse 80i microscope (Nikon Corporation, Japan) at magnifications up to 1000×. Drawings were made with the aid of a drawing tube. The following abbreviations are used:

IKI- = neither amyloid nor dextrinoid, CB+ = cyanophilous, CB- = acyanophilous, SA+ = positive reaction in Sulphobenzaldehyde, SA- = negative reaction in Sulphobenzaldehyde, L = mean spore length, W = mean spore width, Q = L/W ratio, n (a/b) = number of spores (a) measured from the number of specimens (b). Color codes and names follow Kornerup and Wanscher (1978).

DNA extraction and sequencing

A CTAB plant genomic DNA extraction kit, DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to extract total genomic DNA from dried specimens, then amplified by the polymerase chain reaction (PCR), according to the manufacturer's instructions. The ITS1-5.8S-ITS2 region was amplified with the primer pair ITS5/ITS4 (White et al. 1990) using the following protocol: initial denaturation at 95 °C for 4 min, followed by 34 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and final extension at 72 °C for 10 min. The D1-D2 region of the nucleic ribosomal LSU was amplified with the primer pair LR0R/LR7 (https://sites.duke.edu/vilgalyslab/rDNA_primers_for_fungi/) employing the following procedure: initial denaturation at 94 °C for 1 min, followed by 34 cycles at 94 °C for 30 s, 50 °C for 1 min and 72 °C for 1.5 min, and final extension at 72 °C for 10 min. DNA sequencing was performed at Beijing Genomics Institute, and newly generated sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/>). BioEdit v.7.0.5.3 (Hall 1999) and Geneious Basic v.11.1.15 (Kearse et al. 2012) were used to review the chromatograms and for contig assembly.

Phylogenetic analyses

The dataset of concatenated ITS1-5.8S-ITS2-nrLSU sequences of the Peniophoraceae was analyzed. *Amylostereum chailletii* (Pers.) Boidin and *A. laevigatum* (Fr.) Boidin were selected as the outgroup (Larsson and Larsson 2003; Xu et al. 2023). Sequences including those from Larsson and Larsson (2003) were partitioned to ITS1, 5.8S, ITS2 and nrLSU, and then aligned separately using MAFFT v.7.4 (<http://mafft.cbrc.jp/alignment/server/>, Katoh et al. 2017) with the G-INS-I iterative refinement algorithm and optimized manually in BioEdit v.7.0.5.3. The separate alignments were then concatenated using Mesquite v.3.5.1 (Maddison and Maddison 2018). The dataset was deposited in TreeBase (<http://treebase.org/treebase-web/home.html>, submission ID: 30453).

Maximum likelihood (ML) analyses, and Bayesian inference (BI) were carried out by using RAxML v.8.2.10 (Stamatakis 2014) and MrBayes 3.2.6 (Ronquist et al. 2012), respectively. In ML analysis, statistical support values were obtained using rapid bootstrapping with 1000 replicates, with default settings for other parameters. For BI, the best-fit substitution model was estimated with jModeltest v.2.1.7 (Darriba et al. 2012). Four Markov chains were run for 2,000,000 generations for the dataset; until the split deviation frequency value was lower than 0.01. Trees were sampled every 100th generation. The first quarter of the trees, which represented the burn-in phase of the analyses, were discarded, and the remaining trees were used to calculate posterior probabilities (BPP) in the majority rule consensus tree.

Results

Phylogenetic analyses

The concatenated ITS1-5.8S-ITS2-nrLSU dataset contained 58 ITS and 52 nrLSU sequences from 61 samples, representing 33 ingroup taxa and the outgroup (Table 1), and had an aligned length of 2628 characters. jModelTest suggested GTR+I+G, K80+I, HKY+I+G, GTR+I+G to be the best-fit models of nucleotide evolution for ITS1, 5.8S, ITS2, and nrLSU markers, respectively, for the Bayesian analysis. The average standard deviation of split frequencies of BI was 0.005711 at the end of the run. BI analyses resulted in almost identical tree topologies with the ML analysis. Only the ML tree is provided in Fig. 1 with the likelihood bootstrap values ($\geq 50\%$, first) and Bayesian posterior probabilities (≥ 0.95 , second) labelled along the branches.

In the tree, *Scytinostroma* s.s. clade received a moderately strong support value in ML analysis (bootstrap value = 56) but a strong value in BI (Bayesian posterior probabilities = 1). Four new distinct lineages corresponding to *Scytinostroma beijingensis*, *S. boidinii*, *S. subduriusculum* and *S. subrenisporum* spp. nov. were recognized. Sequences of *S. portentosum* and *S. hemidichophyticum* from Europe formed a strongly supported lineage sister to the *S. portentosum* sample from Canada. Samples of *S. duriusculum* from France and those from Sri Lanka (the type locality) formed a lineage sister to *S. subduriusculum*. *Scytinostroma incrustatum* (S.H. He, S.L. Liu & Nakasone) K.H. Larss. and *S. artocreas* (Berk. & M.A. Curtis) K.H. Larss., which were formerly placed in *Michenera*, were nested within *Scytinostroma* s.s. clade.

Table 1. Species and sequences used in the phylogenetic analyses. New species are set in bold with type specimens indicated with an asterisk (*).

| Species | Specimen No. | Locality | GenBank Accession No. | | Reference |
|--|--------------|---------------|-----------------------|----------|--------------------------|
| | | | ITS | nrLSU | |
| <i>Asterostroma laxum</i> | EL33-99 | Estonia | AF506410 | AF506410 | Larsson and Larsson 2003 |
| <i>Asterostroma muscicola</i> | KHL9537 | Puerto Rico | AF506409 | AF506409 | Larsson and Larsson 2003 |
| <i>Baltazarria galactina</i> | CBS 752.86 | France | MH862034 | MH873721 | Vu et al. 2019 |
| <i>Baltazarria neogalactina</i> | CBS 755.86 | French Guiana | MH862037 | MH873724 | Vu et al. 2019 |
| <i>Confertobasidium olivaceoalbum</i> | FP 90196 | USA | AF511648 | AF511648 | Larsson and Larsson 2003 |
| <i>Dichostereum durum</i> | CBS 707.81 | France | MH861450 | MH873192 | Vu et al. 2019 |
| <i>Dichostereum effuscatum</i> | GG930915 | France | AF506390 | AF506390 | Larsson and Larsson 2003 |
| <i>Gloiothele lactescens</i> | EL8-98 | Sweden | AF506453 | AF506453 | Larsson and Larsson 2003 |
| <i>Gloiothele lamellosa</i> | KHL11031 | Venezuela | AF506454 | AF506454 | Larsson and Larsson 2003 |
| <i>Lachnocladium schweinfurthianum</i> | KM49740 | Cameroon | MH260033 | MH260051 | Leal-Dutra et al. 2018 |
| <i>Lachnocladium</i> sp. | KHL10556 | Jamaica | AF506461 | AF506461 | Larsson and Larsson 2003 |
| <i>Metulodonta nivea</i> | NH 13108 | Russia | AF506423 | AF506423 | Larsson and Larsson 2003 |
| <i>Peniophora quercina</i> | CBS 407.50 | France | MH856687 | MH868204 | Vu et al. 2019 |
| <i>Peniophora tristicula</i> | He 4775 | China | MH669235 | MH669239 | Liu and He 2018 |
| <i>Peniophora versiformis</i> | He 3029 | China | MK588756 | MK588796 | Xu et al. 2023 |
| <i>Scytinostroma acystidiatum</i> | He 5646 | China | MK625568 | MK625494 | Present study |
| <i>Scytinostroma acystidiatum</i> | He 5668 | China | MK625569 | MK625496 | Present study |
| <i>Scytinostroma alutum</i> | CBS 762.81 | France | MH861482 | MH873221 | Vu et al. 2019 |

| Species | Specimen No. | Locality | GenBank Accession No. | | Reference |
|--|--------------|-----------|-----------------------|----------|------------------------------------|
| | | | ITS | nrLSU | |
| <i>Scytinostroma alutum</i> | CBS 763.81 | France | MH861483 | MH873222 | Vu et al. 2019 |
| <i>Scytinostroma artocreas</i> | GHL-2016-Oct | USA | MH142900 | MH204691 | Liu et al. 2018 |
| <i>Scytinostroma beijingensis</i> | He 7203 | China | — | OQ729729 | Present study |
| <i>Scytinostroma beijingensis</i> | He 7668 | China | — | OQ729730 | Present study |
| <i>Scytinostroma beijingensis</i> | He 7768* | China | OQ731943 | OQ729731 | Present study |
| <i>Scytinostroma boidinii</i> | He 2499 | China | MK625573 | — | Present study |
| <i>Scytinostroma boidinii</i> | He 5138 | China | MK625572 | MK625497 | Present study |
| <i>Scytinostroma boidinii</i> | He 6911* | China | OQ731934 | OQ729724 | Present study |
| <i>Scytinostroma boidinii</i> | He 7465a | China | OQ731935 | — | Present study |
| <i>Scytinostroma boidinii</i> | He 7465b | China | OQ731936 | — | Present study |
| <i>Scytinostroma caudisporum</i> | CBS 746.86 | Gabon | MH862030 | AY293210 | Vu et al. 2019; Binder et al. 2005 |
| <i>Scytinostroma duriusculum</i> | He 5748 | Sri Lanka | OQ865248 | — | Present study |
| <i>Scytinostroma duriusculum</i> | He 5756 | Sri Lanka | OQ865249 | — | Present study |
| ' <i>Scytinostroma duriusculum'</i> | CBS 757.81 | France | MH861477 | MH873216 | Vu et al. 2019 |
| ' <i>Scytinostroma duriusculum'</i> | CBS 758.81 | France | MH861478 | MH873217 | Vu et al. 2019 |
| <i>Scytinostroma hemidichophyticum</i> | CBS 702.84 | Belgium | MH861818 | MH873509 | Vu et al. 2019 |
| <i>Scytinostroma hemidichophyticum</i> | CBS 759.81 | France | MH861479 | MH873218 | Vu et al. 2019 |
| <i>Scytinostroma hemidichophyticum</i> | CBS 760.81 | France | MH861480 | MH873219 | Vu et al. 2019 |
| <i>Scytinostroma incrustatum</i> | He 2841 | China | MH142906 | MH142910 | Liu et al. 2018 |
| <i>Scytinostroma incrustatum</i> | He 5368 | China | MH204689 | MH204690 | Liu et al. 2018 |
| <i>Scytinostroma portentosum</i> | CBS 503.48 | Canada | MH856447 | AF518723 | Vu et al. 2019 |
| <i>Scytinostroma portentosum</i> | EL11-99 | Sweden | AF506470 | AF506470 | Larsson and Larsson 2003 |
| <i>Scytinostroma portentosum</i> | GEL3225 | — | — | AJ406488 | Langer 2002 |
| <i>Scytinostroma renisporum</i> | CBS 771.86 | Indonesia | MH862051 | MH873738 | Vu et al. 2019 |
| <i>Scytinostroma renisporum</i> | CBS 772.86 | Indonesia | MH862052 | MH873739 | Vu et al. 2019 |
| <i>Scytinostroma subduriusculum</i> | He 3590 | China | MK625571 | MK625499 | Present study |
| <i>Scytinostroma subduriusculum</i> | He 4146 | Thailand | MK625570 | MK625498 | Present study |
| <i>Scytinostroma subduriusculum</i> | He 7134 | China | OQ731937 | — | Present study |
| <i>Scytinostroma subduriusculum</i> | He 7141 | China | OQ731938 | OQ729725 | Present study |
| <i>Scytinostroma subduriusculum</i> | He 7148 | China | OQ731939 | — | Present study |
| <i>Scytinostroma subduriusculum</i> | He 7150 | China | OQ731940 | OQ729726 | Present study |
| <i>Scytinostroma subduriusculum</i> | He 7657* | China | OQ731941 | OQ729727 | Present study |
| <i>Scytinostroma subduriusculum</i> | He 7717 | China | OQ731942 | OQ729728 | Present study |
| <i>Scytinostroma subrenisporum</i> | He 4384 | China | MK625567 | MK625495 | Present study |
| <i>Scytinostroma subrenisporum</i> | He 4792* | China | MK625566 | MK625493 | Present study |
| <i>Scytinostroma yunnanense</i> | CLZhao 10802 | China | MT611446 | — | Wang et al. 2020 |
| <i>Scytinostroma yunnanense</i> | CLZhao 11010 | China | MT611447 | — | Wang et al. 2020 |
| <i>Vararia amphithallica</i> | He 4330 | China | MK674474 | MK625542 | Present study |
| <i>Vararia investiens</i> | TAA164122 | Norway | AF506484 | AF506484 | Larsson and Larsson 2003 |
| <i>Vesiculomyces citrinus</i> | He 3716 | China | KY860369 | KY860429 | Present study |
| <i>Vesiculomyces citrinus</i> | EL53-97 | Sweden | AF506486 | AF506486 | Larsson and Larsson 2003 |
| OUTGROUP | | | | | |
| <i>Amylostereum chailletii</i> | NH 8031 | Sweden | AF506406 | AF506406 | Larsson and Larsson 2003 |
| <i>Amylostereum laevigatum</i> | NH 12863 | Sweden | AF506407 | AF506407 | Larsson and Larsson 2003 |

Peniophoraceae

Scytinostroma s.s.

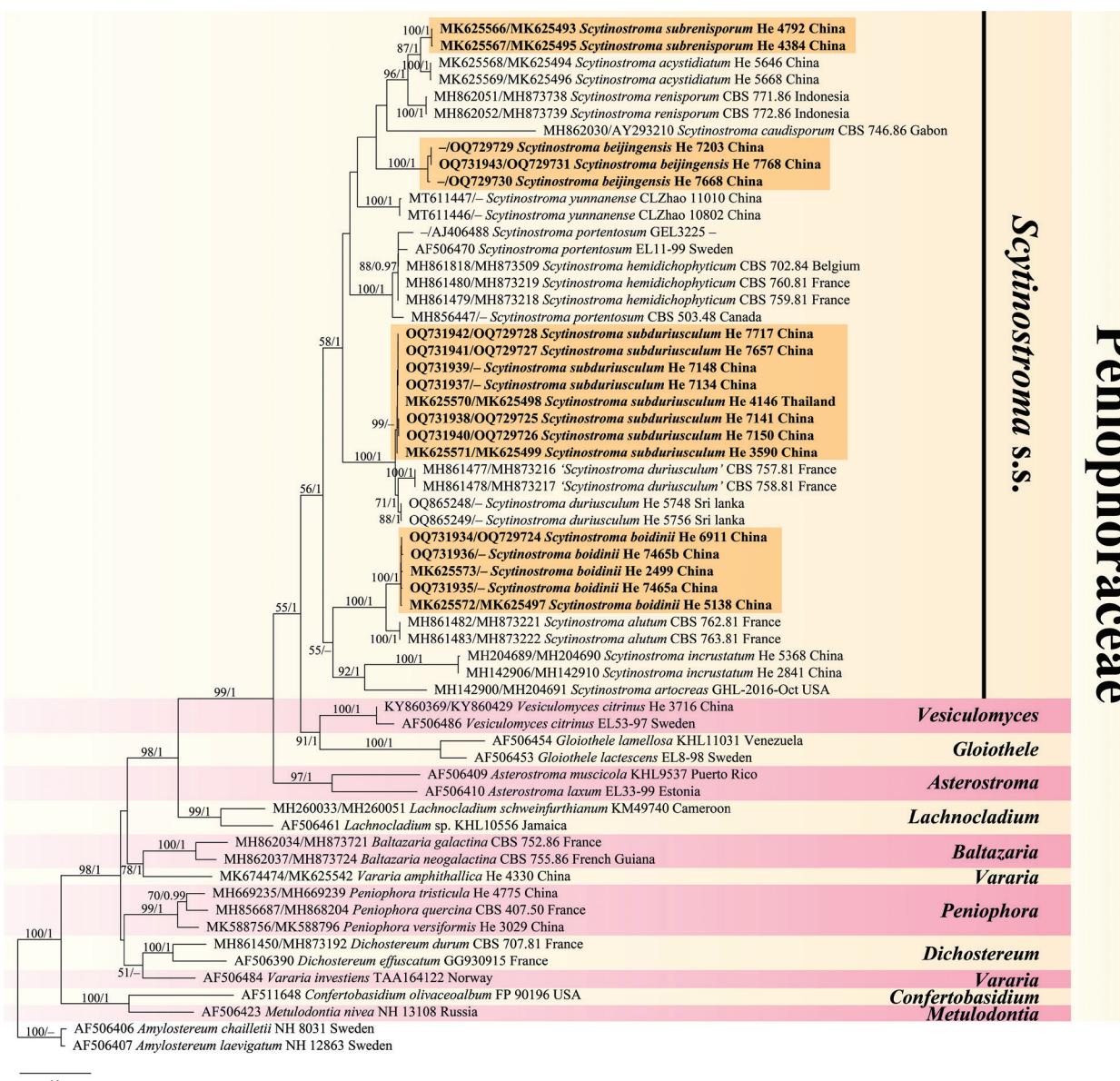


Figure 1. Phylogenetic tree of ML analysis from the ITS1-5.8S-ITS2-nrLSU sequences of Peniophoraceae taxa. Branches are labelled with likelihood bootstrap values ($\geq 50\%$, first) and Bayesian posterior probabilities (≥ 0.95 , second). New species are set in bold and highlighted.

Taxonomy

Scytinostroma beijingensis Yue Li, S.L. Liu & S.H. He, sp. nov.

Mycobank No: 848268

Figs 2, 3

Type. CHINA, Beijing, Haidian District, Yangtaishan Forest Park, on dead *Pyrus* tree, 4 September 2022, He 7768 (BJFC 038905, holotype).

Etymology. Refers to the type locality in Beijing, China.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, coriaceous, first as small patches, later confluent up to 12 cm long, 4.5 cm wide, up to 200 μm thick in section. Hymenophore smooth, greyish yellow (4B5) to greyish orange (5B5), unchanged in KOH, not

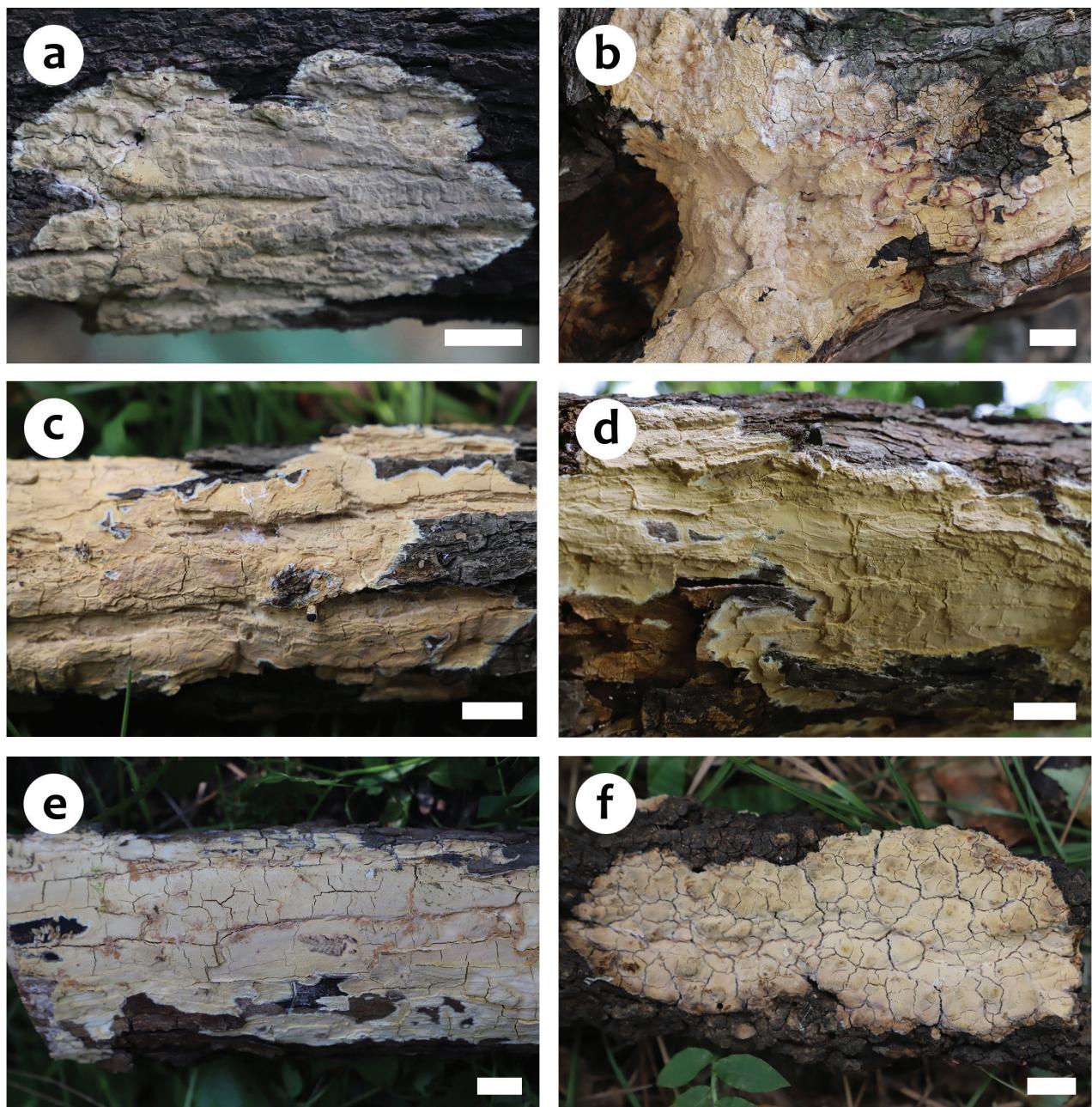


Figure 2. Basidiomes of *Scytinostroma beijingensis* **a** He 7768 (BJFC 038905, holotype) **b** He 7201 (BJFC 036518) **c** He 7203 (BJFC 036520) **d** He 7220 (BJFC 036537) **e** He 7668 (BJFC 038804) **f** He 7759 (BJFC 038896). Scale bars: 1 cm (a-f).

cracked or deeply cracked with age; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context yellow.

Microscopic structures. Hyphal system dimictic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, thin-walled, 2–3 μm in diam., IKI–, CB–. Skeletal hyphae dominant, colorless to yellow, distinctly thick-walled, moderately branched, 2.5–4 μm in diam., weakly dextrinoid, CB+. Catahymenium composed of skeletal hyphae, gloeocystidia, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, frequently dichotomous-branched with acute tips, 1–2 μm wide at lowest part. Gloeocystidia abundant, SA+, with two shapes (1) ventricose, colorless, thin- to slightly thick-walled, mostly embedded, usually

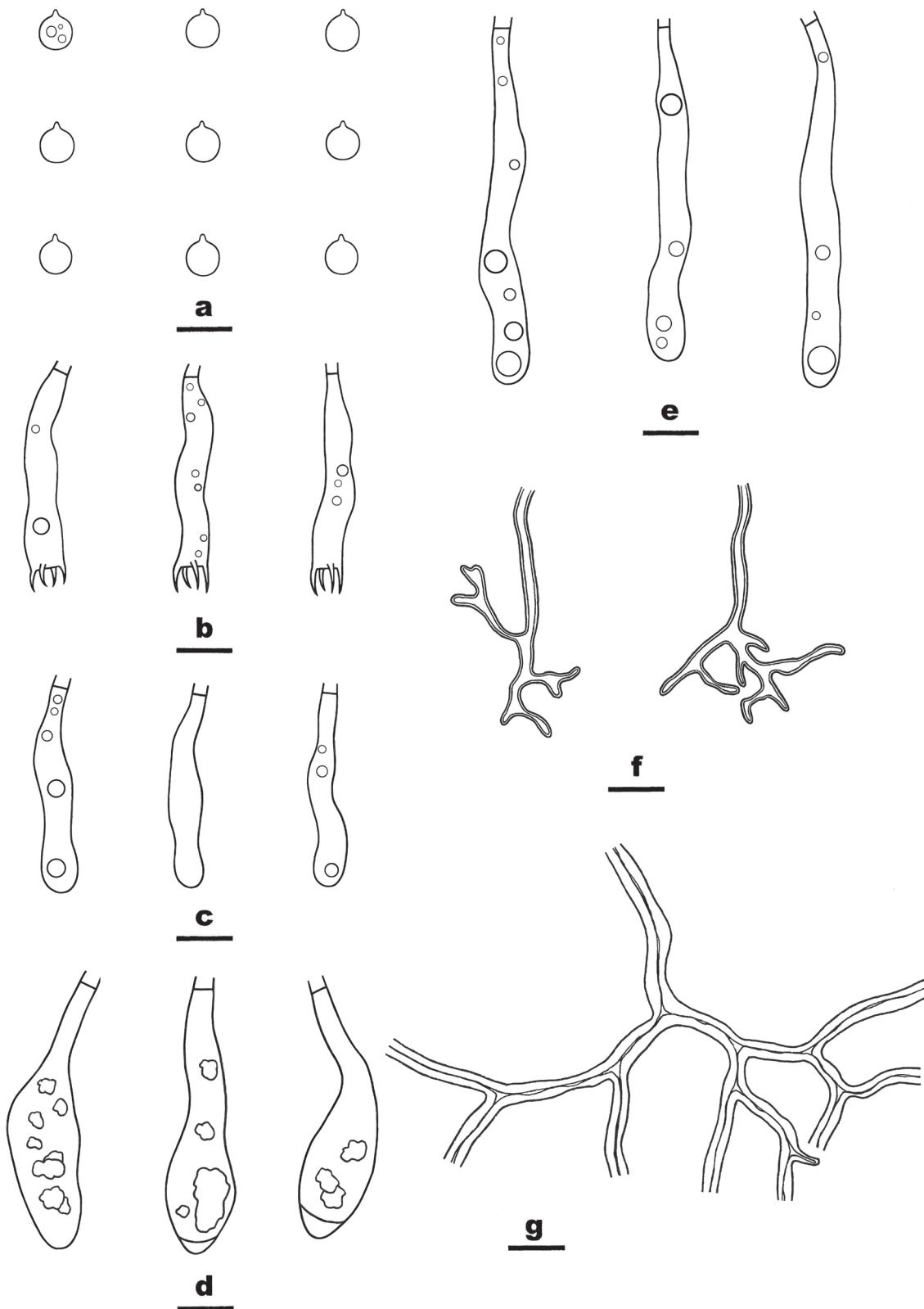


Figure 3. Microscopic structures of *Scytinostroma beijingensis* (from the holotype He 7768) **a** basidiospores **b** basidia **c** basidioles **d**, **e** gloeocystidia **f** skeletal hyphae from hymenium **g** skeletal hyphae from subiculum. Scale bars: 10 µm (a–g).

with contents, $28\text{--}40 \times 8\text{--}15 \mu\text{m}$; (2) subcylindrical, colorless, thin- to slightly thick-walled, mostly projecting beyond the hymenium, usually with contents, $45\text{--}65 \times 5\text{--}7 \mu\text{m}$. Basidia subcylindrical, slightly curved, thin-walled, colorless,

smooth, with four sterigmata and a basal simple septum, $30\text{--}36 \times 4.5\text{--}6.5 \mu\text{m}$; basidioles in shape similar to basidia, but slightly smaller. Basidiospores sub-globose, with a distinct apiculus, thin-walled, colorless, smooth, occasionally with oil-drops, amyloid, CB-, $5.5\text{--}6.5 (-6.8) \times (5-) 5.2\text{--}6.2 (-6.5) \mu\text{m}$, L = $5.9 \mu\text{m}$, W = $5.8 \mu\text{m}$, Q = $1.01\text{--}1.02$ ($n = 90/3$).

Additional specimens examined. CHINA, Beijing, Haidian District, Jiufeng Forest Park, on dead *Pyrus* tree, 26 August 2022, He 7759 (BJFC 038896); Xiangshan Park, on dead *Pyrus* tree, 16 July 2022, He 7668 (BJFC 038804); Mi-yun District, Yunmengshan Scenic Spot, on dead *Pyrus* branch, 7 August 2021, He 7201 (BJFC 036518) & He 7203 (BJFC 036520) & He 7220 (BJFC 036537).

Notes. *Scytinostroma beijingensis* is characterized by having two kinds of gloeocystidia and short branched skeletal hyphae in hymenium, and growing on *Pyrus*. In the phylogenetic tree (Fig. 1), *S. beijingensis* formed a distinct lineage with strong support values that is sister to the clade comprising *S. renisporum* Boidin, Lanq. & Gilles, *S. subrenisporum*, *S. acystidiatum* Q.Y. Zhang, L.S. Bian & Q. Chen and *S. caudisporum* Boidin, Lanq. & Gilles. *Scytinostroma renisporum* differs from *S. beijingensis* by having cylindrical, subclavate or fusoid gloeocystidia ($20\text{--}35 \times 6\text{--}10 \mu\text{m}$), ovoid to reniform basidiospores ($5.2\text{--}6.5 \times 3.2\text{--}4.8 \mu\text{m}$) and a distribution in Côte d'Ivoire, western Africa (Boidin and Lanquetin 1987). *Scytinostroma subrenisporum* and *S. acystidiatum* can be easily distinguished from *S. beijingensis* by the absence of gloeocystidia (Zhang et al. 2023). *Scytinostroma caudisporum* is unique in the group for its distinctly large basidiospores ($15\text{--}30 \times 3\text{--}3.5 \mu\text{m}$, Boidin and Lanquetin 1987).

***Scytinostroma boidinii* Yue Li, S.L. Liu & S.H. He, sp. nov.**

Mycobank No: 848267

Figs 4, 5

Type. CHINA, Beijing, Mentougou District, Xiaolongmen Forest Park, on dead angiosperm branch, 28 August 2020, He 6911 (BJFC 033860, holotype).

Etymology. Named to honor Dr. Jacques Boidin (Lyon, France) who contributed much to the taxonomy of *Scytinostroma*.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, membranaceous to coriaceous, first as small patches, later confluent up to 9 cm long, 3.5 cm wide, up to 300 μm thick in section. Hymenophore smooth, pale yellow (4A3), greyish yellow (4B4) to greyish orange [5B(3–4)], unchanged in KOH, not cracked; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context pale yellow.

Microscopic structures. Hyphal system dimictic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, slightly thick-walled, $2\text{--}3 \mu\text{m}$ in diam., IKI-, CB-. Skeletal hyphae dominant, colorless to yellow, distinctly thick-walled, moderately branched, $1.5\text{--}2 \mu\text{m}$ in diam., dextrinoid, CB+. Catahymenium composed of skeletal hyphae, gloeocystidia, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, dichotomous-branched with acute tips, $1\text{--}1.5 \mu\text{m}$ wide at lowest part. Gloeocystidia abundant, subcylindrical to subfusiform, colorless, slightly thick-walled, with or without contents, weakly SA+, $50\text{--}80 \times 5\text{--}10 \mu\text{m}$. Basidia subclavate to subcylindrical, thin-walled, colorless, smooth, with four

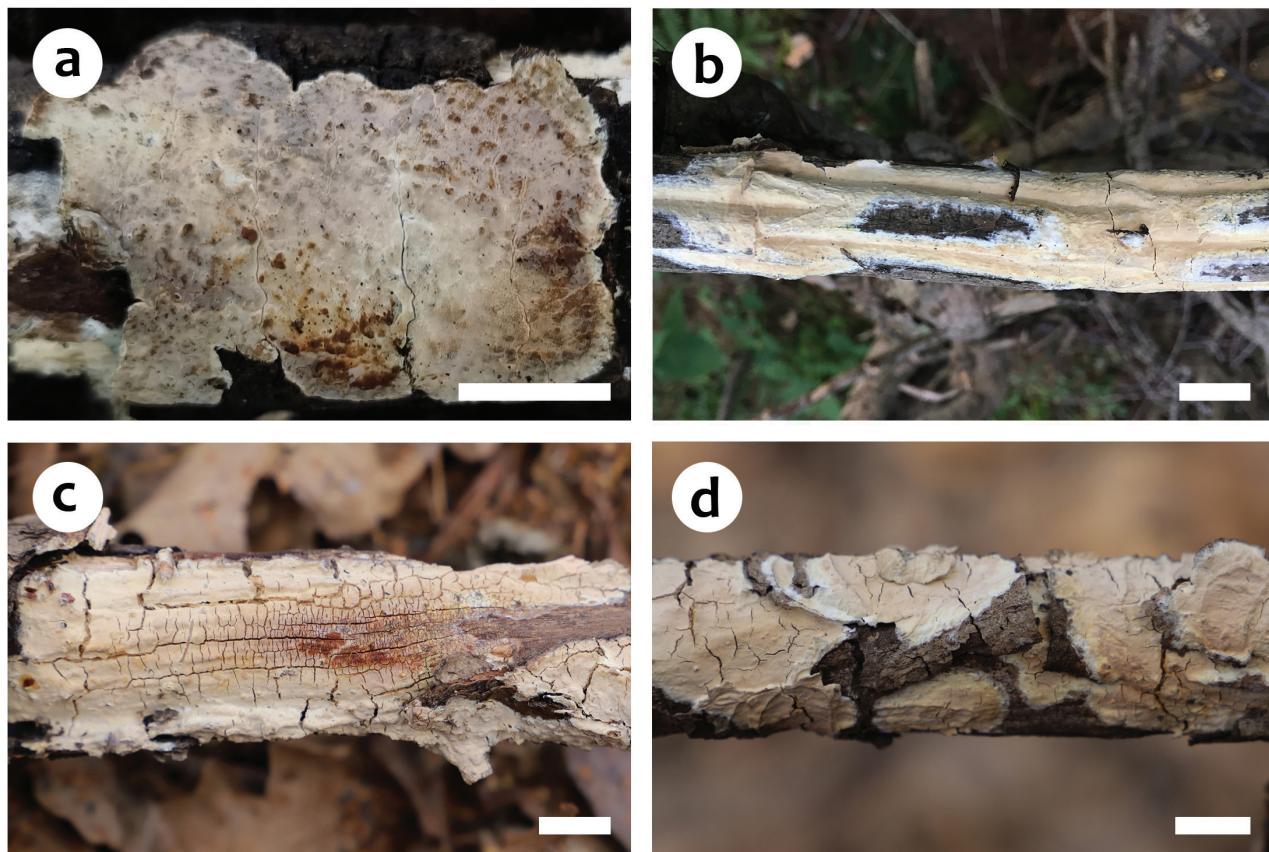


Figure 4. Basidiomes of *Scytinostroma boidinii* **a** He 6911 (BJFC 033860, holotype) **b** He 4985 (BJFC 024503) **c** He 7465a (BJFC 038600) **d** He 7465b (BJFC 038601). Scale bars: 1 cm (**a–d**).

sterigmata and a basal simple septum, $30–50 \times 4–7 \mu\text{m}$; basidioles in shape similar to basidia, but slightly smaller. Basidiospores subglobose, with a distinct apiculus, thin-walled, colorless, smooth, occasionally with oil-drops, amyloid, CB–, $(4.5–) 5–5.5 (–6.5) \times (4–) 4.5–5.5 (–6.2) \mu\text{m}$, L = $5.1 \mu\text{m}$, W = $5.0 \mu\text{m}$, Q = $1.02–1.04$ ($n = 60/2$).

Additional specimens examined. CHINA, Beijing, Mentougou District, Ling-shan Scenic Spot, on dead angiosperm branch, 10 April 2022, He 7465a (BJFC 038600) & He 7465b (BJFC 038601); Gansu Province, Tianshui County, Dangchuan Forest Farm, on dead *Quercus* tree, 9 August 2015, He 2499 (BJFC 020952); Hebei Province, Xinglong County, Wulingshan Nature Reserve, on dead angiosperm branch, 2 September 2017, He 4985 (BJFC 024503); Jilin Province, Jiaohé County, forestry experimental area, on fallen angiosperm trunk, 3 September 2017, He 5138 (BJFC 024656).

Notes. *Scytinostroma boidinii* is characterized by the relatively long gloeo-cystidia and subglobose basidiospores. In the phylogenetic tree (Fig. 1), *S. boidinii* formed a distinct lineage sister to *S. alutum* Lanq., which differs in having cracked basidiomes, slightly larger basidiospores ($5–7 \times 5–7.5 \mu\text{m}$) and a distribution in France, Spain and Pakistan (Boidin and Lanquetin 1987; Bernicchia and Gorjón 2010). *Scytinostroma yunnanense* C.L. Zhao from Yunnan Province, southwestern China, has similar-sized basidiospores ($4.5–5.5 \times 4.2–5.2 \mu\text{m}$) to *S. boidinii*, but differs in having white to cream hymenophore, smaller gloeo-cystidia ($28–33 \times 4–5 \mu\text{m}$) and smaller basidia ($21–28 \times 4–5.5 \mu\text{m}$, Wang et al. 2020).

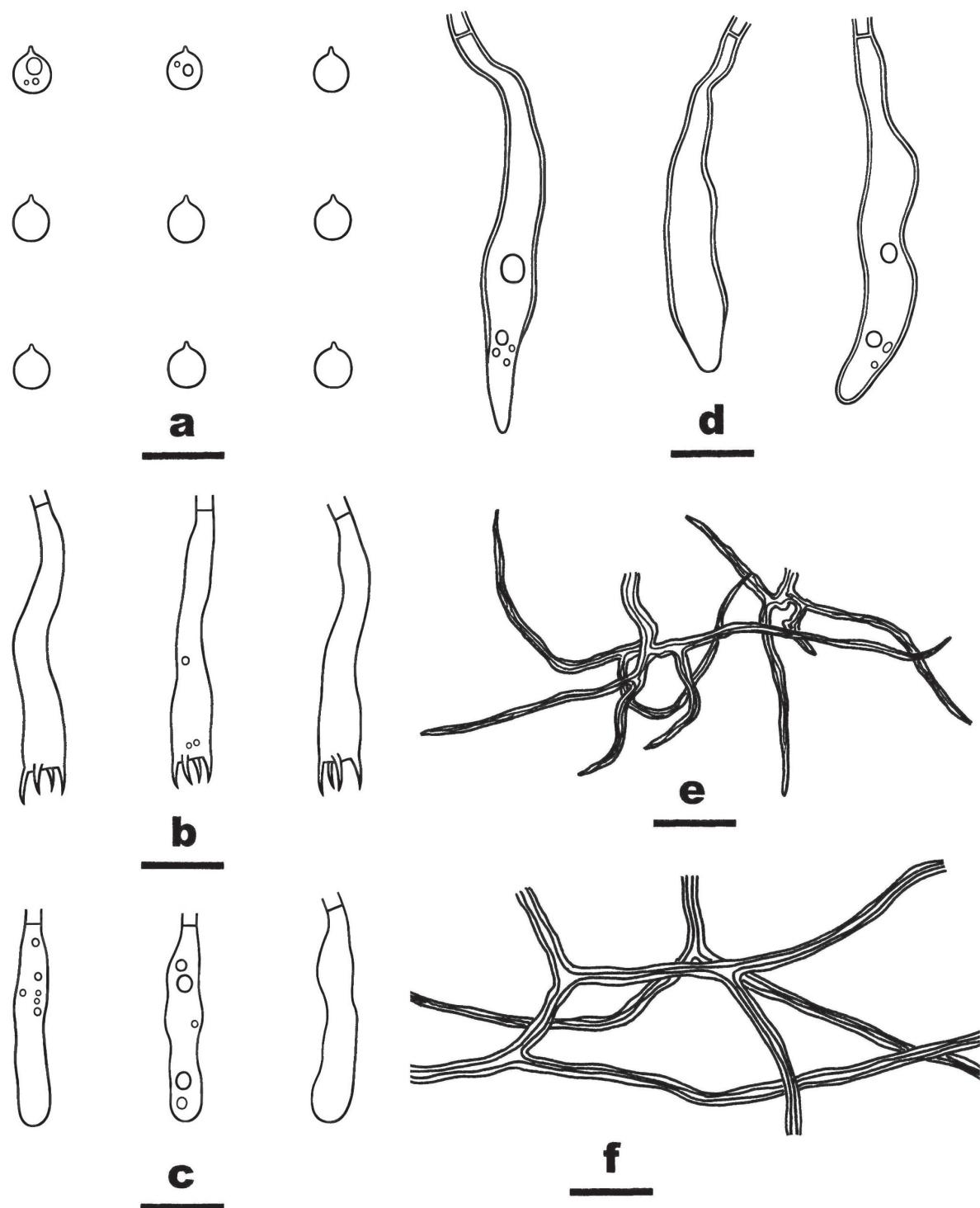


Figure 5. Microscopic structures of *Scytinostroma boidinii* (from the holotype He 6911) **a** basidiospores **b** basidia **c** basidioles **d** gloeocystidia **e** skeletal hyphae from hymenium **f** skeletal hyphae from subiculum. Scale bars: 10 µm (a-f).

***Scytinostroma subduriusculum* Yue Li, S.L. Liu & S.H. He, sp. nov.**

Mycobank No: 848266

Figs 6, 7

Type. CHINA, Beijing, Haidian District, Beijing Botanical Garden, on dead angiosperm branch, 15 July 2022, He 7657 (BJFC 038793, holotype).

Etymology. Refers to the morphological similarity and close phylogenetic relationship with *S. duriusculum*.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, membranaceous to coriaceous, first as small patches, later confluent up to 18 cm long, 3 cm wide, up to 160 µm thick in section. Hymenophore smooth, light yellow (4A4) to greyish orange (5B4), unchanged in KOH, not cracked; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context pale yellow.

Microscopic structures. Hyphal system dimitic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, thin-walled, 2–3 µm in diam., IKI–, CB–. Skeletal hyphae dominant, colorless to pale yellow, distinctly thick-walled, moderately branched, 2.5–4.5 µm in diam., dextrinoid, CB+. Catahymenium composed of skeletal hyphae, gloeocystidia, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, 1–1.5 µm in diam. Gloeocystidia abundant, subclavate to subcylindrical, colorless, thin-walled, usually with contents, SA+, 50–70 × 6–9 µm. Basidia subclavate to subcylindrical, slightly curved, thin-walled, colorless, smooth, with four sterigmata and a basal simple septum, 30–45 × 6–7.5 µm; basidioles in shape similar to basidia, but slightly smaller. Basidiospores subglobose, with a distinct apiculus, thin-walled, colorless, smooth, occasionally with oil-drops, amyloid, CB–, (6–) 6.2–7 (–7.5) × (5.5–) 5.8–6.8 (–7) µm, L = 6.5 µm, W = 6.3 µm, Q = 1.01–1.04 (n = 90/3).

Additional specimens examined. CHINA, Beijing, Changping District, Baiyanggou Scenic Spot, on dead angiosperm branch, 21 July 2021, He 7134 (BJFC 036451); Daxing District, Nanhizi Park, on dead angiosperm branch, 31 July 2021, He 7148 (BJFC 036465); Fangshan District, Qinglonghu Park, on dead Sabina branch, 31 July 2021, He 7150 (BJFC 036467); Fengtai District, Yungang Forest Park, on dead Sabina tree, 25 July 2021, He 7141 (BJFC 036458); Haidian District, Bajia Country Park, on *Sabina* stump, 16 August 2022, He 7717 (BJFC 038853); Guangxi Autonomous Region, on dead angiosperm branch, 16 June 2016, He 3819 (BJFC022318); Guizhou Province, Libo Country, Xiaoqikong Scenic Spot, on dead angiosperm branch, 16 June 2016, He 3822 (BJFC022321); Hainan Province, Baoting Country, Qixianling Forest Park, on dead angiosperm branch, 18 March 2016, He 3590 (BJFC022090) & He 3593 (BJFC022092); Haikou City, Jinniuling Park, on dead twig of living *Araucaria*, 7 June 2016, He 3825 (BJFC022327); Wanning City, Xinglong Tropical Botanical Garden, on dead angiosperm branch, 19 March 2016, He 3603 (BJFC022101); Yunnan Province, Qiubei Country, Puzhehei Scenic Spot, on dead angiosperm branch, 26 July 2014, He 20140726-5 (BJFC019218) & He 20140726-6 (BJFC019219); Ruili City, Moli Tropical Rain Forest Scenic Spot, on fallen angiosperm trunk, 2 December 2015, He 3497 (BJFC021894). THAILAND, Chiang Rai, Mae Fah Luang University, on fallen angiosperm trunk, 21 July 2016, He 4045 (BJFC023484); Krabi, on dead angiosperm branch, 28 July 2016, He 4146 (BJFC023588). VIETNAM, Ho Chi Minh City Animal and Botanical Garden, on fallen angiosperm trunk, 4 September 2017, He 5204 (BJFC024722).

Notes. *Scytinostroma subduriusculum* is characterized by subcylindrical gloeocystidia, subglobose, relatively large basidiospores, and growth on both angiosperm and gymnosperm trees. It is widely distributed in China, and also found in Thailand and Vietnam. In the phylogenetic tree (Fig. 1), *S. subduriusculum* formed a distinct lineage sister to *S. duriusculum* (Berk. & Broome) Donk. There are 24

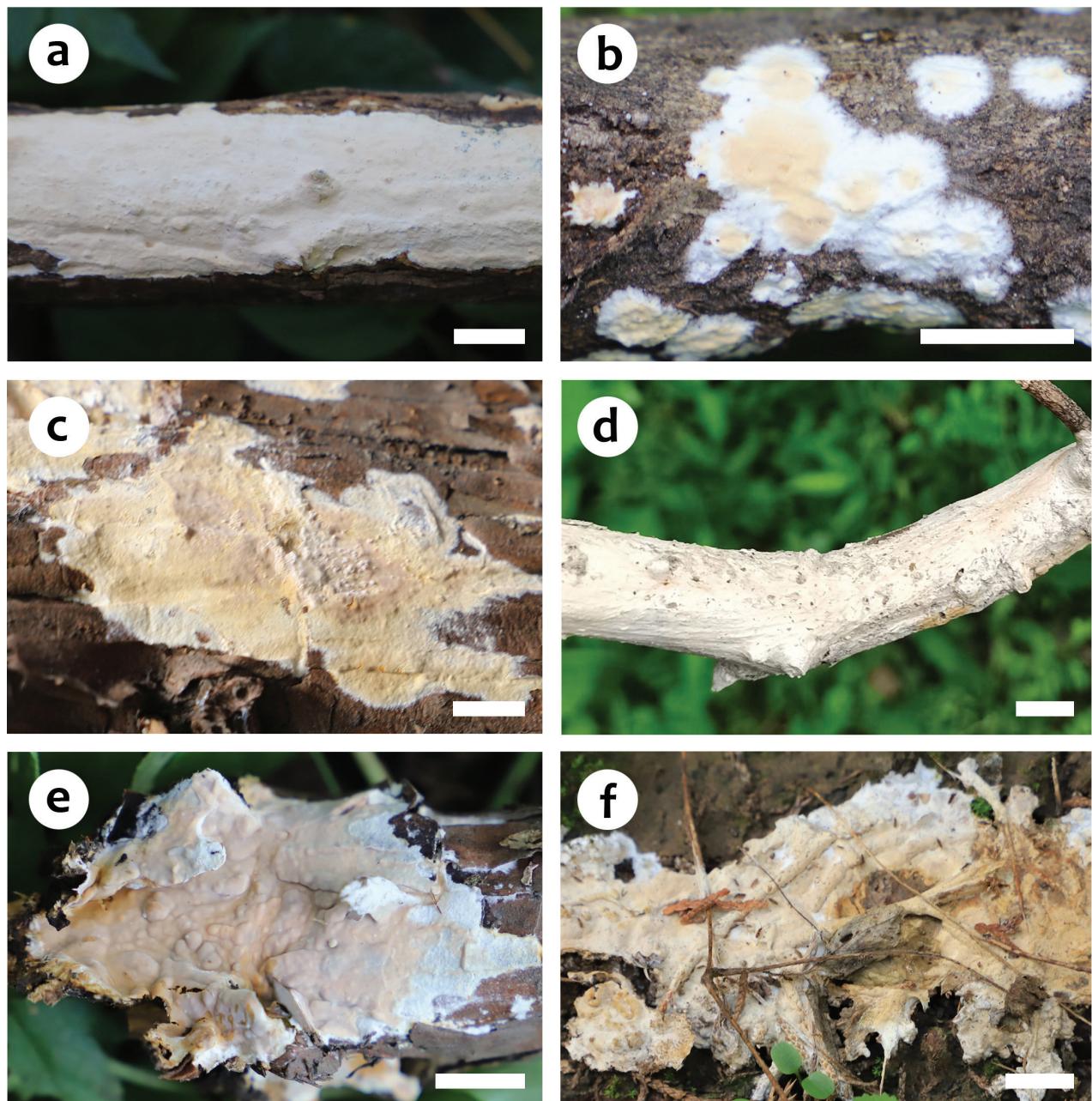


Figure 6. Basidiomes of *Scytinostroma subduriusculum* **a** He 7657 (BJFC 038793, holotype) **b** He 7134 (BJFC 036451) **c** He 7141 (BJFC 036458) **d** He 7148 (BJFC 036465) **e** He 7150 (BJFC 036467) **f** He 7717 (BJFC 036467). Scale bars: 1 cm (**a–f**).

base pair differences between *S. subduriusculum* (He 4146, Thailand) and *S. duriusculum* (He 5748, Sri Lanka), and 66 differences between *S. subduriusculum* and *S. duriusculum* (CBS 757.81, France) of total 665 base pairs of ITS1+5.8S+ITS2 sequences. The similarities are 96.4% (He 4146 vs. He 5748) and 90.1% (He 4146 vs. CBS 757.81). The French samples may represent an undescribed species because their ITS1+5.8S+ITS2 sequences largely differ from those of Sri Lankan samples (71 differences of total 665 base pairs with only 89.3% similarity). Morphologically, the two species share subclavate to subcylindrical gloeocystidia and subglobose basidiospores. However, *S. duriusculum* has shorter basidia (20–25 µm) and smaller basidiospores (6–6.5 × 5.5–6 µm, measured from He 5748 from Sri Lanka).

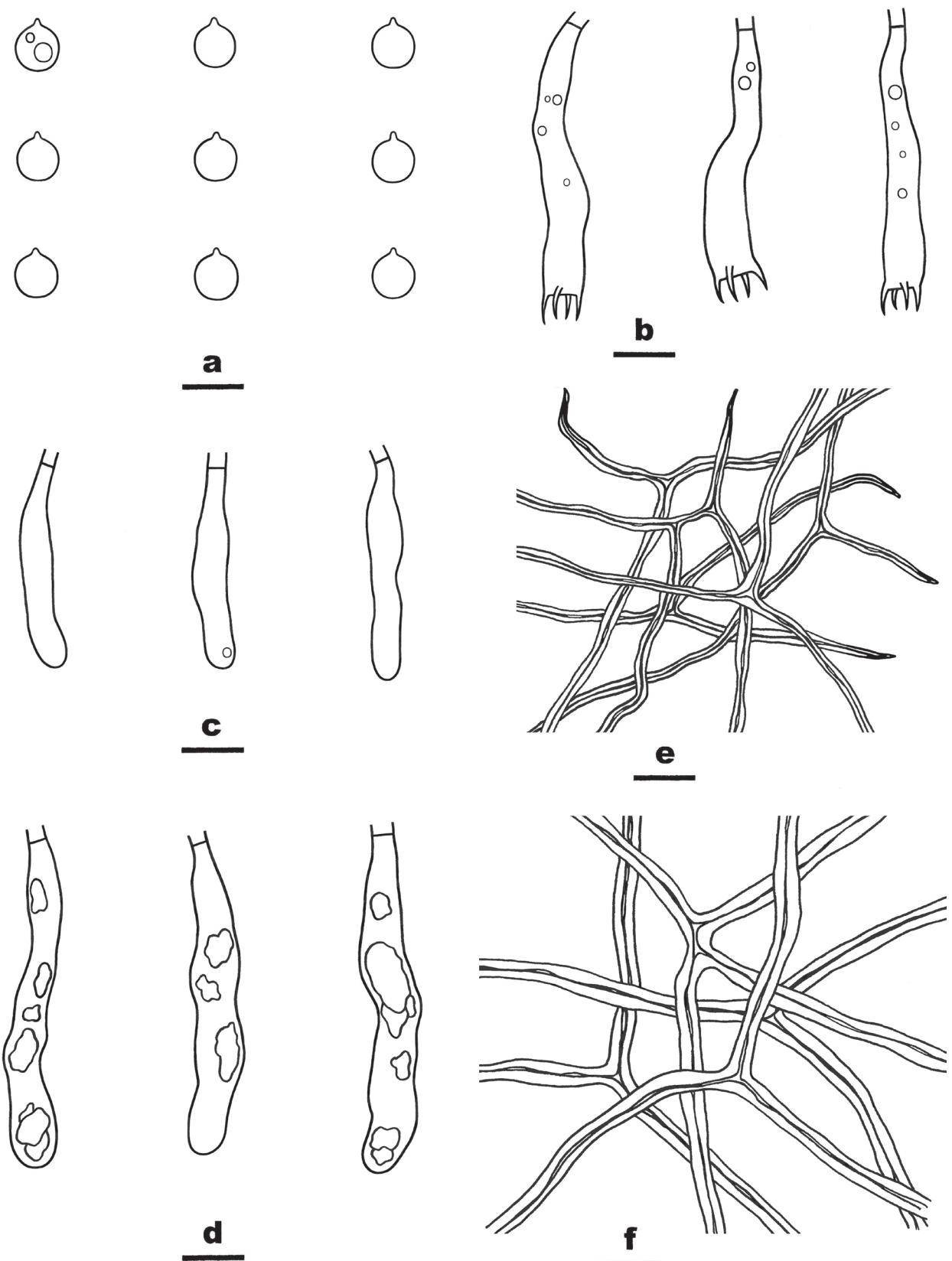


Figure 7. Microscopic structures of *Scytinostroma subduriusculum* (from the holotype He 7657) **a** basidiospores **b** basidia **c** basidioles **d** gloeocystidia **e** skeletal hyphae from hymenium **f** skeletal hyphae from subiculum. Scale bars: 10 µm (a-f).

***Scytinostroma subrenisporum* Yue Li, S.L. Liu & S.H. He, sp. nov.**

Mycobank No: 848269

Fig. 8

Type. CHINA, Guizhou Province, Libo County, Maolan Nature Reserve, on dead angiosperm branch, 11 July 2017, He 4792 (BJFC 024311, holotype).

Etymology. Refers to the morphological similarity and close phylogenetic relationship with *S. renisporum*.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, membranaceous to coriaceous, first as small patches, later confluent up to 10 cm long, 2.5 cm wide, up to 100 µm thick in section. Hymenophore smooth, pale orange (5A3), light orange (5A4) to greyish orange [5B(5–6)], unchanged in KOH, not cracked; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context pale yellow.

Microscopic structures. Hyphal system dimitic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, thin-walled, 2–3 µm in diam., IKI–, CB–. Skeletal hyphae dominant, colorless to yellow, distinctly thick-walled, moderately branched, 1.5–2 µm in diam., dextrinoid, CB+. Catahymenium composed of skeletal hyphae, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, moderately branched with acute tips, 1.5–2 µm wide at lowest part. Gloeocystidia absent. Basidia subcylindrical, slightly curved, thin-walled, colorless, smooth, with four sterigmata and a basal simple septum, 35–45 × 4.5–6.5 µm; basidioles in shape similar to basidia, but slightly smaller. Basidiospores ellipsoid to reniform, with a distinct apiculus, thin-walled, colorless, smooth, amyloid, CB–, (5.5–) 6–6.5 (–7) × (3.8–) 4–5 (–5.5) µm, L = 6.2 µm, W = 4.4 µm, Q = 1.35–1.45 (n = 60/2).

Additional specimens examined. CHINA, Anhui Province, Qimen County, Guniujiang Nature Reserve, on dead angiosperm branch, 8 August 2013, He 1720 (BJFC 016187); Fujian Province, Wuyishan County, Wuyishan Nature Reserve, on dead angiosperm branch, 3 October 2018, He 5685 (BJFC 026747) & He 5686 (BJFC 026748); Guangxi Autonomous Region, Huanjiang County, Mulun National Nature Reserve, on dead angiosperm branch, 10 July 2017, He 4751 (BJFC 024270); Guizhou Province, Libo County, Maolan Nature Reserve, on angiosperm tree, 15 June 2016, He 3792 (BJFC 022291); Hunan Province, Guzhang County, Gaowangjie National Nature Reserve, on dead angiosperm branch, 3 August 2018, He 5626 (BJFC 026688); Jiangxi Province, Ji'an County, Jinggangshan Scenic Spot, on dead angiosperm branch, 11 August 2016, He 4303 (BJFC 023745); Lianping County, Jiulianshan Nature Reserve, on dead Liana branch, 14 August 2016, He 4384 (BJFC 023825); Yifeng County, Guanshan Nature Reserve, on dead angiosperm branch, 9 August 2016, He 4170 (BJFC 023612) & He 4199 (BJFC 023641).

Notes. *Scytinostroma subrenisporum* is characterized by the absence of gloeocystidia and ellipsoid to reniform basidiospores. In the phylogenetic tree (Fig. 1), *S. subrenisporum* is closely related to *S. acystidiatum* and *S. renisporum*. *Scytinostroma acystidiatum* that was recently described from China, is similar to *S. subrenisporum* by sharing the absence of gloeocystidia but differs in having smaller basidiospores (5.2–6 × 3.5–4.5 µm, measured from the type by the authors, Zhang et al. 2023). *Scytinostroma renisporum* is similar to

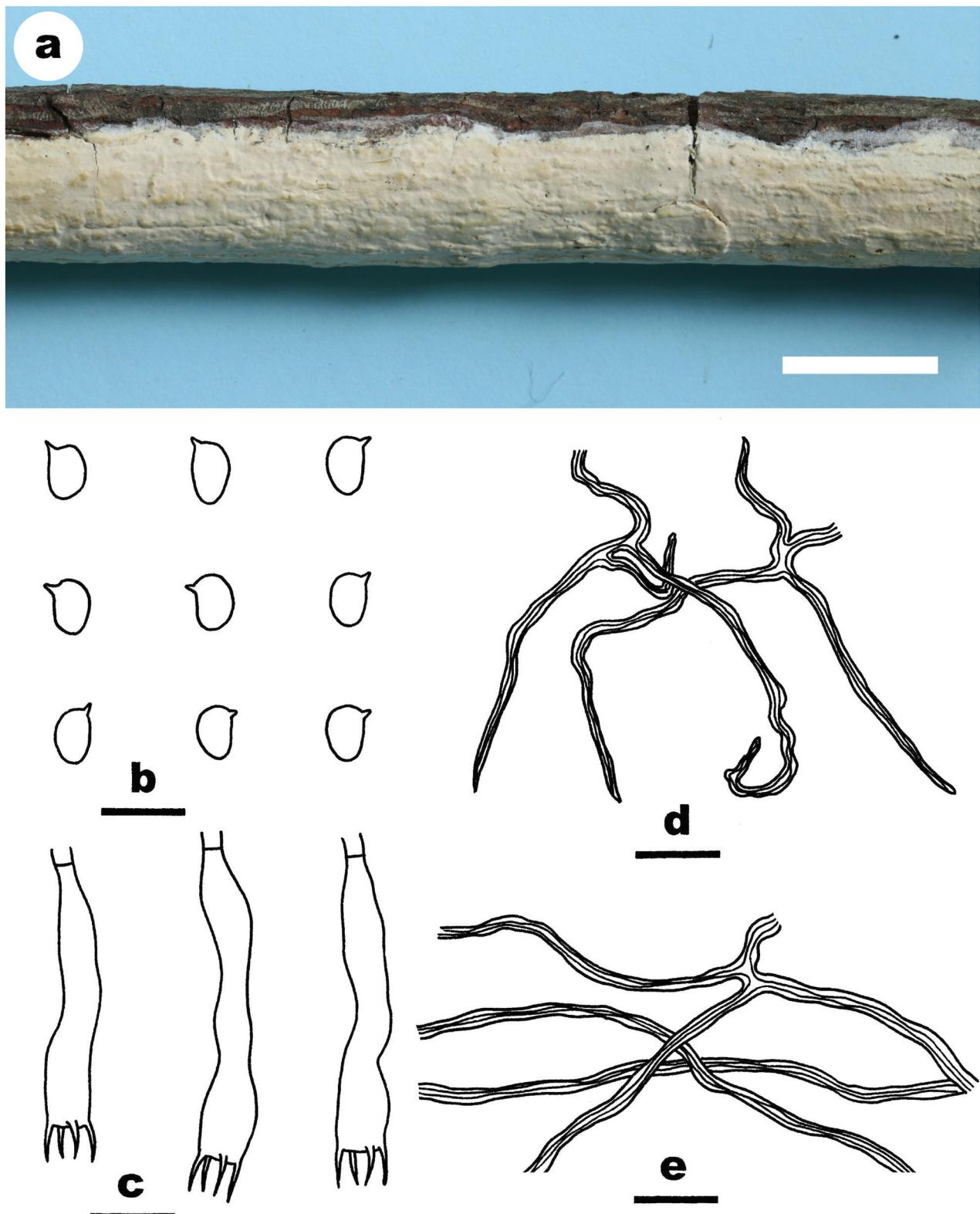


Figure 8. *Scytinostroma subrenisporum* (from the holotype He 4792) **a** basidiomes **b** basidiospores **c** basidia **d** skeletal hyphae from hymenium **e** skeletal hyphae from subiculum. Scale bars: 1 cm (**a**); 10 µm (**b–e**).

S. subrenisporum by sharing ellipsoid to reniform basidiospores but differs by having cylindrical, subclavate or fusoid gloeocystidia and a distribution in Côte d'Ivoire, western Africa (Boidin and Lanquetin 1987).

Discussion

Previous studies showed that *Scytinostroma* is polyphyletic (Larsson and Larsson 2003). In this study, we performed phylogenetic analyses of Peniophoraceae based on ITS1-5.8S-ITS2-nrLSU sequences of samples of *Scytinostroma* s.s. and representative taxa of other genera. Species of *Scytinostroma* s.s. including the type, *S. portentosum*, formed a moderately supported clade in the likelihood analysis but a strongly supported clade in the Bayesian analysis. For the moment, we prefer to treat this clade as a monophyletic genus and believe that the support values could be higher if more samples of Peniophoraceae are included. Since a sequence of *S. portentosum* (type species, described from Pennsylvania) from Canada was distinct from the strongly supported sister lineage comprised of sequences of *S. portentosum* and *S. hemidichophyticum* from Europe, we suppose that all the European sequences represent *S. hemidichophyticum* and *S. portentosum* is restricted in distribution to North America. The two species, *S. artocreas* and *S. incrustatum* transferred from *Michenera* by Stalpers et al. (2021) based on morphological evidence, were nested within the *Scytinostroma* s.s. *Scytinostroma duriusculum* is a cosmopolitan species and has been reported from many countries in subtropical and tropical areas (Boidin and Lanquetin 1987; Bernicchia and Gorjón 2010). However, our phylogenetic analyses demonstrated that it could be a species complex, because three lineages were recognized from the samples of France, Sri Lanka, and China, Thailand and Vietnam.

On the one hand, species in *Scytinostroma* s.s. clade have some common morphological characters, for example, simple-septate generative hyphae, and ovoid, reniform to subglobose basidiospores with amyloid reactions in Melzer's reagent. However, this doesn't mean species with inamyloid basidiospores could not belong to *Scytinostroma* s.s. On the other hand, the shape of skeletal hyphae, presence of gloeocystidia and encrusted cystidia, and size of basidiospores varies in different species. Based on our phylogenetic and morphological study results, we recognized 14 species of *Scytinostroma* s.s. worldwide. Until now, seven species have been reported from China, all of which were newly described in the present study and other recently published papers (Liu et al. 2018; Wang et al. 2020; Zhang et al. 2023). It seems that China, especially its temperate areas, is rich in species diversity of *Scytinostroma* s.s. Although *Scytinostroma* s.s. is well studied in the present paper, the species diversity, taxonomy and phylogeny of *Scytinostroma* s.l. and related genera are still unresolved. A comprehensive study on this issue is urgently needed.

A key to species of *Scytinostroma* s.s. worldwide

| | | |
|---|----------------------------------|-------------------------|
| 1 | Gloeocystidia absent..... | 2 |
| - | Gloeocystidia present | 3 |
| 2 | Basidiospores > 6 µm long | <i>S. subrenisporum</i> |
| - | Basidiospores < 6 µm long | <i>S. acystidiatum</i> |
| 3 | Basidiospores > 15 µm long | 4 |
| - | Basidiospores < 15 µm long | 6 |

| | | |
|----|---|-----------------------------|
| 4 | Basidiospores fusiform to navicular..... | <i>S. caudisporum</i> |
| - | Basidiospores subglobose to globose..... | 5 |
| 5 | Lamprocystidia present, basidiospores 17–22 × 16–21 µm.... | <i>S. incrassatum</i> |
| - | Lamprocystidia absent, basidiospores 16–19 × 14–16 µm.... | <i>S. artocreas</i> |
| 6 | Basidiospores ovoid to reniform | <i>S. renisporum</i> |
| - | Basidiospores subglobose | 7 |
| 7 | Distributed in subtropical and tropical areas..... | 8 |
| - | Distributed in temperate areas | 10 |
| 8 | Gloeocystidia < 50 µm long | <i>S. yunnanense</i> |
| - | Gloeocystidia > 50 µm long | 9 |
| 9 | Reported from Sri Lanka, basidia 20–25 µm long, basidiospores 6–6.5 × 5.5–6 µm..... | <i>S. duriusculum</i> |
| - | Reported from China, Thailand, Vietnam, basidia 30–45 µm long, basidiospores 6.2–7 × 5.8–6.8 µm | <i>S. subduriusculum</i> |
| 10 | Reported from occidental countries | 11 |
| - | Reported from China | 13 |
| 11 | North American species | <i>S. portentosum</i> |
| - | European species | 12 |
| 12 | Skeletal hyphae in hymenium rarely branched | <i>S. alutum</i> |
| - | Skeletal hyphae in hymenium dichotomously branched | <i>S. hemidichophyticum</i> |
| 13 | Gloeocystidia two kinds..... | <i>S. beijingensis</i> |
| - | Gloeocystidia one kind..... | 14 |
| 14 | Basidiospores > 6 µm in diam. | <i>S. subduriusculum</i> |
| - | Basidiospores < 6 µm in diam. | <i>S. boidinii</i> |

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Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization, S.-H.H.; methodology, Y.L. and S.-H.H.; performing the experiment, Y.L., W.-Q.X. and N.Y.; formal analysis, Y.L. and W.-Q.X.; validation, Y.L., W.-Q.X., S.-L.L. and S.-H.H.; resources, S.-H.H.; writing—original draft preparation, Y.L. and S.-L.L.; writing—review and editing, S.-H.H.; visualization, Y.L. and S.-L.L.; supervision, S.-H.H.; project administration, S.-H.H.; funding acquisition, S.-H.H. All authors have read and agreed to the published version of the manuscript.

Author ORCIDs

- Yue Li  <https://orcid.org/0000-0003-4091-1506>
Wei-Qi Xu  <https://orcid.org/0009-0000-5675-386X>
Shi-Liang Liu  <https://orcid.org/0000-0001-7556-2575>
Ning Yang  <https://orcid.org/0009-0007-6900-5669>
Shuang-Hui He  <https://orcid.org/0000-0003-4702-3034>

Data availability

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

References

- Bernicchia A, Gorjón SP (2010) Corticiaceae s.l. Fungi Europaei 12. Edizioni Candusso. Alassio, Italia.
- Binder M, Hibbett DS, Larsson KH, Larsson E, Langer E, Langer G (2005) The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). *Systematics and Biodiversity* 3(2): 113–157. <https://doi.org/10.1017/S147720005001623>
- Boidin J, Lanquetin P (1987) Le genre *Scytinostroma* Donk. *Bibliotheca Mycologica* 114: 1–130.
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9(8): 772. <https://doi.org/10.1038/nmeth.2109>
- Hall TA (1999) Bioedit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98. <https://doi.org/10.1021/bk-1999-0734.ch008>
- Katoh K, Rozewicki J, Yamada KD (2017) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20(4): 1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Keasey M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Genious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28(12): 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>
- Kornerup A, Wanscher JH (1978) Methuen handbook of colour. 3rd edn. E. Methuen and Co., Ltd., London.
- Langer E (2002) Phylogeny of non-gilled and gilled Basidiomycetes: DNA sequence inference, ultrastructure, and comparative morphology. *Habilitationsschrift*, University of Tübingen, Tübingen.
- Larsson E, Larsson KH (2003) Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphyllophoralean taxa. *Mycologia* 95(6): 1037–1065. <https://doi.org/10.1080/15572536.2004.11833020>
- Leal-Dutra CA, Neves MA, Griffith GW, Reck MA, Clasen LA, Dentinger BT (2018) Reclassification of *Parapterulicum* Corner (Pterulaceae, Agaricales), contributions to Lachnocladiaceae and Peniophoraceae (Russulales) and introduction of *Baltazaria* gen. nov. *MycoKeys* 37: 39–56. <https://doi.org/10.3897/mycokeys.37.26303>
- Liu SL, He SH (2018) Taxonomy and phylogeny of *Dichostereum* (Russulales), with descriptions of three new species from southern China. *MycoKeys* 40: 111–126. <https://doi.org/10.3897/mycokeys.40.28700>

- Liu SL, Nakasone KK, He SH (2018) *Michenera incrustata* sp. nov. (Peniophoraceae, Russulales) from Yunnan Province, southwestern China. *Nova Hedwigia* 108: 197–206. https://doi.org/10.1127/nova_hedwigia/2018/0500
- Maddison WP, Maddison DR (2018) Mesquite: a modular system for evolutionary analysis. Version 3.5.1. <http://www.mesquiteproject.org>
- Miller SL, Larsson E, Larsson KH, Verbeken A, Nuytinck J (2006) A phylogeny for kingdom fungi (deep hypha) II perspectives in the new russulales. *Mycologia* 98(6): 960–970. <https://doi.org/10.1080/15572536.2006.11832625>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Stalpers J, Redhead S, May TW, Rossman AY, Crouch JA, Cubeta MA, Dai YC, Kirschner R, Langer GJ, Larsson KH, Mack J, Norvell LL, Oberwinkler F, Papp V, Roberts P, Rajchenberg M, Seifert KA, Thorn RG (2021) Competing sexual-aseexual generic names in Agaricomycotina (Basidiomycota) with recommendations for use. *IMA Fungus* 12(1): 1–31. <https://doi.org/10.1186/s43008-021-00061-3>
- Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30(9): 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Vu D, Groenewald M, de Vries M, Gehrmann T, Stielow B, Eberhardt U, Al-Hatmi A, Groenewald JZ, Cardinali G, Houbraken J, Boekhout T, Crous PW, Robert V, Verkley GJM (2019) Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Studies in Mycology* 92(1): 135–154. <https://doi.org/10.1016/j.simyco.2018.05.001>
- Wang H, He X, Zhao CL (2020) *Scytinostroma yunnanense* sp. nov. (Russulales, Basidiomycota) evidenced by morphological characteristics and phylogenetic analyses in China. *Phytotaxa* 451: 145–153. <https://doi.org/10.11646/phytotaxa.451.2.4>
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR protocols: A guide to methods and applications. Academic, San Diego, 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Xu YL, Tian Y, He SH (2023) Taxonomy and phylogeny of *Peniophora* sensu lato (Russulales, Basidiomycota). *Journal of Fungi* 9(1): 93. <https://doi.org/10.3390/jof9010093>
- Zhang QY, Liu HG, Bian LS, Chen Q (2023) Two new species of *Scytinostroma* (Russulales, Basidiomycota) in Southwest China. *Frontiers in Cellular and Infection Microbiology* 13: 1189600. <https://doi.org/10.3389/fcimb.2023.1189600>