Species diversity, molecular phylogeny and ecological habits of *Cyanosporus* (Polyporales, Basidiomycota) with an emphasis on Chinese collections

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Abstract

*Cyanosporus* is a genus widely distributed in Asia, Europe, North America, South America and Oceania. It grows on different angiosperm and gymnosperm trees and can cause brown rot of wood. Blue-tinted basidiomata of *Cyanosporus* makes it easy to distinguish from other genera, but the similar morphological characters make it difficult to identify species within the genus. Phylogeny and taxonomy of *Cyanosporus* were carried out based on worldwide samples with an emphasis on Chinese collections, and the species diversity of the genus is updated. Four new species, *C. flavus*, *C. rigidus*, *C. subungulatus* and *C. tenuicontextus*, are described based on the evidence of morphological characters, distribution areas, host trees and molecular phylogenetic analyses inferred from the internal transcribed spacer (ITS) regions, the large subunit of nuclear ribosomal RNA gene (nLSU), the small subunit of nuclear ribosomal RNA gene (nSSU), the small subunit of mitochondrial rRNA gene (mtSSU), the largest subunit of RNA polymerase II (RPB1), the second largest subunit of RNA polymerase II (RPB2), and the translation elongation factor 1-α gene (TEF). Our study expanded the number of *Cyanosporus* species to 35 around the world including 23 species from China. Detailed descriptions of the four new species and the geographical locations of the *Cyanosporus* species in China are provided.

Keywords

brown-rot fungi, distribution areas, host trees, multi-gene phylogeny, new species

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Introduction

*Cyanosporus* was proposed as a monotypic genus for *Polyporus caesius* (Schrad.) Fr. based on its cyanophilous basidiospores (McGinty 1909). However, *Tyromyces caesius* (Schrad.) Murrill and *Postia caesia* (Schrad.) P. Karst. were frequently used instead of *Cyanosporus caesius* (Schrad.) McGinty in subsequent studies (Donk 1960; Jahn 1963; Lowe 1975). Later, four species in the *Postia caesia* complex were described from Europe, viz., *P. luteocaesia* (A. David) Jülich, *P. subcaesia* (A. David) Jülich, *P. alni* Niemelä & Vampola and *P. mediterraneocaesia* M. Pieri & B. Rivoire (David 1974, 1980; Jahn 1979; Pieri and Rivoire 2005). Then, the subgenus *Cyanosporus* (McGinty) V. Papp was proposed for the species of *P. caesia* complex (Papp 2014). Miettinen et al. (2018) revised the species concept of the *P. caesia* complex based on morphology and two gene markers (ITS and TEF) and raised the species number of the complex to 24, including six species from China.

Previously, species identification of the *P. caesia* complex was only based on morphological characters and host trees in China, and only two species were recorded from China before Dai (2012), viz., *P. alni* and *P. caesia*. Recently, taxonomic studies of *P. caesia* complex in China have been carried out, and some new species have been described based on both morphological characteristics and molecular data. Shen et al. (2019) carried out a comprehensive study on *Postia* and related genera, in which *Cyanosporus* was supported as an independent genus with 12 species were accepted in this genus. Liu et al. (2021a) studied the species diversity and molecular phylogeny of *Cyanosporus* and the number of *Cyanosporus* species was expanded to 31 around the world, including 19 species from China. These studies have greatly enriched the species of *Cyanosporus* in China. Currently, the morphological characteristics of the genus are as follows: basidiomata annual, pileate or resupinate to effused-reflexed, soft corky, corky to fragile. Pileal surface white to cream to greyish brown, usually with blue tint. Pore surface white to cream, frequently bluish; pores round to angular. Context white to cream, corky. Tubes cream, fragile. Hyphal system monomitic; generative hyphae clamped, IKI–, CB–. Cystidia usually absent, cystidioles occasionally present. Basidiospores narrow, allantoid to cylindrical, hyaline, usually slightly thick-walled, smooth, IKI–, weakly CB+.

*Cyanosporus* species usually have blue-tinted basidiomata, which makes it easy to recognize. Some specimens with blue-tinted basidiomata were collected during investigations into the diversity of polypores in China, and four undescribed species of *Cyanosporus* were discovered. To confirm the affinity of the undescribed species to *Cyanosporus*, phylogenetic analyses were carried out based on the combined datasets of ITS+TEF and ITS+nLSU+nSSU+mtSSU+RPB1+RPB2+TEF sequences. During the investigation and study of *Cyanosporus*, the information of host trees and distribution areas of species in the genus from China were also obtained (Table 1). Four new species are described and illustrated in the current study, and the geographical locations of the *Cyanosporus* species distributed in China are indicated on the map (Fig. 1).
Table 1. The main ecological habits of *Cyanosporus* with an emphasis on distribution areas and host trees. New species are shown in bold.

| Species | Distribution in the world | Distribution in China | Climate zone | Host | Reference |
|---------|---------------------------|-----------------------|--------------|------|-----------|
| *C. aequor* (Niemi & Vampola) B.K. Cui, L.L. Shen & Y.C. Dai | Europe (Czech Republic, Denmark, Finland, Germany, Norway, Poland, Russia, Slovakia), East Asia (China) | Guizhou, Hebei | Temperate | Angiosperm (*Alnus*, *Betula*, *Corylus*, *Fagus*, *Populus*, *Quercus*) | Miettinen et al. 2018; present study |
| *C. arbus* (Spirin & Niemela) B.K. Cui & Shun Liu | North America (USA) | | Temperate | Angiosperm (*Arbutus*) | Miettinen et al. 2018 |
| *C. aureoconus* (Spirin & Niemela) B.K. Cui & Shun Liu | Europe (Finland, Poland, Russia), East Asia (China) | Inner Mongolia | Temperate to boreal | Gymnosperm (*Pinus*, *Picea*) | Miettinen et al. 2018; Liu et al. 2021a |
| *C. bifarius* (Spirin) B.K. Cui & Shun Liu | Europe (Russia), East Asia (China, Japan) | Jilin, Sichuan, Yunnan | Cold temperate | Gymnosperm (*Picea, Pinus, Larix*) | Miettinen et al. 2018; present study |
| *C. babalina* B.K. Cui & Shun Liu | East Asia (China) | Yunnan | Temperate | Gymnosperm (*Pinus*) | Liu et al. 2021a |
| *C. caesius* (M. Pieri & B. Riboire) B.K. Cui, L.L. Shen & Y.C. Dai | Europe (Czech Republic, Denmark, Finland, France, Germany, Russia, Slovakia, Spain, UK) | | Common in temperate, rare in south boreal zone | Angiosperm (*Betula, Fagus, Salix*) and gymnosperm (*Abies, Picea*) | Miettinen et al. 2018 |
| *C. cyanescens* (Schrad.) McGinnis | Europe (Estonia, Finland, France, Poland, Russia, Spain, Sweden) | | Temperate to Mediterranean mountains | Gymnosperm (*Abies, Picea, Pinus*) | Miettinen et al. 2018 |
| *C. flavus* B.K. Cui & Shun Liu | East Asia (China) | Sichuan | Plateau humid climate | Gymnosperm (*Abies, Picea*) | Present study |
| *C. fusiformis* B.K. Cui, L.L. Shen & Y.C. Dai | East Asia (China) | Guizhou, Sichuan | North temperate to subtropical | Angiosperm (*Rhododendron*) | Shen et al. 2019 |
| *C. glauc* (Spirin & Miettinen) B.K. Cui & Shun Liu | East Asia (China), Europe (Russia) | Jilin | Cold temperate mountains | Gymnosperm (*Abies, Picea*) | Miettinen et al. 2018 |
| *C. gosypinus* (Motug. & Lév.) B.K. Cui & Shun Liu | Europe (France) | | Temperate | Gymnosperm (*Cedrus*) | Miettinen et al. 2018 |
| *C. hirsutus* B.K. Cui & Shun Liu | East Asia (China) | Qinghai, Sichuan, Yunnan | Temperate to plateau continental climate | Gymnosperm (*Abies, Picea*) | Liu et al. 2021a; present study |
| *C. livens* (Miettinen & Vlasák) B.K. Cui & Shun Liu | North America (Canada, USA) | | Temperate | Angiosperm (*Acer, Betula, Fagus*) and gymnosperm (*Abies, Larix, Picea, Tsuga*) | Miettinen et al. 2018 |
| *C. laterocaudatus* (A. David) B.K. Cui, L.L. Shen & Y.C. Dai | Europe (France) | Mediterranean | | Gymnosperm (*Pinus*) | Miettinen et al. 2018 |
| *C. magnus* (Miettinen) B.K. Cui & Shun Liu | East Asia (China) | Chongjin, Jilin, Hainan, Yunnan | Temperate | Angiosperm (*Populus*) and gymnosperm (*Corylus*) | Miettinen et al. 2018; present study |
| *C. mediterraneocaesius* (M. Pieri & B. Riboire) B.K. Cui, L.L. Shen & Y.C. Dai | Europe (France, Spain) | | Warm temperate to Mediterranean | Angiosperm (*Buxus, Erica, Populus, Quercus*) and gymnosperm (*Cedrus, Juniperus, Pinus*) | Miettinen et al. 2018 |
| *C. microporosus* B.K. Cui, L.L. Shen & Y.C. Dai | East Asia (China) | Yunnan | Subtropical | Angiosperm (undetermined) | Shen et al. 2019 |
| *C. nobilis* B.K. Cui, Shun Liu & Y.C. Dai | Oceania (Australia), South America (Argentina) | | Temperate marine climate | Angiosperm (*Nannophyllum*) | Liu et al. 2021a |
Morphological studies

The examined specimens were deposited in the herbarium of the Institute of microbiology, Beijing Forestry University (BJFC), and some duplicates were deposited at the Institute of Applied Ecology, Chinese Academy of Sciences, China (IFP) and Southwest Forestry University (SWFC). Macro-morphological descriptions were based on the field notes and measurements of herbarium specimens. Special colour terms followed Petersen (1996). Micro-morphological data were obtained from the dried specimens and observed under a light microscope following Cui et al. (2019) and Liu et al. (2021b). Sections were studied at a magnification up to × 1000 using a Nikon Eclipse 80i microscope and phase contrast.
illumination (Nikon, Tokyo, Japan). Drawings were made with the aid of a drawing tube. Microscopic features, measurements and drawings were made from slide preparations stained with Cotton Blue and Melzer’s reagent. Spores were measured from sections cut from the tubes. To present variation in the size of basidiospores, 5% of measurements were excluded from each end of the range and extreme values are given in parentheses.

In the text the following abbreviations were used: IKI = Melzer’s reagent, IKI– = neither amyloid nor dextrinoid, KOH = 5% potassium hydroxide, CB = Cotton Blue, CB + = cyanophilous, CB – = acyanophilous, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios between the specimens studied, n (a/b) = number of spores (a) measured from given number (b) of specimens.

Molecular studies and phylogenetic analysis

A cetyl trimethylammonium bromide (CTAB) rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd, Beijing, China) was used to extract total genomic DNA from dried specimens, and performed the polymerase chain reaction
(PCR) according to the manufacturer’s instructions with some modifications as described by Shen et al. (2019) and Liu et al. (2021a). The ITS regions were amplified with primer pairs ITS5 and ITS4 (White et al. 1990). The nLSU regions were amplified with primer pairs LR0R and LR7 (http://www.biology.duke.edu/fungi/mycolab/primers.htm). The nSSU regions were amplified with primer pairs NS1 and NS4 (White et al. 1990). The mtSSU regions were amplified with primer pairs MS1 and MS2 (White et al. 1990). RPB1 was amplified with primer pairs RPB1-Af and RPB1-Cr (Matheny et al. 2002). RPB2 was amplified with primer pairs fRPB2-f5F and bRPB2-7.1R (Matheny 2005). Part of TEF was amplified with primer pairs EF1-983 F and EF1-1567R (Rehner 2001).

The PCR cycling schedule for ITS, mtSSU and TEF included an initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 54 °C for ITS and mtSSU, 54–55 °C for TEF for 45 s, 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR cycling schedule for nLSU and nSSU included an initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 50 °C for nLSU and 52 °C for nSSU for 1 min, 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. The PCR procedure for RPB1 and RPB2 follow Justo and Hibbett (2011) with slight modifications: initial denaturation at 94 °C for 2 min, followed by 10 cycles at 94 °C for 40 s, 60 °C for 40 s and 72 °C for 2 min, then followed by 37 cycles at 94 °C for 45 s, 55 °C for 1.5 min and 72 °C for 2 min, and a final extension of 72 °C for 10 min. The PCR products were purified and sequenced at Beijing Genomics Institute (BGI), China, with the same primers. All newly generated sequences were deposited at GenBank (Table 1).

Additional sequences were downloaded from GenBank (Table 1). All sequences of ITS, nLSU, nSSU, mtSSU, RPB1, RPB2 and TEF were respectively aligned in MAFFT 7 (Katoh and Standley 2013; http://mafft.cbrc.jp/alignment/server/) and manually adjusted in BioEdit (Hall 1999). Alignments were spliced in Mesquite (Maddison and Maddison 2017). The missing sequences were coded as “N”. Ambiguous nucleotides were coded as “N”. The final concatenated sequence alignment was deposited at TreeBase (http://purl.org/phylo/treebase; submission ID: 29010).

Most parsimonious phylogenies were inferred from the combined 2-gene dataset (ITS+TEF) and 7-gene dataset (ITS+nLSU+nSSU+mtSSU+RPB1+RPB2+TEF), and their congruences were evaluated with the incongruence length difference (ILD) test (Farris et al. 1994) implemented in PAUP* 4.0b10 (Swofford 2002), under heuristic search and 1000 homogeneity replicates. Phylogenetic analyses approaches followed Liu et al. (2019) and Sun et al. (2020). In phylogenetic reconstruction, the sequences of Antrodia serpens (Fr.) Donk and A. tanakae (Murrill) Spirin & Miettinen obtained from GenBank were used as outgroups. Maximum parsimony analysis was applied to the combined multiple genes datasets, and the tree construction procedure was performed in PAUP* version 4.0b10. All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates.
Diversity, phylogeny and ecological habits of *Cyanosporus* (Felsenstein 1985). Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each most Parsimonious Tree (MPT) generated. RAxML v.7.2.8 was used to construct a maximum likelihood (ML) tree with a GTR+G+I model of site substitution including estimation of Gamma-distributed rate heterogeneity and a proportion of invariant sites (Stamatakis 2006). The branch support was evaluated with a bootstrapping method of 1000 replicates (Hillis and Bull 1993). The phylogenetic tree was visualized using FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

MrModeltest 2.3 (Posada and Crandall 1998; Nylander 2004) was used to determine the best-fit evolution model for the combined multi-gene dataset for Bayesian inference (BI). Bayesian inference was calculated with MrBayes 3.1.2 with a general time reversible (GTR) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist and Huelsenbeck 2003). Four Markov chains were run for 2 runs from random starting trees for 1.8 million generations (ITS+TEF), for 3.5 million generations (ITS+nLSU+nSSU+mtSSU+RPB1+RPB2+TEF) and trees were sampled every 100 generations. The first one-fourth generations were discarded as burn-in. A majority rule consensus tree of all remaining trees was calculated. Branches that received bootstrap support for maximum parsimony (MP), maximum likelihood (ML) and Bayesian posterior probabilities (BPP) greater than or equal to 75% (MP and ML) and 0.95 (BPP) were considered as significantly supported, respectively.

### Results

### Phylogeny

The combined 2-gene (ITS+TEF) sequences dataset had an aligned length of 1015 characters, of which 502 characters were constant, 62 were variable and parsimony-uninformative, and 451 were parsimony-informative. MP analysis yielded 10 equally parsimonious trees (TL = 2396, CI = 0.379, RI = 0.735, RC = 0.279, HI = 0.621). The best model for the concatenate sequence dataset estimated and applied in the Bayesian inference was GTR+I+G with equal frequency of nucleotides. ML analysis resulted in a similar topology as MP and Bayesian analyses, and only the ML topology is shown in Fig. 2.

The combined 7-gene (ITS+nLSU+nSSU+mtSSU+RPB1+RPB2+TEF) sequences dataset had an aligned length of 5634 characters, of which 3843 characters were constant, 247 were variable and parsimony-uninformative, and 1544 were parsimony-informative. MP analysis yielded 23 equally parsimonious trees (TL = 5756, CI = 0.468, RI = 0.752, RC = 0.352, HI = 0.532). The best model for the concatenate sequence dataset estimated and applied in the Bayesian inference was GTR+I+G with equal frequency of nucleotides. ML analysis resulted in a similar topology as MP and Bayesian analyses, and only the ML topology is shown in Fig. 3.

The phylogenetic trees inferred from ITS+TEF and ITS+nLSU+nSSU+mtSSU+RPB1+RPB2+TEF gene sequences were all obtained from 106 fungal samples represent-
Figure 2. Maximum likelihood tree illustrating the phylogeny of *Cyanosporus* and its related genera in the antrodia clade based on the combined sequences dataset of ITS+TEF. Branches are labelled with maximum likelihood bootstrap higher than 50%, parsimony bootstrap proportions higher than 50% and Bayesian posterior probabilities more than 0.90 respectively. Bold names = New species.
Figure 3. Maximum likelihood tree illustrating the phylogeny of *Cyanosporus* and its related genera in the antrodia clade based on the combined sequences dataset of ITS+nLSU+nSSU+mtSSU+RPB1+RPB2+TEF. Branches are labelled with maximum likelihood bootstrap higher than 50%, parsimony bootstrap proportions higher than 50% and Bayesian posterior probabilities more than 0.90 respectively. Bold names = New species.
ing 65 taxa of *Cyanosporus* and its related genera within the antrodia clade. 74 samples representing 35 taxa of *Cyanosporus* clustered together and separated from species of *Postia* and other related genera. As for *Cyanosporus*, the sequences used in phylogenetic analyses include 28 holotype specimen sequences, one isotype specimen sequence and one neotype specimen sequence (Table 1).

**Taxonomy**

*Cyanosporus flavus* B.K. Cui & Shun Liu, sp. nov.

MycoBank No: 842319

Figs 4, 5

**Diagnosis.** *Cyanosporus flavus* is characterised by flabelliform to semicircular and hirsute pileus with ash grey to light vinaceous grey pileal surface when fresh, buff to lemon-chrome pore surface when dry, and allantoid and slightly curved basidiospores (4.6–5.2 × 0.8–1.3 μm).

**Holotype.** China. Sichuan Province, Jiuzhaigou County, on stump of *Picea* sp., 19. IX.2020, Cui 18547 (BJFC 035408).

**Etymology.** *Flavus* (Lat.): referring to its lemon-chrome pore surface when dry.

**Fruiting body.** Basidiomata annual, pileate, soft and watery, without odour or taste when fresh, becoming corky to fragile and light in weight upon drying. Pileus flabelliform to semicircular, projecting up to 3.2 cm, 5.7 cm wide and 0.9 cm thick at base. Pileal surface ash-grey to light vinaceous grey when fresh, becoming pale mouse-grey to mouse-grey when dry, hirsute; margin acute to slightly obtuse, white with a little blue tint when fresh, olivaceous buff to greyish brown when dry. Pore surface white to cream when fresh, becoming buff to lemon-chrome when dry; sterile margin narrow to almost lacking; pores angular, 5–7 per mm; dissepiments thin, entire to lacerate. Context white to cream, soft corky, up to 6 mm thick. Tubes pale mouse-grey to ash-grey, fragile, up to 4 mm long.

**Hyphal structure.** Hyphal system monomitic; generative hyphae with clamp connections, IKI–, CB–; hyphae unchanged in KOH.

**Context.** Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, loosely interwoven, 2.7–6.5 μm in diam.

**Tubes.** Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, rarely branched, interwoven, 2.2–4.7 μm in diam. Cystidia absent; cystidioles present, fusoid, thin-walled, 12.3–17.8 × 2.2–3.5 μm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 13.2–16.5 × 3.2–5.5 μm; basidioles dominant, in shape similar to basidia, but smaller, 12.6–15.7 × 2.9–5.2 μm.

**Spores.** Basidiospores slim allantoid, slightly curved, hyaline, thin- to slightly thick-walled, smooth, IKI–, CB–, 4.6–5.2 × 0.8–1.3 μm, L = 5 μm, W = 0.99 μm, Q = 4.96–5.25 (n = 60/2).

**Type of rot.** Brown rot.

**Additional specimen (paratype) examined.** China. Sichuan Province, Jiuzhaigou County, Jiuzhaigou Nature Reserve, on fallen trunk of *Abies* sp., 20.IX.2020, Cui 18562 (BJFC 035423).
Cyanosporus rigidus B.K. Cui & Shun Liu, sp. nov.
MycoBank No: 842320
Figs 6, 7

Diagnosis. *Cyanosporus rigidus* is characterised by corky, hard corycky to rigid basidiomata with a buff yellow to clay-buff and tomentose pileal surface when fresh, becom-
Figure 5. Microscopic structures of *Cyanosporus flavus* (Holotype, Cui 18547) a basidiospores b basidia and basidioles c cystidioles d hyphae from trama e hyphae from context. Drawings by: Shun Liu.
ing olivaceous buff to greyish brown when dry, smaller and cylindrical to allantoid basidiospores (3.7–4.2 × 0.9–1.3 μm).

**Holotype.** China. Yunnan Province, Yulong County, Laojun Mountain, Jiushijiu Longtan, on fallen trunk of *Abies* sp., 15.IX.2018, Cui 17032 (BJFC 030331).
Figure 7. Microscopic structures of *Cyanosporus rigidus* (Holotype, Cui 17032) **a** basidiospores **b** basidia and basidioles **c** hyphae from trama **d** hyphae from context. Drawings by: Shun Liu.
**Etymology.** *Rigidus* (Lat.): referring to the rigid basidiomata.

**Fruiting body.** Basidiomata annual, pileate, corky, without odour or taste when fresh, becoming hard corky to rigid upon drying. Pileus flabelliform, projecting up to 1.6 cm, 3.8 cm wide and 0.6 cm thick at base. Pileal surface tomentose, buff yellow to clay-buff, when fresh, becoming smooth, rugose, olivaceous buff to greyish brown when dry; margin obtuse. Pore surface white to cream when fresh, becoming buff-yellow to pinkish buff when dry; sterile margin narrow to almost lacking; pores angular, 5–8 per mm; dissepiments thin, entire to lacerate. Context cream to buff, hard corky, up to 4 mm thick. Tubes cream to pinkish buff, brittle, up to 5 mm long.

**Hyphal structure.** Hyphal system monomitic; generative hyphae with clamp connections, IKI–, CB–; hyphae unchanged in KOH.

**Context.** Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, rarely branched, loosely interwoven, 2.2–5 μm in diam.

**Tubes.** Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, interwoven, 2–4 μm in diam. Cystidia and cystidioles absent. Basidia clavate, bearing four sterigmata and a basal clamp connection, 12.4–14.8 × 3–4.2 μm; basidioles dominant, in shape similar to basidia, but smaller, 11.8–13.9 × 2.6–4 μm.

**Spores.** Basidiospores allantoid to cylindrical, slightly curved, hyaline, thin- to slightly thick-walled, smooth, IKI–, CB–, (3.5–)3.7–4.2 × (0.8–)0.9–1.3(–1.4) μm, L = 3.94 μm, W = 1.09 μm, Q = 3.66 (n = 60/1).

**Type of rot.** Brown rot.

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**Cyanosporus subungulatus** B.K. Cui & Shun Liu, sp. nov.
MycoBank No: 842321
Figs 8, 9

**Diagnosis.** *Cyanosporus subungulatus* is characterised by shell-shaped pileus with a pale mouse-grey to ash-grey pileal surface when fresh, dark-grey to mouse-grey when dry, allantoid to cylindrical and slightly curved basidiospores (4.5–5.2 × 1.1–1.4 μm).

**Holotype.** China. Yunnan Province, Yangbi County, Shimenguan Nature Reserve, on fallen trunk of *Pinus* sp., 6.IX.2019, Cui 18046 (BJFC 034905).

**Etymology.** *Subungulatus* (Lat.): referring to the species resembling *Cyanosporus ungulatus* in morphology.

**Fruiting body.** Basidiomata annual, pileate, soft corky, without odour or taste when fresh, becoming corky to fragile and light in weight upon drying. Pileus shell-shaped, projecting up to 1.7 cm, 2.8 cm wide and 1.2 cm thick at base. Pileal surface velutinate, pale mouse-grey to ash-grey when fresh, becoming smooth, rugose, dark-grey to mouse-grey when dry; margin obtuse. Pore surface white to cream when fresh, becoming cream to pinkish buff when dry; sterile margin narrow to almost lacking; pores round, 4–6 per mm; dissepiments thin, entire to lacerate. Context white to cream, soft corky, up to 5 mm thick. Tubes pale mouse-grey to ash-grey, fragile, up to 6 mm long.
Figure 8. Basidiomata of *Cyanosporus subungulatus* (Holotype, Cui 18046). Scale bar: 10 mm. The upper figure is the upper surface and the lower figure is the lower surface of the basidiomata.

**Hyphal structure.** Hyphal system monomitic; generative hyphae with clamp connections, IKI–, CB–; hyphae unchanged in KOH.

**Context.** Generative hyphae hyaline, slightly thick-walled with a wide lumen, rarely branched, loosely interwoven, 2.5–6.4 μm in diam.
Figure 9. Microscopic structures of *Cyanosporus subungulatus* (Holotype, Cui 18046) a) basidiospores, b) basidia and basidioles, c) hyphae from trama, d) hyphae from context. Drawings by: Shun Liu.
**Tubes.** Generative hyphae hyaline, slightly thick-walled with a wide lumen, occasionally branched, interwoven, 2–4.2 μm in diam. Cystidia and cystidioles absent. Basidia clavate, bearing four sterigmata and a basal clamp connection, 13.6–17.8 × 3–5.5 μm; basidioles dominant, in shape similar to basidia, but smaller, 12.8–17.2 × 2.4–5.2 μm.

**Spores.** Basidiospores allantoid to cylindrical, slightly curved, hyaline, thin- to slightly thick-walled, smooth, IKI–, CB–, (4.3–)4.5–5.2 × 1.1–1.4 μm, L = 4.73 μm, W = 1.22 μm, Q = 3.48–3.66 (n = 60/2).

**Type of rot.** Brown rot.

**Additional specimen (paratype) examined.** China, Yunnan Province, Xichou County, Xiaqiaoagou Nature Reserve, on fallen angiosperm trunk, 14.I.2019, Zhao 10833 (SWFC 010833).

_Cyanosporus tenuicontextus_ B.K. Cui & Shun Liu, sp. nov.

MycoBank No: 842323

Figs 10, 11

**Diagnosis.** _Cyanosporus tenuicontextus_ is characterised by flabelliform pileus with a velutinate, cream to pinkish buff with a little blue tint pileal surface when fresh, becoming glabrous, light vinaceous grey to pale mouse-grey when dry, small and round pores (6–8 per mm), thin context (up to 0.8 mm) and allantoid basidiospores (3.8–4.3 × 0.8–1.2 μm).

**Holotype.** China. Yunnan Province, Lanping County, Tongdian Town, Luoguqing, on fallen trunk of _Pinus_ sp., 19.IX.2017, Cui 16280 (BJFC 029579).

**Etymology.** _Tenuicontextus_ (Lat.): referring to the species having thin context.

**Fruiting body.** Basidiomata annual, pileate, soft coryx, without odour or taste when fresh, becoming coryx to fragile and light in weight upon drying. Pileus flabelliform, projecting up to 1.3 cm, 3.2 cm wide and 0.5 cm thick at base. Pileal surface velutinate, cream to pinkish buff with a little blue tint when fresh, becoming glabrous, light vinaceous grey to pale mouse-grey when dry; margin acute. Pore surface white to cream when fresh, becoming pinkish buff to buff when dry; sterile margin narrow to almost lacking; pores round, 6–8 per mm; dissepiments thin, entire to lacerate. Context cream to buff, soft coryx, up to 0.8 mm thick. Tubes pale mouse-grey to buff, fragile, up to 4.3 mm long.

**Hyphal structure.** Hyphal system monomitic; generative hyphae with clamp connections, IKI–, CB–; hyphae unchanged in KOH.

**Context.** Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, loosely interwoven, 2.3–5.5 μm in diam.

**Tubes.** Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, interwoven, 2–4 μm in diam. Cystidia absent; cystidioles present, fusoid, thin-walled, 9.5–14.6 × 2.8–3.4 μm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 11.7–16.8 × 3.4–4.3 μm; basidioles dominant, in shape similar to basidia, but smaller, 10.6–14.7 × 2.9–3.6 μm.
Spores. Basidiospores allantoid, slightly curved, hyaline, thin- to slightly thick-walled, smooth, IKI–, CB–, (3.7–)3.8–4.3 × 0.8–1.2 μm, L = 3.97 μm, W = 1.02 μm, Q = 3.78–4.26 (n = 60/2).

Figure 10. Basidiomata of *Cyanosporus tenuicontextus* (Holotype, Cui 16280). Scale bar: 1 cm. The upper figure is the upper surface and the lower figure is the lower surface of the basidiomata.
Figure 11. Microscopic structures of *Cyanosporus tenuicontextus* (Holotype, Cui 16280) a basidiospores b basidia and basidioles. c cystidioles d hyphae from trama e hyphae from context. Drawings by: Shun Liu.
**Type of rot.** Brown rot.

**Additional specimen (paratype) examined.** China. Yunnan Province, Yuxi, Xinning County, Mopanshan National Forest Park, on angiosperm stump, 16.I.2017, Zhao 813 (SWFC 000813).

**Discussion**

In the current phylogenetic analyses based on the combined datasets of ITS+TEF and ITS+nLSU+mtSSU+nSSU+Rpb1+Rpb2+TEF sequences, species of *Cyanosporus* formed a highly supported lineage, distant from *Postia* and other brown-rot fungal genera (Figs 2, 3) and consistent with previous studies (Shen et al. 2019; Liu et al. 2021a). Based on morphological characters and phylogenetic analyses, 35 species are accepted in *Cyanosporus* around the world, including four new species from China, viz., *C. flavus*, *C. rigidus*, *C. subungulatus* and *C. tenuicontextus*. The main ecological habits of the species in *Cyanosporus* with an emphasis on distribution areas and host trees are provided in Table 2.

In the phylogenetic trees, *Cyanosporus flavus* grouped together with *C. fusiformis*, *C. subungulatus* and *C. ungulatus* (Figs 2, 3). *Cyanosporus fusiformis* differs from *C. flavus* by having white to cream pileal surface when fresh, clay-buff pore surface when dry and larger pores (4–5 per mm) and by growing on angiosperm woods (Shen et al. 2019); *C. subungulatus* differs from *C. flavus* in its glabrous pileal surface, cream to pinkish buff pore surface when dry and wider basidiospores (4.5–5.2 × 1.1–1.4 μm); *C. ungulatus* differs from *C. flavus* by having ungulate basidiomata, sulcate pileal surface with olivaceous buff, pinkish buff, cream to ash-grey and white zones when fresh (Shen et al. 2019). *Cyanosporus hirsutus* and *C. subhirsutus* have pileate basidiomata with hirsute, blue tint to the pileal surface and slightly thick-walled basidiospores like *C. flavus*, but *C. hirsutus* differs by having wider basidiospores (4–4.7 × 1.2–1.5 μm; Liu et al. 2021a), while *C. subhirsutus* has larger pores (2–3 per mm; Shen et al. 2019). Besides, *C. hirsutus* and *C. subhirsutus* are distant from *C. flavus* in the phylogenetic analyses (Figs 2, 3). *Cyanosporus subungulatus* and *C. ungulatus* share similar pores and basidiospores; however, *C. ungulatus* differs by having ungulate basidiomata, glabrous and sulcate pileal surface, narrower context hyphae and tramal hyphae (Shen et al. 2019).

Phylogenetically, *Cyanosporus rigidus* form a separate lineage different from other species in the genus. Morphologically, *C. submicroporus* share similar pores and basidiospores with *C. rigidus*, but *C. submicroporus* differs by having cream to pinkish buff pileal surface and white to smoke grey pore surface when fresh, buff to buff-yellow pileal surface and buff to olivaceous buff pore surface when dry. *Cyanosporus auricomus* and *C. luteocaesius* resemble *C. rigidus* in morphology by producing yellow-colored basidiomata, but *C. auricomus* differs from *C. rigidus* by having a hirsute pileal surface and larger basidiospores (4.4–5.6 × 1.5–1.8 μm; Miettinen et al. 2018); *C. luteocaesius* differs from *C. rigidus* by having larger pores (3–5 per mm) and basidiospores (4.3–6.1 × 1.5–1.9 μm; Miettinen et al. 2018).
Table 2. A list of species, specimens, and GenBank accession number of sequences used for phylogenetic analyses in this study.

| Species                     | Sample no.          | Localities                | GenBank accessions                      | References                |
|-----------------------------|---------------------|---------------------------|-----------------------------------------|---------------------------|
| *Amaruspora hinokianensis*  | Cui 13739 (holotype) | China                     | KX900099, KX900579, KX901053, KX90123, KX901171, KX901223 | Han et al. 2019           |
| *A. stiptica*               | Cui 10193           | China                     | KX900906, KX900976, KX901046, KX901119, KX901167, KX901219 | Han et al. 2019           |
| *Anglycarya lapponica*      | HHIB-13400          | United States             | KC585237, KC585059                      | Ortiz-Santana et al. 2013|
| *A. lapponica*              | OKM-4418            | United States             | KC585238, KC585060                      | Ortiz-Santana et al. 2013|
| *Antrodia armata*           | Dai 7465            | Luxembourg                | KR60581, KR605752, KR606013, KR60913, KR610832, KR610742 | Han et al. 2016           |
| *A. tanakae*                | Cui 9743            | China                     | KR60581, KR605753, KR606014, KR60914, KR610833, KR610743 | Han et al. 2016           |
| *Calkiporia guttulata*      | Cui 10018           | China                     | KF727432, KF68478, KX901065, KX901138, KX901181, KX901236, KX901276 | Shen et al. 2019          |
| *C. guttulata*              | Cui 10028           | China                     | KF727432, KF68479, KX901086, KX901139, KX901182, KX901237, KX901277 | Shen et al. 2019          |
| *Gymnoporus abei*           | Spirin 12.10.1995   | Slovakia                  | MG137026                                 | Miettinen et al. 2018     |
| *G. abii*                   | Cui 7185            | China                     | KX900879, KX900949, KX901017, KX901092, KX901155, KX901202, KX901254 | Shen et al. 2019          |
| *G. abii*                   | Dai 14945           | Island                    | KX900880, KX900950, KX901018, KX901093, KX901156, KX901203, KX901255 | Shen et al. 2019          |
| *G. arbuti*                 | Vicheslav Spirin 8327 | United States             | MG137039                                 | Miettinen et al. 2018     |
| *G. xeromus*                | Cui 13518           | China                     | KX900887, KX900957, KX901025, KX901100, KX901209 | Shen et al. 2019          |
| *G. xeromus*                | Cui 13519           | China                     | KX900888, KX900958, KX901026, KX901101 | Shen et al. 2019          |
| *G. xeromus*                | Tizemo Nielé 8310   | Finland                   | MG137040                                 | Miettinen et al. 2018     |
| *G. hifera*                 | Vicheslav Spirin 6402 | Russia                   | MG137043, MG137043                      | Miettinen et al. 2018     |
| *G. hifera*                 | Cui 17534           | China                     | OL42598*, OL42608*, OL437195*, OL42620*, OL44985*, OL44999*, OL44999* | Present study             |
| *G. hifera*                 | Cui 16277           | China                     | OL42599*, OL42609*, OL437196*, OL43621*, OL44986*, OL44700*, OL44999* | Present study             |
| *G. huihelious*             | Cui 16976           | China                     | MW182172, MW182225, MW182208, MW182189, MW191547, MW191563 | Liu et al. 2021a          |
| *G. huihelious*             | Cui 16985           | China                     | MW182173, MW182226, MW182209, MW182190, MW191548, MW191564 | Liu et al. 2021a          |
| *G. caninimimus*            | Vicheslav Spirin 4199 | Russia                   | MG137061                                 | Miettinen et al. 2018     |
| *G. caninimimus*            | Otto Miettinen 16796 | United States             | MG137054                                 | Miettinen et al. 2018     |
| *C. canarius*               | Gerhard Schuster 51 | Germany                   | MG137045                                 | Miettinen et al. 2018     |
| *C. canarius*               | Otto Miettinen 14156 | Finland                  | MG137048                                 | Miettinen et al. 2018     |
| *C. canarius*               | Dai 18630           | France                    | OL42660*, OL42610*, OL437197*, OL42362* | Present study             |
| *C. canarius af GB*         | K 32713             | United Kingdom            | AY99576                                  | Miettinen et al. 2018     |
| *C. canarius af GB*         | K 32425             | United Kingdom            | AY99575                                  | Miettinen et al. 2018     |
| *C. cupreoviridis*          | Otto Miettinen 12214 | Indonesia                | MG137063                                 | Miettinen et al. 2018     |
| *C. cupreoviridis*          | Otto Miettinen 12214 | Indonesia                | MG137063                                 | Miettinen et al. 2018     |
| *C. comatus*                | Otto Miettinen 14755,5 (holotype) | United States | MG137066                                 | Miettinen et al. 2018     |
| *C. cyanescens*             | Otto Miettinen 13602 | Finland                  | MG137067                                 | Miettinen et al. 2018     |
| *C. cyanescens*             | Otto Miettinen 15919,2 | Spain                 | MG137071                                 | Miettinen et al. 2018     |
| *C. flavus*                 | Cui 18547           | China                     | MW448564*, MW448561*, MW448557*, MW452596*, MW452599* | Present study             |
| *C. flavus*                 | Cui 18562 (holotype) | China                     | MW448565*, MW448562*, MW448558*, MW452597*, MW452600* | Present study             |
| *C. fusiformis*             | Cui 1077s           | China                     | KX900868, KX900938, KX901006, KX901081, KX901191, KX901245 | Shen et al. 2019          |
| Species          | Sample no. | GenBank accession | TFS | mLSU | nSSU | RPB1 | TEF | References          |
|------------------|------------|-------------------|-----|------|------|------|-----|---------------------|
| *C. glaucus*     | Cui 12158  | KX900867          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. glaucus*     | Cui 16983  | KX900868          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. hirsutus*    | Cui 1805   | MG137103          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. livens*      | Cui 1805   | MG137104          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. luteocaesia* | Cui 1805   | MG137105          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. magnus*      | Cui 1805   | MG137106          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. mediterraneocaesius* | Cui 1805 | MG137107          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. populi*      | Cui 1805   | MG137108          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. subhirsutus* | Cui 1805   | MG137109          |     |      |      |      |     | Miettinen et al. 2018 |
| *C. subviridis*  | Cui 1805   | MG137110          |     |      |      |      |     | Miettinen et al. 2018 |

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| Species                  | Sample no.          | Locality          | GenBank accessions | References          |
|-------------------------|---------------------|-------------------|--------------------|---------------------|
| **C. tenuicontextus**   | Cui 16280 (holotype) | China             | OL423607*          | Present study       |
|                         |                     |                   | OL423618*          |                     |
|                         |                     |                   | OL437205*          |                     |
|                         |                     |                   | OL423630*          |                     |
| **C. tenuis**           | Zhao 813            | China             | MG231802*          | Present study       |
|                         |                     |                   | OL423619*          |                     |
|                         |                     |                   | OL437206*          |                     |
|                         |                     |                   | OL423631*          |                     |
| **C. tricolor**         | Cui 12233 (holotype) | China             | KX900884           | Shen et al. 2019    |
|                         |                     |                   | KX900954           |                     |
|                         |                     |                   | KX901014           |                     |
|                         |                     |                   | KX900989           |                     |
|                         |                     |                   | KX901161           |                     |
| **C. ungulatus**        | Cui 10778           | China             | KX900875           | Shen et al. 2019    |
|                         |                     |                   | KX900945           |                     |
|                         |                     |                   | KX901013           |                     |
|                         |                     |                   | KX900888           |                     |
| **C. yanae**            | Heikki Kotiranta 27406 | Russia           | MG137122          | Miettinen et al. 2018 |
|                         |                     |                   | MG137121          |                     |
| **Cystidiopostia hibernica** | Cui 2658         | China             | KX900905           | Shen et al. 2019    |
|                         |                     |                   | KX900975           |                     |
|                         |                     |                   | KX901044           |                     |
| **C. inocybe**          | LY BR 3703          | France            | KX900903           | Shen et al. 2019    |
|                         |                     |                   | KX900973           |                     |
|                         |                     |                   | KX901116           |                     |
| **C. pileata**          | Cui 10034           | China             | KX900909           | Shen et al. 2019    |
|                         |                     |                   | KX900956           |                     |
|                         |                     |                   | KX901050           |                     |
| **Fuscopostia duplicate** | Dai 13411        | China             | KF699125           | Han et al. 2016     |
|                         |                     |                   | KF68876            |                     |
|                         |                     |                   | KR606027           |                     |
| **F. fragilis**         | JV 0610-8           | Czech             | JF950573           | Vampola et al. 2014 |
|                         |                     |                   |                   |                     |
| **F. lateritia**        | Dai 2652            | China             | KX900913           | Shen et al. 2019    |
|                         |                     |                   | KX900983           |                     |
| **F. brunomallotella**  | Cui 9599            | China             | KF699123           | Shen et al. 2019    |
|                         |                     |                   | KF68876            |                     |
|                         |                     |                   | KR60528            |                     |
|                         |                     |                   | KR61085            |                     |
|                         |                     |                   | KR61075            |                     |
| **Jahnoborus brachiatius** | X 3252             | Russia            | KU165781           | Spin et al. 2015    |
| **J. hirtus**           | Spinosa 10 X 2014   | United States     | KU165784           | Spin et al. 2015    |
|                         |                     |                   | KY940944           |                     |
| **J. oreinus**          | X 3241              | Russia            | KU165785           | Spin et al. 2015    |
| **Oligoporus rennyi**   | TN-6645             | Finland           | KC59529            | Ortiz-Santana et al. 2013 |
|                         |                     |                   | KC59529            |                     |
| **O. siccodomata**      | Cui 9870            | China             | KX900920           | Shen et al. 2019    |
|                         |                     |                   | KX900990           |                     |
|                         |                     |                   | KX901068           |                     |
| **O. obscura**          | Cui 10074           | China             | KX900924           | Shen et al. 2019    |
|                         |                     |                   | KX900994           |                     |
|                         |                     |                   | KX901071           |                     |
| **O. undosa**           | Dai 7105            | China             | KX900921           | Shen et al. 2019    |
|                         |                     |                   | KX900991           |                     |
|                         |                     |                   | KX901069           |                     |
| **Portia amurenensis**  | Dai 903 (holotype)  | China             | KX900901           | Shen et al. 2019    |
|                         |                     |                   | KX900971           |                     |
| **P. birsta**           | Cui 11237 (holotype) | China             | KF68470            | Shen et al. 2019    |
|                         |                     |                   | KF68804            |                     |
| **P. lactea**           | Cui 12141           | China             | KX900892           | Shen et al. 2019    |
|                         |                     |                   | KX900962           |                     |
| **P. buiei**            | Cui 9585            | China             | KX900898           | Shen et al. 2019    |
|                         |                     |                   | KX900968           |                     |
|                         |                     |                   | KX901035           |                     |
| **P. oblanceolata**     | Cui 10802 (holotype) | China             | KM107903           | Shen et al. 2019    |
|                         |                     |                   | KM107908           |                     |
|                         |                     |                   | KX901041           |                     |
| **P. subclavata**       | Cui 9595 (holotype)  | China             | KX900900           | Shen et al. 2019    |
|                         |                     |                   | KX900970           |                     |
|                         |                     |                   | KX901037           |                     |
| **Spongious gloeoporus** | Dai 12610        | Finland           | KX900879           | Shen et al. 2019    |
|                         |                     |                   | KM107904           |                     |
| **S. floriformis**      | Cui 10292           | China             | KX900915           | Shen et al. 2019    |
|                         |                     |                   | KX900985           |                     |
|                         |                     |                   | KX901060           |                     |
| **S. floriformis**      | Dai 13887           | China             | KX900914           | Shen et al. 2019    |
|                         |                     |                   | KX900984           |                     |

*Newly generated sequences for this study. New species are shown in bold.
Phylogenetically, *C. tenuicontextus* is closely related to *C. caesiosimulans*, *C. cyanescens*, *C. populi*, *C. subviridis* and *C. yanae* (Figs 2, 3). Morphologically, they share similar pores; but *C. caesiosimulans* differs by having larger basidiospores (4.2–5.5 × 1.1–1.4 μm), and a wide distribution area (Europe and North America; Miettinen et al. 2018); *C. cyanescens* differs in having light bluish-greyish tint in older and dry specimens and larger basidiospores (4.7–6.1 × 1.1–1.6 μm; Miettinen et al. 2018); *C. populi* differs in its larger basidiospores (4.2–5.6 × 1–1.3 μm), and a wide distribution area (East Asia, Europe and North America; Miettinen et al. 2018; Liu et al. 2021a); *C. subviridis* differs in its conchate basidiomata, distributed in Europe and North America and grows only on gymnosperms (*Abies* sp., *Picea* sp. and *Pinus* sp.; Miettinen et al. 2018); *C. yanae* differs by having narrower generative hyphae (3–4 μm in context, 2.2–2.9 μm in tubes), larger basidiospores (4.3–5.8 × 1.2–1.6 μm), distributed in Europe and grows only on gymnosperm (*Larix* sp., *Pinus* sp.; Miettinen et al. 2018). *Cyanosporus bifarius* is also distributed in Lanping County, Yunnan Province of China, they share similar pores and basidiospores, but *C. bifarius* grows only on gymnosperm trees (*Picea* sp., *Pinus* sp., *Larix* sp.; Miettinen et al. 2018), and *C. bifarius* is distant from *C. tenuicontextus* in the phylogenetic analyses (Figs 2, 3).

The natural distribution of plant-associated fungi across broad geographic ranges is determined by a combination of the distributions of suitable hosts and environmental conditions (Lodge 1997; Brandle and Brandl 2006; Gilbert et al. 2007, 2008). Species in *Cyanosporus* have a wide distribution range (Asia, Europe, North America, South America and Oceania; Table 2) and variable host type (angiosperms and gymnosperms). As for distribution ranges, 23 species of *Cyanosporus* are distributed in Asia, 16 species in Europe, seven species in North America, one species in South America and one species in Oceania. As for host trees, nine species of *Cyanosporus* grow only on angiosperm trees, 15 species only on gymnosperm trees, and eleven species both on angiosperm and gymnosperm trees (Table 1). In some cases, some *Cyanosporus* species have host specificity, at least regionally, such as in Europe, *C. auricomus* only growth on *Pinus sylvestris*, *C. cyanescens* only growth on *Picea abies*, *C. populi* prefers *Populus tremula*, and *C. luteocaesia* have been recorded only from *Pinus* sp. (Miettinen et al. 2018).

In the current study, 77 samples of *Cyanosporus* throughout China and 11 samples outside of China have been morphologically examined in detail. The specimens collected from China representing 21 species were sequenced here and referred to in our phylogeny, viz., *C. alni*, *C. auricomus*, *C. bifarius*, *C. bubalinus*, *C. coeruleivirens*, *C. comatus*, *C. flavus*, *C. fusiformis*, *C. hirsutus*, *C. magnus*, *C. microporus*, *C. piceicola*, *C. populi*, *C. rigidus*, *C. subhirsutus*, *C. submicroporus*, *C. subungulatus*, *C. tenuicontextus*, *C. tricolor* and *C. ungulatus*. Another two species reported in a previous study, viz., *C. glauca* (=*Postia glauca* Spirin & Miettinen) and *C. simulans* (=*Postia simulans* (P. Karst.) Spirin & Rivoire; Miettinen et al. 2018) were also found from China. Among these *Cyanosporus* species, 15 are endemic to China so far, viz., *C. bubalinus*, *C. flavus*, *C. fusiformis*, *C. hirsutus*, *C. microporus*, *C. piceicola*, *C. rigidus*, *C. subhirsutus*, *C. submicroporus*, *C. subungulatus*, *C. tenuicontextus*, *C. tricolor* and *C. ungulatus*. The *Cyanosporus* species formed a distribution center in Southwest China. This may be due
to the complex and diverse ecological environment and diverse host trees in this region, which provide a rich substrate for the growth of *Cyanosporus* species. The geographical locations of the *Cyanosporus* species distributed in China are indicated on the map (Fig. 1).

In summary, we performed a comprehensive study on the species diversity and phylogeny of *Cyanosporus* with an emphasis on Chinese collections. So far, 35 species are accepted in the *Cyanosporus* around the world, including 23 species from China. Currently, *Cyanosporus* is characterized by an annual growth habit, resupinate to effused-reflexed or pileate, soft corky, corky, fragile to hard corky basidiomata, velutinate to hirsute or glabrous pileal surface with blue-tinted, white to cream or yellow-colored, white to cream pore surface with round to angular pores, a monomitic hyphal system with clamped generative hyphae, and hyaline, thin- to slightly thick-walled, smooth, narrow, allantoid to cylindrical basidiospores that are usually weakly cyanophilous; it grows on different angiosperm and gymnosperm trees, causes a brown rot of wood and has a distribution in Asia, Europe, North America, Argentina in South America and Australia in Oceania (McGinty 1909; Shen et al. 2019; Liu et al. 2021a).

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