Species Diversity and Molecular Phylogeny of Cyanosporus (Polyporales, Basidiomycota)

Shun Liu1,2, Lu-Lu Shen3, Yan Wang1,2, Tai-Min Xu1,2, Genevieve Gates4 and Bao-Kai Cui1,2*

1 Beijing Advanced Innovation Center for Tree Breeding by Molecular Design, Beijing Forestry University, Beijing, China, 2 School of Ecology and Nature Conservation, Institute of Microbiology, Beijing Forestry University, Beijing, China, 3 Yichang Academy of Agricultural Science, Yichang, China, 4 Tasmanian Institute of Agriculture, Hobart, TAS, Australia

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Cyanosporus is a cosmopolitan brown-rot fungal genus, recognizable by blue-tinted basidiocarps. Species in this genus were usually treated as belonging to the Postia caesia complex, however, recent phylogenetic analyses showed that this complex represents an independent genus. During further studies on Cyanosporus, five new species were discovered based on morphological features and molecular data. Phylogenetic analyses of Cyanosporus were conducted using 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); illustrated descriptions of the new species are provided. In addition, fifteen species previously belonging to the Postia caesia complex are transferred to Cyanosporus and proposed as new combinations.

Keywords: brown-rot fungi, multi-loci phylogeny, new species, Postia caesia complex, species identification

INTRODUCTION

Boletus caesius Schrad. was described based on material from Germany (Schrader, 1794), and this name was subsequently sanctioned by Fries (1821), who considered B. coerules Schumach. a synonym of Polyporus caesius (Schrad.) Fr. In 1881 Karsten transferred Boletus caesius to Postia Fr. as Postia caesia (Schrad.) P. Karst. (Karsten, 1881). Murrill (1907) transferred this species to Tyromyces P. Karst. as T. caesius (Schrad.) Murrill and later McGinty (1909) proposed a new monotypic genus Cyanosporus McGinty for Polyporus caesius, based on its cyanophilous basidiospores, but Cyanosporus caesius was not widely used in subsequent studies (Donk, 1960; Jahn, 1963; Lowe, 1975), while Tyromyces caesius was commonly used. Later, Postia caesia was widely used (Papp, 2014). David (1974, 1980) described another two species: P. luteocaesia (A. David) Jülich and P. subcaesia (A. David) Jülich from Europe besides Postia caesia (Schrad.) P. Karst. Jahn (1979) noted that David's P. subcaesia included many forms and introduced P. subcaesia "f. minor," which was described as P. alni Niemelä & Vampola by Niemelä et al. (2001). Subsequently, Pieri and Rivoire (2005) introduced the fifth European species, P. mediterraneocaesia...
M. Pieri & B. Rivoire in the Postia caesia complex. Papp (2014) provided a detailed nomenclatural review on the Postia caesia complex and proposed the subgenus Postia subg. Cyanosporus (McGinty) V. Papp for this complex which included five species viz., P. alni, P. caesia, P. lutocaea, P. mediterraneocaesia and P. subcaesia. Miettinen et al. (2018) focused on the taxonomy of the Postia caesia complex based on morphological features and molecular evidence and increased the species number of the Postia caesia complex from 10 to 24. In their study, they only focused on the species concept of the Postia caesia complex, the taxonomic status of this complex among Postia and related genera are not mentioned.

Shen et al. (2019) carried out a comprehensive study on Postia and related genera and confirmed that the genus Cyanosporus is an independent genus rather than subgenus which containing 12 accepted species including seven new species of the Postia caesia complex. Furthermore, phylogenetic analyses showed that Cyanosporus belongs to the antrodia clade (Shen et al., 2019). Morphologically, Cyanosporus differs from other related genera by its bluish basidiocarps, usually narrow allantoid and thinly to slightly thick-walled basidiospores (McGinty, 1909; Shen et al., 2019). In the current study, the phylogenetic analysis of Cyanosporus was carried out based on the combined sequence dataset of ITS + nLSU + nSSU + mtSSU + RPB1 + RPB2 + TEF rRNA gene regions. Combining morphological characters and molecular evidence, thirty-one species belonging to the Postia caesia complex are now recognized in Cyanosporus, including five new species and fifteen new combinations.

MATERIALS AND METHODS

Taxa Sampling and Morphological Study

The examined specimens were deposited at the herbarium of the Institute of Microbiology, Beijing Forestry University (BJFC) with some duplicates at the Institute of Applied Ecology, Chinese Academy of Sciences (IFP). Morphological descriptions and abbreviations used in this study following Liu et al. (2019); Sun et al. (2020).

DNA Extraction and Molecular Analyses

The procedures for DNA extraction and polymerase chain reaction (PCR) used in this study were the same as described by Chen et al. (2017); Song and Cui (2017). The primer pairs ITS5 and ITS4 for ITS regions, LR0R and LR7 for nLSU regions, NS1 and NS4 for nSSU regions, MS1 and MS2 for mtSSU regions, RPB1-Af and RPB1-Cr for RPB1 gene, RPB2-f5F and bRPB2-7.1R for RPB2 gene, EF1-983 F and EF1-1567R for TEF gene used in this study are the same as previous studies (White et al., 1990; Rehner, 2001; Matheny et al., 2002; Matheny, 2005).

The PCR cycling schedules for different DNA sequences of ITS, nLSU, nSSU, mtSSU, RPB1, RPB2, and TEF genes used in this study followed those used in Liu et al. (2019); Shen et al. (2019), Zhu et al. (2019); Sun et al. (2020) with some modifications. The PCR products were purified and sequenced at the Beijing Genomics Institute (BGI), China, with the same primers. All newly generated sequences were deposited in GenBank (Table 1).

Additional sequences for phylogenetic analyses were downloaded from GenBank (Table 1). All sequences were aligned in MAFFT 7 (Katoh and Standley, 2013) 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” following Chen et al. (2017). The final concatenated sequence alignment was deposited in TreeBase (submission ID: 27274).

Phylogenetic analyses approaches used in this study followed Han et al. (2016); Cui et al. (2019). The congruences of the 7-gene (ITS, nLSU, nSSU, mtSSU, RPB1, RPB2, and TEF) 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. The sequences of Antrodia serpens (Fr.) Donk obtained from GenBank were used as outgroups for phylogenetic reconstruction. Maximum parsimony (MP) analysis was performed in PAUP* version 4.0b10 (Swofford, 2002). Maximum Likelihood (ML) analysis was performed in RAxML v.7.2.8 with a GTR + G + I model (Stamatakis, 2006). Bayesian inference (BI) was calculated by MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) with a general time reversible (GTR) model of DNA substitution and a gamma distribution rate variation across sites determined by MrModeltest 2.3 (Posada and Crandall, 1998; Nylander, 2004). Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates (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. The branch support was evaluated with a bootstrapping method of 1000 replicates (Hillis and Bull, 1993). Branches that received bootstrap supports for MP, ML greater than or equal to 75% and Bayesian posterior probabilities (BPP) greater than or equal to 0.95 were considered as significantly supported. The phylogenetic tree was visualized using FigTree v1.4.2.

RESULTS

Molecular Phylogeny

The ITS + TEF sequences dataset had an aligned length of 1166 characters, of which 646 characters were constant, 68 were variable and parsimony-uninformative, and 452 were parsimony-informative. MP analysis yielded 4 equally parsimonious trees (TL = 1983, CI = 0.417, RI = 0.726, RC = 0.303, HI = 0.583). The best model for the concatenate sequence dataset estimated and applied in the Bayesian inference was GTR + I + G with an equal frequency of nucleotides. ML analysis resulted in a similar topology as MP and Bayesian analyses, and only the ML topology is shown in Figure 1.

The combined three-gene (ITS + nLSU + TEF) sequences dataset had an aligned length of 2475 characters, of which 1752

1http://mafft.cbrc.jp/alignment/server/
2http://www.treebase.org
3http://tree.bio.ed.ac.uk/software/figtree/
TABLE 1 | A list of species, specimens, and GenBank accession number of sequences used for phylogenetic analyses in this study.

| Species | Sample no. | Locality | GenBank accessions |
|---------|------------|----------|--------------------|
|         |            |          | ITS | nLSU | nSSU | mtSSU | RPB1 | RPB2 | TEF |
| Amaropostia stipica | Cui 10043 | China | KX900906 | KX900976 | KX901119 | KX901046 | KX901167 | KX901219 | / |
| A. stipica | Cui 10981 | China | KX900907 | KX900977 | KX901120 | KX901047 | KX901168 | KX901220 | / |
| Amylocystis lapponica | HHB-13400-Sp | United States | KC585237 | KC585059 | KX901219 | / | / | / | / |
| A. lapponica | OKM-4418-Sp | United States | KC585238 | KC585060 | / | / | / | / | / |
| Antrodia serpens | Dai 7465 | Luxemburg | KR605813 | KR605752 | KR605913 | KR606013 | / | KF610832 | KF610742 |
| A. serpens | Dai 14850 | Poland | MG787582 | MG787624 | MG787731 | MG787674 | / | MG787798 | MG787849 |
| Cyanosporus ahni | Petr Vampola 12.10.1995 | Slovakia | MG137026 | / | / | / | / | / | / |
| C. ahni | Cui 7185 | China | KX900879 | KX900949 | KX901092 | KX901017 | KX901155 | KX901202 | KX901254 |
| C. ahni | OKM-4418-Sp | United States | KC585238 | KC585060 | / | / | / | / | / |
| C. arbuti | Viacheslav Spirin 8327 | United States | MG137039 | / | / | / | / | / | / |
| C. auricoma | Dai 20992 | Belarus | MW182169 | / | / | / | / | / | / |
| C. auricoma | Cui 13518 | China | KX900887 | KX900957 | KX901100 | KX901025 | / | KX901209 | / |
| C. auricoma | Cui 13519 | China | KX900888 | KX900958 | KX901101 | KX901026 | / | / | / |
| C. auricoma | Tuomo Niemelä 8310 | Finland | MG137040 | / | / | / | / | / | / |
| C. auricoma | Viacheslav Spirin 4586 | Russia | MG137042 | / | / | / | / | / | / |
| C. bifaria | Viacheslav Spirin 6402 | Russia | MG137043 | / | / | / | / | / | / |
| C. bifaria | Cui 17445 | China | MW182170 | MW182223 | MW182187 | MW182206 | / | MW191562 | MW191528 |
| C. bifaria | Cui 17806 | China | MW182171 | MW182224 | MW182188 | MW182207 | MW191546 | / | MW191529 |
| C. bubalinus | Cui 16976 | China | MW182172 | MW182225 | MW182189 | MW182208 | MW191547 | MW191563 | MW191530 |
| C. bubalinus | Cui 16985 | China | MW182173 | MW182226 | MW182190 | MW182209 | MW191548 | MW191564 | MW191531 |
| C. caesiosimulans | Viacheslav Spirin 4199 | Russia | MG137061 | / | / | / | / | / | / |
| C. caesiosimulans | Otto Miettinen 16976 | United States | MG137054 | / | / | / | / | / | / |
| C. caesius | Otto Miettinen 14156 | Finland | MG137048 | / | / | / | / | / | / |
| C. caesius | Gerhard Schuster 51 | Germany | MG137045 | / | / | / | / | / | / |
| C. caesius aff AR | CIEFAP 350 | Argentina | JX090110 | JX090130 | / | / | / | / | / |
| C. caesius aff AR | CIEFAP 174 | Argentina | JX090109 | JX090129 | / | / | / | / | / |
| C. caesius aff GB | K 32713 | United Kingdom | AF599576 | / | / | / | / | / | / |
| C. caesius aff GB | K 32425 | United Kingdom | AF599575 | / | / | / | / | / | / |
| C. coerulivirens | Dai 11834 | China | KF699119 | / | / | / | / | / | / |
| C. coerulivirens | Otto Miettinen 12214 | Indonesia | MG137063 | / | / | / | / | / | / |
| C. coerulivirens | Dai 19220 | China | MW182174 | MW182227 | MW182191 | MW182210 | MW191549 | / | MW191532 |
| C. cornata | Otto Mettinen 14755,1 | United States | MG137066 | / | / | / | / | / | / |
| C. cornata | Cui 18338 | China | MW182175 | MW182228 | MW182192 | / | MW191550 | / | MW191533 |
| C. cornata | Cui 18546 | China | / | / | / | / | / | / | / |
| C. cyanescens | Otto Miettinen 13602 | Finland | MG137067 | / | / | / | / | / | / |
| C. cyanescens | Otto Miettinen 15919,2 | Spain | MG137071 | / | / | / | / | / | / |
| C. fusiformis | Cui 10775 | China | KX900868 | KX900938 | KX901081 | KX901006 | / | KX901191 | KX901245 |
| C. fusiformis | Dai 15036 | China | KX900867 | KX900937 | KX901080 | KX901005 | / | KX901190 | KX901244 |
| C. glauca | Viacheslav Spirin 5317 | Russia | MG137078 | / | / | / | / | / | / |

(Continued)
| Species          | Sample no.          | Locality         | GenBank accessions |
|------------------|---------------------|------------------|--------------------|
|                  |                     |                  | ITS    | nLSU  | nSSU  | mtSSU  | RPB1   | RPB2   | TEF    |
| C. glauca        | Viacheslav Spirin   | Russia           | MG137081 / / / / / | MG137145 |
| C. gossypina     | Bernard Rivoire     | France           | /       / / / / / | /       MG137146 |
| C. hirsutus      | Cui 17050           | China            | MW182176 MW182230 MW182194 MW182211 MW191551 MW191565 MW191535 |
| C. hirsutus      | Cui 17053           | China            | MW182177 MW182231 MW182195 MW182212 MW191552 MW191566 MW191536 |
| C. hirsutus      | Cui 17055           | China            | MW182178 MW182232 MW182196 MW182213 MW191553 MW191567 MW191537 |
| C. hirsutus      | Cui 17083           | China            | MW182179 MW182233 MW182197 MW182214 MW191554 MW191568 MW191538 |
| C. livers        | Viacheslav Spirin   | Russia           | MG137090 / / / / / | MG137150 |
| C. livers        | Otto Miettinen      | United States    | MG137082 / / / / / | /       MG137147 |
| C. luteocaesia   | Bernard Rivoire     | France           | /       / / / / / | /       / |
| C. magna         | Cui 16983           | China            | MW182180 MW182234 MW182198 MW182215 MW191555 MW191569 MW191539 |
| C. magna         | Dai 10854           | China            | KF699117 / / / / / | /       / |
| C. magna         | Otto Miettinen      | China            | KC596944 KC596944 / / / / / | / | MG137151 |
| C. mediterraneocaesius | LY BR 4274 | France           | KO900886 / KO901099 KO901024 / / | / |
| C. microporus    | Cui 11014           | China            | KO900878 KO900948 KO901091 KO901016 / KO901201 / |
| C. microporus    | Dai 11717           | China            | KO900877 KO900947 KO901090 KO901015 / KO901200 / |
| C. nothofagicaola| Cui 16697           | Australia        | MW182181a MW182235a MW182199a MW182216a MW191556a MW191570a MW191540a |
| C. nothofagicaola| Dai 18765           | Australia        | MW182182a MW182236a MW182200a MW182217a MW191557a / MW191541a |
| C. piceicola     | Cui 10626           | China            | KO900862 KO900932 KO901075 KO901001 / KO901185 / |
| C. piceicola     | Dai 12158           | China            | KO900866 KO900936 KO901079 KO901004 KO901153 KO901189 KO901243 |
| C. populi        | Cui 17087a          | China            | MW182183 MW182237 MW182201 MW182218 MW191558 MW191571 MW191542 |
| C. populi        | Cui 17549           | China            | /       MW182238 MW182202 MW182219 MW191559 MW191572 MW191543 |
| C. populi        | Tuomo Niemelä       | Finland          | MG137097 / / / / / | / | MG137154 |
| C. populi        | Otto Miettinen      | United States    | MG137092 / / / / / | / | MG137153 |
| C. simulans      | Otto Miettinen      | Finland          | MG137110 / / / / / | / | MG137160 |
| C. simulans      | Tuomo Niemelä       | Finland          | MG137103 / / / / / | / |
| C. subcaesius    | Josef Vlasák 0110/24 | Czech Republic   | MG137117 / / / / / | / | MG137164 |
| C. subcaesius    | Aix David 652       | France           | MG137116 / / / / / | / |
| C. subhirsutus   | Cui 11330           | China            | KO900873 KO900943 KO901086 KO901011 / KO901196 KO901250 |
| C. subhirsutus   | Dai 14892           | China            | KO900871 KO900941 KO901084 KO901009 / KO901194 KO901248 |
| C. submicroporus | Cui 16506           | China            | MW182184 MW182239 MW182203 MW182220 MW191560 MW191573 MW191544 |
| C. submicroporus | Cui 17750           | China            | MW182185 MW182240 MW182204 MW182221 MW191561 / MW191545 |
| C. submicroporus | Dai 18156           | China            | MW182186 MW182241 MW182205 MW182222 / MW191574 / |
| C. subviridis    | Viacheslav Spirin   | United States    | MG137120 / / / / / | / | MG137166 |
| C. subviridis    | Reijo Penttilä 14376 | Finland          | /       / / / / / | / | MG137165 |
| C. tenuis        | Cui 10788           | China            | KO900885 KO900955 KO901098 KO901023 KO901181 KO901208 / |
| C. tenuis        | Dai 12974           | China            | KO900884 KO900954 KO901097 KO901022 KO901160 KO901207 KO901258 |
| C. tricolor      | Cui 12233           | China            | KO900876 KO900946 KO901089 KO901014 / KO901199 KO901253 |
| C. tricolor      | Dai 10790           | China            | KO900875 KO900945 KO901088 KO901013 KO901198 KO901252 |
| C. ungulatus     | Cui 10778           | China            | KO900870 KO900940 KO901083 KO901008 KO901193 KO901247 |
| C. ungulatus     | Dai 12897           | China            | KO900869 KO900939 KO901082 KO901007 KO901154 KO901192 KO901246 |

(Continued)
Bayesian inference was GTR + the concatenate sequence dataset estimated and applied in the RI = 0.806, RC = 0.471, HI = 0.415). The best model for and 1361 were parsimony-informative. MP analysis yielded 8 equally parsimonious trees (TL = 2222, CI = 0.473, RI = 0.770, RC = 0.365, HI = 0.527). The best model analysis yielded 8 equally parsimonious trees (TL = 2222, CI = 0.473, RI = 0.770, RC = 0.365, HI = 0.527). 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 Figure 2.

The combined seven-gene (ITS + nLSU + nSSU + mtSSU + RPB1 + RPB2 + TEF) sequences dataset had an aligned length of 5855 characters, of which 4194 characters were constant, 134 were variable and parsimony-uninformative, and 589 were variable and parsimony-informative. MP analysis yielded 8 equally parsimonious trees (TL = 2222, CI = 0.473, RI = 0.770, RC = 0.365, HI = 0.527). 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 Figure 2.

The phylogenetic trees (Figures 1–3) inferred from ITS + TEF, ITS + nLSU + TEF and ITS + nLSU + nSSU + mtSSU + RPB1 + RPB2 + TEF gene sequences were obtained from 99 fungal samples representing 45 taxa of Cyanosporus and its related genera in the antrodia clade. Seventy-five samples representing thirty-one taxa of Cyanosporus clustered together and separated from species of Postia and other related genera.

**Taxonomy**

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

(MycoBank: MB 838417)

Dissers from other *Cyanosporus* species by its tomentose, cream to buff pileal surface when fresh becoming cream to pinkish buff when dry and a white to cream pore surface when fresh becoming straw yellow to buff when dry, and round to angular small pores (5–8 per mm).

**Type.** — *CHINA*. Yunnan Province, Binchuan County, Jizu Mountain, on fallen branch of *Pinus*, 14 September 2018, *Cui* 16985 (holotype, BJFC).

**Etymology.** — *Bubalinus* (Lat.): refers to the cream to buff pileal surface.

*Basidiocarps.* — Annual, pileate, solitary, soft and watery when fresh, becoming soft corky to fragile upon drying. *Pileus* shell-shaped, projecting up to 2.5 cm, 3.5 cm wide and 1.5 cm thick at base. *Pileal surface* white to cream when fresh, finely tomentose, becoming cream to pinkish buff upon drying; margin acute. *Pore surface* white to cream when fresh, becoming straw yellow to buff when dry; sterile margin narrow to almost lacking; *pores* round to angular, 5–8 per mm; *dissepiments* thin, entire to lacerate. *Context* white, corky, up to 1.2 cm thick. *Tubes* cream, fragile, up to 5 mm long.
Hyphal structure. — Hyphal system monomitic; generative hyphae with clamp connections, IKI–, CB–; tissues unchanged in KOH.

Context. — Generative hyphae hyaline, slightly thick-walled with a wide lumen, occasionally branched, loosely interwoven, 2.5–7.3 μm in diam.

Tubes. — Generative hyphae hyaline, thin- to slightly thick-walled, occasionally branched, interwoven, 2–4.2 μm in diam. Cystidia absent; cystidioles present, fusoid, thin-walled, 13.3–23.4 × 2.9–4.2 μm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 11.6–19.8 × 4.3–5.6 μm; basidioles dominant, in shape similar to basidia, but smaller.

Basidiospores. — Cylindrical, slightly curved, hyaline, thin- to slightly thick-walled, smooth, occasionally with small oily drops, IKI–, CB–, (4.2–)4.3–4.8 × 1.2–1.7(–1.8) μm, L = 4.65 μm, W = 1.55 μm, Q = 2.98–3.09 (n = 60/2).

Notes. — In the phylogenetic trees (Figures 1–3), two specimens of Cyanosporus bubalinus formed a highly supported lineage (Figures 1–3), closely related to C. coeruliciviridis (Corner) B.K. Cui, Shun Liu & Y.C. Dai, C. magna (Miettinen) B.K. Cui & Shun Liu and C. subhirsutus B.K. Cui, L.L. Shen &
C. coeruleivirens

Y.C. Dai. Morphologically, Liu et al. Taxonomy and Phylogeny of Cyanosporus differs by having a hirsute pileal surface when dry, larger pores (2–3 per mm), smaller basidia (10–12 × 4–6 μm) and smaller basidiospores (4–4.5 × 0.9–1.3 μm) (Table 2). Cyanosporus microporus B.K. Cui, L.L. Shen & Y.C. Dai and C. piceicola B.K. Cui, L.L. Shen & Y.C. Dai were also discovered from Yunnan Province. Cyanosporus microporus differs from the new species by its narrower basidiospores (4.5–4.9 × 1–1.2 μm, Table 2); C. piceicola differs by having a velutinate, cream to clay-buff pileal surface, with bluish gray zonation when fresh, larger and round pores (3–5 per mm) and narrower basidiospores (4–4.5 × 0.9–1.3 μm). Cyanosporus bifaria (Spirin) B.K. Cui & Shun Liu, C. glauca (Spirin & Miettinen) B.K. Cui & Shun Liu and C. subviridis (Riyvarden & Guzmán) B.K. Cui & Shun Liu are similar to C. bubalinus as they all have pileate basidiocarps and similar pores, however, they differ by narrower tramaal hyphae (2.5–3.8 μm in C. bifaria, 2.6–3.3 μm in C. glauca, 2.5–3.2 μm in C. subviridis) and smaller basidia (9.8–14.8 × 3.4–4.5 μm in C. bifaria, 9.8–14.8 × 3.1–4.3 μm in C. glauca, 10–13 × 3.2–4.4 μm in C. subviridis) (Table 2); in addition, they are distantly related from C. bubalinus in phylogeny.

Additional specimen (paratype) examined: CHINA. Yunnan Province, Binchuan County, Jizu Mountain, on wood of Pinus, 14 September 2018, Cui 16976 (BJFC).

Cyanosporus hirsutus B.K. Cui & Shun Liu, sp. nov. (Figures 4C–D, 6)

MycoBank: MB 838418

Diffs from other Cyanosporus species by its flabelliform to semicircular and distinctly hirsute pileus with ash gray to light grayish brown pileal surface, and cylindrical and slightly curved basidiospores (4.1–4.7 × 1.2–1.5 μm).

Type. — CHINA. Yunnan Province, Lijiang, Yulong Snow Mountain, on fallen trunk of Picea, 14 September 2018, Cui 17083 (holotype, BJFC).

Etymology. — Hirsutus (Lat.): refers to the distinctly hirsute pileal surface.

Basidiocarps. — Annual, pileate, soft corty, without odor or taste when fresh, becoming corty to fragile upon drying. Pileus flabelliform to semicircular, projecting up to 5.2 cm, 9.5 cm wide and 1.5 cm thick at base. Pileal surface ash gray to light grayish brown with bluish gray zone when fresh, becoming grayish to grayish brown when dry, distinctly hirsute; margin acute. Pore surface cream when fresh, becoming straw yellow to olivaceous buff when dry; sterile margin narrow to almost lacking; pores angular, 5–7 per mm; dissepiments thin, entire. Context white, soft corty, up to 9 mm thick. Tubes cream, fragile, up to 7 mm long.

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

Context. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, loosely interwoven, 2.7–8.2 μm in diam.

Tubes. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, interwoven, 2–5 μm in diam. Cystidia absent; cystidioles present, fusoid, thin-walled, 13.2–22.5 × 2.7–4.3 μm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 13.6–15.5 × 3.4–4.7 μm; basidioles dominant, in a shape similar to basidia, but smaller.
**Basidiospores.** — Cylindrical, slightly curved, hyaline, thin- to slightly thick-walled, smooth, occasionally with small oily drops, IKI−, CB−, 4–4.7(−4.9) × (1−)1.2–1.5(−1.8) µm, $L = 4.42$ µm, $W = 1.33$ µm, $Q = 3.18$–3.52 ($n = 90/3$).

**Notes.** — Phylogenetically, *Cyanosporus hirsutus* grouped together with *C. caesius*, *C. glauca*, *C. gossypina* (Moug. & Lév.) B.K. Cui & Shun Liu, *C. mediterraneocaesius* (M. Pieri & B. Rivoire) B.K. Cui, L.L. Shen & Y.C. Dai and *C. piceicolora*. 

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**FIGURE 4** | Basidiocarps of *Cyanosporus* species. (A,B) *C. bubalinus*; (C,D) *C. hirsutus*; (E,F) *C. nothofagicola*; (G,H) *C. submicroporus*; (I,J) *C. tenuis* (scale bars: A,B,I,J = 1 cm; C,D,E,F,G,H = 2 cm).
FIGURE 5 | Microscopic structures of Cyanosporus bubalinus (drawn from the holotype). (A) Basidiospores; (B) Basidia and basidioles; (C) Cystidioles; (D) Hyphae from trama; (E) Hyphae from context. Bars: (A) = 5 µm; (B–E) = 10 µm.
### TABLE 2 | Comparisons of the main morphological characters of species in *Cyanosporus*.

| Species       | Distribution                                                                 | Basidio-Carps       | Pileal surface when dry | Pores per mm | Context hyphae (µm) | Tramal hyphae (µm) | Basidia (µm) | Basidiospores | Ref.        |
|---------------|------------------------------------------------------------------------------|---------------------|-------------------------|--------------|---------------------|-------------------|--------------|--------------|-------------|
| *C. alni*     | China (Guizhou, Hebei), Czech Republic, Denmark, Finland, Germany, Norway, Poland, Russia, Slovakia | Pileate/Effused-reflexed | Velutinate              | 4–6          | 3.9–5.5             | 2.9–3.6           | 10–14.8 x 3.3–4.2 | 4.3–6.1 x 3.3–4.2 | 4.22        | Miettinen et al., 2018 |
| *C. arbuti*   | United States                                                               | Pileate/Effused-reflexed | Glabrous                | 6–8          | 3.2–4.6             | 2.4–3.1           | 11–17 x 3.3–4.2   | 4.1–5.1 x 3.3–4.2   | 4           | Miettinen et al., 2018 |
| *C. auricoma* | China (Inner Mongolia), Finland, Poland, Russia                              | Pileate/Effused-reflexed/Resupinate | Hirsute                | 4–6          | 4.2–5.2             | 3.1–4.0           | 14–20 x 3.8–5.3   | 4.4–5.6 x 3.5–6.5   | 3.06        | Miettinen et al., 2018 |
| *C. bifaria*  | China (Jilin, Sichuan), Japan, Russia                                        | Pileate              | Velutinate              | 6–8          | 4–7                 | 2.5–3.8           | 9.8–14.8 x 3.4–4.5 | 3.7–4.4 x 1–1.2     | 3.6         | Miettinen et al., 2018 |
| *C. bubalinus*| China (Yunnan)                                                               | Pileate              | Tomentose               | 5–8          | 2.5–7.3             | 2–4.2             | 11.6–19.8 x 4.3–5.6 | 4.3–4.8 x 1.5–2    | 2.6–2.83    | this study |
| *C. caesius*  | Czech Republic, Denmark, Finland, France, Germany, Russia, Slovakia, Spain, United Kingdom | Pileate/Effused-reflexed | Hirsute                | 4–5          | 3.7–5.2             | 2.8–3.6           | 10–15 x 3.7–4.5   | 4.1–5.3 x 1.3–1.7   | 3.13        | Miettinen et al., 2018 |
| *C. caesiosimulans* | Finland, Russia, United States                                      | Pileate/Effused-reflexed | Glabrous                | 5–7          | 3.4–5.2             | 2.9–3.8           | 10.5–15.5 x 3.2–5.2 | 4.2–5.5 x 1.1–1.4 | 3.93        | Miettinen et al., 2018 |
| *C. coerulivirens* | China (Hunan, Jilin, Zhejiang), Indonesia, Russia                | Pileate              | Velutinate              | 6–8          | 3.6–6               | 2.4–3.4           | 8.8–13.5 x 3.3–4.3 | 3.8–4.6 x 1–1.3    | 3.64        | Miettinen et al., 2018 |
| *C. comata*   | China (Sichuan, Xizang), United States                                     | Pileate/Effused-reflexed | Velutinate             | 4–6          | 4.2–5.3             | 2.8–3.8           | 8.8–14.2 x 3.7–4.9 | 4.1–4.9 x 1–1.3    | 3.62        | Miettinen et al., 2018 |
| *C. cyanescens* | Estonia, Finland, France, Poland, Russia, Spain, Sweden          | Pileate/Effused-reflexed | Glabrous                | 5–6          | 4.1–5.2             | 2.9–3.7           | 11.4–19.8 x 3.7–5.4 | 4.7–6.1 x 1–1.6    | 3.92        | Miettinen et al., 2018 |
| *C. fusiformis* | China (Guizhou, Sichuan)                                                  | Pileate/Effused-reflexed | Tomentose               | 4–5          | 3–5                 | 2–4              | 12–15 x 4.5–6     | 4.5–5.2 x 0.8–1.1  | 5.21–5.45    | Shen et al., 2019 |
| *C. glauca*   | China (Jilin), Russia                                                      | Pileate              | Hirsute                 | 5–8          | 3.4–5.1             | 2.6–3.3           | 9.8–14.8 x 3.1–4.3 | 4.1–5.4 x 1–1.5    | 3.64        | Miettinen et al., 2018 |
| *C. gossypina* | France                                                                     | Pileate              | Glabrous                | 4–6          | 3.6–4.8             | 2.3–3             | 8.7–16.8 x 3.8–5   | 4.1–5.1 x 1–2.7    | 3.11        | Miettinen et al., 2018 |
| *C. hirsutus* | China (Yunnan)                                                             | Pileate              | Hirsute                 | 5–7          | 2.7–8.2             | 2–5              | 13.6–15.5 x 3–4.7  | 4.4–7.2 x 1.2–1.5  | 3.18–3.52    | this study    |
| *C. livens*   | Canada, United States                                                     | Pileate              | Velutinate              | 4–6          | 3.7–5.3             | 2.9–4             | 9.3–14.3 x 4–5.3   | 4.1–5.7 x 1–1.5    | 3.74        | Miettinen et al., 2018 |

(Continued)
| Species               | Distribution                                      | Basidio-Carps          | Pileal surface when dry | Pores per mm | Context hyphae (µm) | Tramal hyphae (µm) | Basidia (µm) | Basidiospores | Ref.          |
|----------------------|---------------------------------------------------|------------------------|-------------------------|--------------|---------------------|-------------------|--------------|---------------|--------------|
|                     |                                                   |                        |                         |              |                     |                   |              |               |              |
| C. luteocaesius      | France                                           | Pileate/Effused-reflexed | Tomentose               | 3–5          | 4.1–5.8             | 2.7–3.2           | 11.1–16.2 x 4.5 | 4.3–6.1 x 1.5 | 3.02 Miettinen et al., 2018 |
| C. magna             | China (Jilin, Hainan, Yunnan)                     | Pileate                | Velutinate              | 4–5          | 4.2–6               | 2.2–3.3           | 10–12.5 x 3.4  | 3.6–4.4 x 1  | 3.51 Miettinen et al., 2018  |
| C. mediterraneocaesius | France, Spain                                      | Pileate/Effused-reflexed | Velutinate              | 5–6          | 3.1–4               | 2.3–3.2           | 12–18.5 x 3.5  | 4.2–5.8 x 1.3 | 3.26 Miettinen et al., 2018  |
| C. microporus        | China (Yunnan)                                    | Pileate                | Velutinate              | 6–8          | 3.5–6               | 2–4               | 11–13.5 x 4.5  | 4.5–4.9 x 1 | 4.47–4.52 Shen et al., 2019  |
| C. nothofagicola     | Australia                                         | Pileate/Effused-reflexed | Tomentose               | 4–6          | 2.3–7.5             | 2–5               | 13.6–17.2 x 3.4 | 3.8–5 x 1 | 4.08–4.22 this study  |
| C. piceicola         | China (Sichuan, Xizang, Yunnan)                   | Pileate                | Velutinate              | 3–5          | 5–7                 | 2.5–4             | 13–16 x 4.5  | 4–4.5 x 0.9 | 3.75–3.97 Shen et al., 2019  |
| C. populi            | China (Jilin, Sichuan, Yunnan), Finland, Norway, Poland, Russia, United States | Pileate/Effused-reflexed | Glabrous                | 5–7          | 3.2–4.8             | 2.7–3.3           | 10–16 x 3.5  | 4.2–5.6 x 1 | 3.14 Miettinen et al., 2018  |
| C. simulans          | Canada, China, Estonia, Finland, France, Germany, Norway, Russia, United States | Pileate/Effused-reflexed/Resupinate | Glabrous                | 5–7          | 3.9–5               | 2.8–3.6           | 10–14.8 x 3.7  | 4.4–6.3 x 1.3 | 3.6 Miettinen et al., 2018  |
| C. subcaesius        | Czech Republic, Finland, France, Russia, United Kingdom | Pileate/Effused-reflexed | Glabrous                | 4–6          | 4.2–6.6             | 3.1–4.1           | 10.3–17.8 x 3.3  | 4–5.3 x 1.4 | 3.8 Miettinen et al., 2018  |
| C. subhirsutus       | China (Guizhou, Fujian, Yunnan)                   | Pileate                | Hirsute                 | 2–3          | 4–6                 | 3–4.5             | 10–12 x 4–6  | 4–4.5 x 0.9 | 3.67–3.79 Shen et al., 2019  |
| C. submicroporus     | China (Sichuan, Yunnan)                           | Pileate                | Velutinate              | 6–9          | 2.3–6.2             | 2–4.8             | 12.2–20.5 x 3.4  | 3.6–4.7 x 1 | 3.45–3.52 this study  |
| C. subviridis        | Finland, Mexico, United States                    | Pileate                | Glabrous                | 6–8          | 4.8–5.8             | 2.5–3.2           | 10–13 x 3.2  | 3.8–4.5 x 1 | 3.58 Miettinen et al., 2018  |
| C. tricolor          | China (Sichuan, Xizang)                           | Pileate                | Velutinate              | 4–5          | 3–5                 | 2–3               | 12–15 x 4–5 | 4–4.8 x 0.8 | 4.55–4.87 Shen et al., 2019  |
| C. tenuis            | China (Sichuan)                                   | Pileate/Effused-reflexed | Tomentose               | 5–7          | 2.6–7               | 2.2–4.8           | 18.2–27.6 x 3.7  | 4.7–6 x 1.3 | 2.89–2.93 This study  |
| C. unguulatus        | China (Sichuan)                                   | Pileate                | Glabrous                | 4–6          | 2.5–4.5             | 2–3               | 12–15 x 4–5 | 4.5–5 x 0.9 | 4.79–4.83 Shen et al., 2019  |
| C. yanae             | Russia                                            | Pileate/Effused-reflexed | Glabrous                | 5–7          | 3–4                 | 2.2–2.9           | 9–14 x 3.5  | 4.3–5.8 x 1 | 3.56 Miettinen et al., 2018  |
Morphologically, *C. hirsutus* is similar to *C. caesius* as both species share hairy and distinctly bluish basidiocarps, but *C. caesius* differs from *C. hirsutus* by its larger pores (4–5 μm), and narrower hyphae of the context (3.7–5.2) (Table 2); *C. hirsutus* and *C. glauca* have similar-sized basidiocarps, but *C. glauca* has a plumbeous to bluish gray or grayish brown pileal surface (Miettinen et al., 2018); *C. hirsutus* and *C. gossypina* have similar-sized pores and basidiocarps, but *C. gossypina* has larger basidiocarps (projecting up to 3 cm, 5.5 cm wide and 1.8 cm thick at base), thinner hyphae in the context (5–7 μm) and smaller basidia (13–16 × 4–5 μm) (Shen et al., 2019). *Cyanosporus microporus* and *C. subhirsutus* both have a flabelliform pileus, with bluish gray zonate pileal surface, similar-sized pores and basidiocarps, but *C. picecola* has smaller basidiocarps (projecting up to 3 cm, 5.5 cm wide and 1.8 cm thick at base), thinner hyphae in the context (5–7 μm) and smaller basidia (13–16 × 4–5 μm) (Shen et al., 2019). *Cyanosporus nothofagicola* differs from other *C. hirsutus* and *C. picecola* both have a flabelliform pileus, with bluish gray zonate pileal surface, similar-sized pores and basidiocarps, but *C. picecola* has smaller basidiocarps (projecting up to 3 cm, 5.5 cm wide and 1.8 cm thick at base), thinner hyphae in the context (5–7 μm) and smaller basidia (13–16 × 4–5 μm) (Shen et al., 2019). *Cyanosporus microporus* and *C. subhirsutus* both have pileate basidiocarps with a blue tint to the pileal surface and slightly thick-walled basidiocarps like *C. hirsutus*, but *C. microporus* differs in its smaller pores (6–8 per mm and basidia (11–13.5 × 4–5 μm) (Table 2); *C. subhirsutus* differs in having larger pores (2–3 per mm) and smaller basidia (10–12 × 4–6 μm) (Table 2).

Additional specimens (paratypes) examined. CHINA. Yunnan Province, Lijiang, Yulong Snow Mountain, on fallen trunk of *Picea*, 14 September 2018, Cui 17050, 17053, 17055, 17070, 17082 (BJFC).

*Cyanosporus nothofagicola* B.K. Cui, Shun Liu & Y.C. Dai, sp. nov. (Figures 4E–F, 7)

MycoBank: MB 838419

Differs from other *Cyanosporus* species by its cream to pinkish buff pileal surface and white to smoke gray pore surface when fresh, buff to buff yellow pileal surface and white to buff yellow pileal surface and similar pores to *C. nothofagicola*, but it differs from the later by its plumbeous to bluish gray or grayish brown pileal surface (Miettinen et al., 2018). Additional specimen (paratype) examined. AUSTRALIA. Tasmania, Arve River Streamside Reserve, on fallen trunk of *Nothofagus*, 15 May 2018, Dai 18765 (BJFC).

*Cyanosporus submicroporus* B.K. Cui & Shun Liu, sp. nov. (Figures 4G–H, 8)

MycoBank: MB 838420

Differs from other *Cyanosporus* species by its cream to pinkish buff pileal surface and white to smoke gray pore surface when fresh, buff to buff yellow pileal surface and white to olivaceous buff pore surface when dry. Type. — CHINA. Yunnan Province, Baoshan, Gaoligongshan Nature Reserve, on angiosperm wood, 8 November 2019, Cui 18156 (holotype, BJFC).

Etymology. — *Submicroporus* (Lat.): refers to the new species resembling *Cyanosporus microporus* in morphology.

Basidiocarps. — Annual, effused-reflexed to pileate, solitary, soft and watery, without odor or taste when fresh, becoming corky to woody hard upon drying. *Pileus* flabelliform to semicircular, projecting up to 2.4 cm, 4.2 cm wide and 0.7 cm thick at base. *Pileal surface* buff to olivaceous buff when fresh, finely tomentose, becoming smooth, pale mouse gray to buff yellow when dry; margin acute. *Pore surface* white to cream when fresh, becoming cream to buff yellow when dry; sterile margin narrow to lacerate; *pores* angular, 4–6 per mm; *disseminations* thin, entire. *Context* cream to buff, corky, up to 5 mm thick. *Tubes* pale mouse gray to cream, fragile, up to 7 mm long.

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

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

Context. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, loosely interwoven, 2.3–7.5 μm in diam.

Tubes. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, interwoven, 2–5 μm in diam. *Cystidia* absent; *cystidioides* present, fusoid, thin-walled, 14.2–16.7 × 2.6–5.2 μm. *Basidia* clavate, bearing four sterigmata and a basal clamp connection, 13.6–17.2 × 3.4–4.2 μm; *basidioles* dominant, in shape similar to basidia, but smaller.

Basidiocarps. — Cylindrical to allantoid, slightly curved, hyaline, thin- to slightly thick-walled, smooth, IKI–, CB–, 3.8–5 × (0.8–)1–1.7 μm, L = 4.62 μm, W = 1.15 μm, Q = 4.08–4.22 (n = 60/2).

Notes. — *Cyanosporus caesius* is also found in Tasmania, Australia. It has pileate or effused reflexed basidiocarps with a tomentose pileal surface and similar pores to *C. nothofagicola*, but it differs from the later by its plumbeous to bluish gray or grayish brown pileal surface (Miettinen et al., 2018). Additional specimen (paratype) examined. AUSTRALIA. Tasmania, Arve River Streamside Reserve, on fallen trunk of *Nothofagus*, 15 May 2018, Dai 18765 (BJFC).

*Cyanosporus submicroporus* B.K. Cui & Shun Liu, sp. nov. (Figures 4G–H, 8)

MycoBank: MB 838420

Differs from other *Cyanosporus* species by its cream to pinkish buff pileal surface and white to smoke gray pore surface when fresh, buff to buff yellow pileal surface and white to olivaceous buff pore surface when dry.

Type. — CHINA. Yunnan Province, Baoshan, Gaoligongshan Nature Reserve, on angiosperm wood, 8 November 2019, Cui 18156 (holotype, BJFC).

Etymology. — *Submicroporus* (Lat.): refers to the new species resembling *Cyanosporus microporus* in morphology.

Basidiocarps. — Annual, pileate, soft and watery, without odor or taste when fresh, becoming corky to woody hard upon drying. *Pileus* flabelliform to semicircular, projecting up to 3.2 cm, 6.5 cm wide and 1.3 cm thick at base. *Pileal surface* cream to pinkish buff when fresh, velutinate, becoming rugose, buff to buff yellow when dry; margin acute. *Pore surface* white to smoke gray when fresh, becoming buff to olivaceous buff when dry; sterile margin narrow to almost lacking; *pores* round, 6–9 per mm; *disseminations* thin, entire. *Context* cream to buff, corky, up to 5 mm thick. *Tubes* pale mouse gray to cream, fragile, up to 7 mm long.

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

Context. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, rarely branched, loosely interwoven, 2.3–6.2 μm in diam.

Tubes. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, interwoven, 2–4.8 μm in diam. *Cystidia* and *cystidioides* absent. *Basidia* clavate, bearing four sterigmata and a basal clamp connection, 12.2–20.5 × 3.4–5.6 μm; *basidioles* dominant, in shape similar to basidia, but smaller.
FIGURE 6 | Microscopic structures of *Cyanosporus hirsutus* (drawn from the holotype). (A) Basidiospores; (B) Basidia and basidioles; (C) Cystidioles; (D) Hyphae from trama; (E) Hyphae from context. Bars: (A) = 5 µm; (B–E) = 10 µm.
Basidiospores. — Allantoid, slightly curved, hyaline, thin- to slightly thick-walled, smooth, occasionally with small oil drops, IKI−, weakly CB+, 3.6–4.7 × (0.9–)1–1.3 μm, $L = 4.18 \, \mu m$, $W = 1.19 \, \mu m$, $Q = 3.45–3.52$ ($n = 90/3$).

Notes. — In the phylogenetic tree the three specimens of *Cyanosporus submicroporus* formed a highly supported lineage (Figures 1-3), and are usually grouped together with *C. bifaria*, *C. comata* (Miettinen) B.K. Cui & Shun Liu, *C. fusiformis* B.K. Cui, L.L. Shen & Y.C. Dai and *C. ungulatus* B.K. Cui, L.L. Shen & Y.C. Dai. Morphologically, both *C. submicroporus* and *C. bifaria* have similar pores and basidiospores, but *C. bifaria* differs in having ochraceous hues, a strigose pileal surface, and...
FIGURE 8 | Microscopic structures of Cyanosporus submicroporus (drawn from the holotype). (A) Basidiospores; (B) Basidia and basidioles; (C) Hyphae from trama; (D) Hyphae from context. Bars: (A) = 5 µm; (B–D) = 10 µm.
smaller basidiospores (9.8–14.8 × 3.4–4.5 µm) (Table 2); C. comata has similar basidiospores to C. submicroporus, but differs in having conchate or effused-reflexed basidiocarps, and smaller basidia (8.8–14.2 × 3.7–4.9 µm) (Table 2); C. fusiformis and C. ungulatus differ in having larger pores (Table 2). Cyanosporus submicroporus is similar to C. microporus by having piletate basidiocarps with a velutinate pileal surface, and small and angular pores, but C. microporus differs in having thick-walled trama generative hyphae, smaller basidia (11–13.5 × 1–2 µm) and longer basidiospores (4.5–4.9 × 1–1.2 µm) (Table 2).

Additional specimens (paratypes) examined. CHINA. Sichuan Province, Shimian County, on fallen angiosperm trunk, 14 September 2019, Cui 17750 (BJFC); Yunnan Province, Chuxiong, Zizixhan Nature Reserve, on fallen angiosperm trunk, 20 September 2017, Cui 16306 (BJFC).

Cyanosporus tenuis B.K. Cui, Shun Liu & Y.C. Dai, sp. nov. (Figures 4I–J, 9)

MycoBank: MB 838421

Differs from other Cyanosporus species by the thin basidiocarps, larger cystidioles (16.4–25.4 × 2.8–4.2 µm), and bigger basidiospores (4.7–6 × 1.3–2 µm).

Type. — CHINA. Sichuan Province, Luding County, Hailuogou Forest Park, on fallen trunk of Picea, 20 October 2012, Cui 10788 (BJFC).

Etymology. — Tenuis (Lat.): refers to the thin basidiocarps.

Basidiocarps. — Annual, effused-reflexed to pileate, soft corky, without odor or taste when fresh, becoming corky to fragile upon drying. Pileus flabelliform, projecting up to 1.5 cm, 1.8 cm wide and 0.4 cm thick at base. Pileal surface buff to olivaceous buff when fresh, finely tomentose, becoming cream to olivaceous buff when dry; sterile context white to cream when fresh, becoming buff yellow to pinkish buff when dry; sterile margin acute. Pore surface white to cream when fresh, becoming buff yellow to pinkish buff when dry; sterile margin narrow to almost lacking; pores angular, 5–7 per mm; dissepiments thin, entire to lacerate. Context cream, soft corky, up to 2 mm thick. Tubes pinkish buff, fragile, up to 2 mm long.

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

Context. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, loosely interwoven, 2.6–7 µm in diam.

Tubes. — Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, occasionally branched, interwoven, 2.2–4.8 µm in diam. Cystidia absent; cystidioles present, fusoid, thin-walled, 16.4–25.4 × 2.8–4.2 µm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 18.2–27.6 × 3.7–6 µm; basidioles dominant, in a shape similar to basidia, but smaller.

Basidiospores. — Cylindrical, slightly curved, hyaline, thin- to slightly thick-walled, smooth, occasionally with small oil drops, IKI–, weakly CB+, (4.5–)4.7–6 × 1.3–2 µm, L = 5.44 µm, W = 1.76 µm, Q = 2.89–2.93 (n = 60/2).

Notes. — Phylogenetically, Cyanosporus tenuis grouped together with C. arbuti (Spirin) B.K. Cui & Shun Liu, C. luteocaesius (A. David) B.K. Cui, L.L. Shen & Y.C. Dai and C. simulans (P. Karst.) B.K. Cui & Shun Liu. Morphologically, C. arbuti differs in having narrower hyphae in the context and smaller basidiospores (4.1–5.1 × 1–1.2 µm) (Table 2); C. luteocaesius differs in larger pores (3–5 per mm; Table 2); C. simulans differs in smaller basidia (10–14.8 × 3.7–5.2 µm; Table 2). Cyanosporus fusiformis, C. picicola, C. tricolor B.K. Cui, L.L. Shen & Y.C. Dai and C. ungulatus are also distributed in Sichuan Province, but C. fusiformis has a semi-circular pileus, fusiform cystidioles presenting in the hymenium and narrow allantoid basidiospores (4.5–5.2 × 0.8–1.1 µm) (Table 2); C. picicola has sub-rotund pileus, small angular pores, and slightly thick-walled and allantoid basidiospores (4.4–4.5 × 0.9–1.3 µm) (Table 2); C. tricolor has a white, blue, and pale mouse gray pileal surface when fresh (Shen et al., 2019); C. ungulatus has unglelate basidiocarps (Shen et al., 2019).

Additional specimen (paratype) examined. CHINA. Sichuan Province, Puge County, Luoji Mountain, on fallen trunk of Picea, 19 September 2012, Dai 12974 (BJFC).

Cyanosporus arbuti (Spirin) B.K. Cui & Shun Liu, comb. nov.

MycoBank: MB 838422

Basionym: Postia arbuti Spirin, Fungal Systematics and Evolution 1: 113, 2018.

Notes. — Postia arbuti was described from the United States (Miettinen et al., 2018). It is characterized by conchate, pendant to effused-reflexed basidiocarps with almost glabrous to matt pileal surfaces. It usually grows on Arbutus menziesii and is widely distributed in temperate areas of North America (North-West). In our study, the phylogenetic analysis (Figures 1–3) strongly supports its placement in Cyanosporus. For a detailed description of Postia arbuti, see Miettinen et al. (2018).

Cyanosporus auricoma (Spirin & Niemelä) B.K. Cui & Shun Liu, comb. nov.

MycoBank: MB 838423

Basionym: Postia auricoma Spirin & Niemelä, Fungal Systematics and Evolution 1: 115, 2018.

= Cyanosporus mongolicus B.K. Cui, L.L. Shen & Y.C. Dai, Persoonia 42: 115, 2019.

Notes. — Postia auricoma was described by Miettinen et al. (2018) and Cyanosporus mongolicus was described by Shen et al. (2019). Phylogenetically, the two species formed a highly supported lineage (Figures 1–3) and as the morphological characters of C. mongolicus fit well with Postia auricoma, we treat C. mongolicus as a synonym of P. auricoma, and P. auricoma is transferred to Cyanosporus as a new combination.

Specimens examined. CHINA. Inner Mongolia, Ewenk, Honghuajerji Nature Reserve, on fallen trunk of Pinus, 19 October 2015, Cui 13518, 13519 (BJFC).

Cyanosporus bifaria (Spirin) B.K. Cui & Shun Liu, comb. nov.

MycoBank: MB 838424

Basionym: Postia bifaria Spirin, Fungal Systematics and Evolution 1: 115, 2018.

Notes. — Postia bifaria was described by Miettinen et al. (2018). The morphological characters of the two specimens from China fit well with Postia bifaria and phylogenetically they clustered together within the genus Cyanosporus. Based on morphological characters and phylogenetic analysis, we transferred Postia bifaria to Cyanosporus as a new combination. For a detailed description of Postia bifaria, see Miettinen et al. (2018).
FIGURE 9 | Microscopic structures of Cyanosporus tenuis (drawn from the holotype). (A) Basidiospores; (B) Basidia and basidioles; (C) Cystidioles; (D) Hyphae from trama; (E) Hyphae from context. Bars: (A) = 5 µm; (B–E) = 10 µm.
Specimens examined: CHINA. Sichuan Province, Xiangcheng County, on fallen trunk of Pinus, 12 August 2019, Cui 17445 (BJFC); Zhaojue County, on stump of Pinus, 16 September 2019, Cui 17806 (BJFC).

*Cyanosporus caesiosimulans* (G.F. Atk.) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838425

Basionym: *Tyromyces caesiosimulans* G.F. Atk., Annales Mycologici 6: 61, 1908.

= *Postia caesiosimulans* (G.F. Atk.) Spirin & Miettinen, Fungal Systematics and Evolution 1: 117, 2018.

Note. — *Tyromyces caesiosimulans* was introduced primarily based on its globose basidiospores (Atkinson, 1908). Miettinen et al. (2018) transferred it to the *Postia caesia* complex based on morphological and molecular evidence. In our study, the phylogenetic analysis strongly supports its placement in *Cyanosporus* (Figures 1–3). For a detailed description of *Postia caesiosimulans*, see Miettinen et al. (2018).

*Cyanosporus coeruleivirens* (Corner) B.K. Cui, Shun Liu & Y.C. Dai, *comb. nov.*

MycoBank: MB 838426

Basionym: *Tyromyces coeruleivirens* Corner, Beihefte zur Nova Hedwigia 96: 163, 1989.

= *Postia coeruleivirens* (Corner) V. Papp, Mycotaxon 129(2): 411, 2015.

Note. — *Tyromyces coeruleivirens* was described from Borneo (Corner, 1989). It has a greenish pileus, a monomitic hyphal system, and allantoid inamayoi basidiospores (Corner, 1989; Hattori, 2002), and was considered as a member of the *Postia caesia* group (Hattori, 2002). Papp (2014) transferred *Tyromyces coeruleivirens* to the *Postia caesia* complex as a new combination. In our study, *Postia coeruleivirens* is transferred to *Cyanosporus* as a new combination; phylogenetically it is closely related to *C. subhirsutus* (Figures 1–3). Morphologically, both *C. coeruleivirens* and *C. subhirsutus* have annual basidiocarps, a monomitic hyphal system and allantoid basidiospores, but *C. subhirsutus* differs in having a disc-shaped pileus, hirsute and zonate pileal surface and larger pores (2–3 per mm; Shen et al., 2019). For a detailed description of *Postia coeruleivirens*, see Miettinen et al. (2018).

Specimens examined: CHINA. Hunan Province, Changde, Hefu Forest Park, on fallen angiosperm trunk, 17 October 2018, Dai 19220 (BJFC); Zhejiang Province, Hangzhou, Jiuxi Forest Park, on fallen angiosperm trunk, 17 October 2010, Dai 11834 (BJFC).

*Cyanosporus comata* (Miettinen) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838427

Basionym: *Postia comata* Miettinen, Fungal Systematics and Evolution 1: 118, 2018.

Note. — *Postia comata* was described from the United States (Miettinen et al., 2018). It is morphologically similar to *P. livens* Miettinen & Vlasák but differs in having mostly thick-walled tramal hyphae and slightly smaller basidiospores (Miettinen et al., 2018). Its closest relative is the East Asian *P. bifaria*, which has smaller pores (6–8 per mm) and basidiospores (3.7–4.4 × 1.0–1.2 µm), and thin-walled tramal hyphae that collapse (Miettinen et al., 2018). *Postia comata* is transferred to *Cyanosporus* as a new combination based on morphological characters and molecular phylogeny. For a detailed description of *Postia comata*, see Miettinen et al. (2018).

Specimens examined: CHINA. Sichuan Province, Jiuzhaigou County, Zhangsha, on stump of Picea, 19 September 2020, Cui 18546 (BJFC); Xizang (Tibet), Mangkang County, on stump of Abies, 8 September 2020, Cui 18388 (BJFC).

*Cyanosporus cyanescens* (Miettinen) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838428

Basionym: *Postia cyanescens* Miettinen, Fungal Systematics and Evolution 1: 119, 2018.

Notes. — *Postia cyanescens* was described by Miettinen et al. (2018). This species is characterized by thin, conchate to flabelliform basidiocarps with light bluish grayish tinted pore surfaces, and long and narrow basidiospores (4.7–6.1 × 1.1–1.6 µm). In our study, the phylogenetic analysis (Figures 1–3) strongly supports its placement in *Cyanosporus*, so we transferred *P. cyanescens* to *Cyanosporus* as a new combination. For a detailed description of *Postia cyanescens*, see Miettinen et al. (2018).

*Cyanosporus glauca* (Spirin & Miettinen) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838429

Basionym: *Postia glauca* Spirin & Miettinen, Fungal Systematics and Evolution 1: 120, 2018.

Notes. — *Postia glauca* was described by Miettinen et al. (2018). It is characterized by thin, small and conchate basidiocarps with plumbeous to bluish gray or grayish brown pileal surfaces, and cream to light bluish grayish pore surfaces. In our study, the phylogenetic analysis (Figures 1–3) supports its placement in *Cyanosporus*, so we transferred it to *Cyanosporus* as a new combination. For a detailed description of *Postia glauca*, see Miettinen et al. (2018).

*Cyanosporus gossypina* (Moug. & Lév.) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838430

Basionym: *Polyporus gossypinus* Moug. & Lév., Annales des Sciences Naturelles Botanique 9: 124, 1848.

= *Postia gossypina* (Moug. & Lév.) Spirin & B. Rivoire, Fungal Systematics and Evolution 1: 120, 2018.

Notes. — *Postia gossypina* was proposed by Miettinen et al. (2018). Based on morphological characters and phylogenetic analysis, we transferred *P. gossypina* to *Cyanosporus* as a new combination. For a detailed description of *Postia gossypina*, see Miettinen et al. (2018).

*Cyanosporus livens* (Miettinen & Vlasák) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838431

Basionym: *Postia livens* Miettinen & Vlasák, Fungal Systematics and Evolution 1: 120, 2018.

Notes. — *Postia livens* was described from North America. It is the most common representative of the *P. caesia* complex in North America, and it can be easily identified by its plumbeous to bluish gray to ochraceous pileal surface often with bluish tints (Miettinen et al., 2018). In our study, it grouped with other species of the *P. caesia* complex in *Cyanosporus* (Figures 1–3),...
so, we transferred it into *Cyanosporus* as a new combination. For a detailed description of *Postia livens*, see Miettinen et al. (2018).

**Cyanosporus magna** (Miettinen) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838432

Basionym: *Postia magna* Miettinen, Fungal Systematics and Evolution 1: 121, 2018.

Notes. — *Postia magna* was described from China (Miettinen et al., 2018). Although we did not find the type specimen, we have examined two specimens from China, and its morphological characters fit well with this species. The phylogenetic analysis (Figures 1–3) also strongly supports its placement in *Cyanosporus*. So, we transferred *Postia magna* to *Cyanosporus* as a new combination. For a detailed description of *Postia magna*, see Miettinen et al. (2018).

Specimens examined: CHINA. Hainan Province, Ledong County, Jianfengling Nature Reserve, on fallen angiosperm trunk, 12 May 2009, Cui 10854 (BJFC); Jilin Province, Fusong County, Lushuimei Forest Park, on fallen angiosperm branch, 11 August 2011, Cui 10094 (BJFC); Yunnan Province, Pinxian County, Jizu Mountain, on fallen angiosperm branch, 14 September 2018, Cui 16983 (BJFC).

**Cyanosporus populi** (Miettinen) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838433

Basionym: *Postia populi* Miettinen, Fungal Systematics and Evolution 1: 122, 2018.

Notes. — *Postia populi* was described by Miettinen et al. (2018). Based on morphological characters and phylogenetic analyses, we transferred *P. populi* to *Cyanosporus* as a new combination. For a detailed description of *Postia populi*, see Miettinen et al. (2018).

Specimens examined: CHINA. Sichuan Province, Muli County, on fallen trunk of *Pinus*, 16 August 2019, Cui 17549 (BJFC); Yunnan Province, Lijiang, Yulong Snow Mountain, on fallen trunk of *Picea*, 16 September 2018, Cui 17087a (BJFC).

**Cyanosporus simulans** (P. Karst.) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838434

Basionym: *Bjerkandera simulans* P. Karst., Revue Mycologique Toulouse 10: 73, 1888.

= *Postia simulans* (P. Karst.) Spirin & B. Rivoire, Fungal Systematics and Evolution 1: 123, 2018.

Notes. — This species was described by Karsten (1888) as *Bjerkandera simulans*. Recently, *Bjerkandera simulans* was treated as an independent species in the *Postia caesia* complex by Miettinen et al. (2018). In our study, the phylogenetic analysis (Figures 1–3) supports its placement in *Cyanosporus*. For a detailed description of *Postia simulans*, see Miettinen et al. (2018).

**Cyanosporus subviridis** (Ryvarden & Guzmán) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838435

Basionym: *Tyromyces subviridis* Ryvarden & Guzmán, Mycotaxon 78: 252, 2001.

= *Postia subviridis* (Ryvarden & Guzmán) Spirin, Fungal Systematics and Evolution 1: 125, 2018.

Notes. — *Tyromyces subviridis* was described from a highland conifer forest in Mexico (Guzmán and Ryvarden, 2001). Miettinnen et al. (2018) studied the type specimen, and transferred it to the *Postia caesia* complex. In our study, the phylogenetic analysis (Figures 1–3) supports its placement in *Cyanosporus*. For a detailed description of *Postia subviridis*, see Miettinen et al. (2018).

**Cyanosporus yanae** (Miettinen & Kotiranta) B.K. Cui & Shun Liu, *comb. nov.*

MycoBank: MB 838436

Basionym: *Postia yanae* Miettinen & Kotir., Fungal Systematics and Evolution 1: 125, 2018.

Notes. — *Postia yanae* was described by Miettinen et al. (2018). It is characterized by effused-reflexed or resupinate basidiocarps with detached or adnate margins, and white, with light to strong bluish grayish tinted pore surfaces. In our study, the phylogenetic analysis (Figures 1–3) supports its placement in *Cyanosporus*. For a detailed description of *Postia yanae*, see Miettinen et al. (2018).

### Other Specimens of *Cyanosporus*

**Examined**

*Cyanosporus alni* (Niemelä & Vampola) B.K. Cui, L.L. Shen & Y.C. Dai. CHINA. Guizhou Province, Suiyang County, Kuankuoshui Nature Reserve, on fallen angiosperm trunk, 26 June 2014, Dai 15060 (BJFC); Hebei Province, Xinglong County, Wulingshan Nature Reserve, on fallen angiosperm trunk, 29 August 2009, Cui 7185 (BJFC). CZECH REPUBLIC. Ceske Budejovice, on fallen trunk of *Fagus*, 22 November 2011, Dai 12709 (BJFC).

**FINLAND.** Uusimaa, Vantaa, Tamisto Nature Reserve, on fallen trunk of *Pupulus*, 4 November 2011, Dai 12641 (BJFC). POLAND. Brańka, Mcrow, on fallen trunk of *Fagus*, 3 October 2014, Dai 14845 (BJFC).

*Cyanosporus caesius*. FINLAND. Uusimaa, Vantaa, Tamisto Nature Reserve, on fallen trunk of *Picea*, 3 November 2011, Dai 12605 (BJFC). SPAIN. Cadiz Province, Sierra Grazalema Natural Park, on fallen trunk of *Abies*, 22 November 2005, Dai 7438 (BJFC).

*Cyanosporus fusiformis*. CHINA. Guizhou Province, Suiyang County, Kuankuoshui Nature Reserve, on dead angiosperm tree, 26 November 2014, Dai 15036 (BJFC, holotype); Sichuan Province, Luding County, Hailuogou Forest Park, on dead tree of *Rhododendron*, 20 October 2012, Cui 10775 (BJFC, paratype).

*Cyanosporus microporus*. CHINA. Yunnan Province, Pu’er, Taiyanghe National Forest Park, on fallen angiosperm trunk, 8 July 2013, Cui 11014 (BJFC, holotype); Chuxiong, Zixishan Nature Reserve, on dead angiosperm tree, 28 August 2010, Dai 11717 (BJFC, paratype).

*Cyanosporus piceicola*. CHINA. Sichuan Province, Jiuzhaigou County, Jiuzhaigou Nature Reserve, on stump of *Picea*, 11 October 2012, Dai 10626 (BJFC, holotype), on fallen trunk of *Picea*, 11 October 2012, Dai 10617 (BJFC, paratype); Xizang (Tibet), Linzi, Sejila Mountain, on fallen trunk of *Picea*, 18 September 2014, Cui 12158 (BJFC, paratype); Milin County, Nanyigou Forest Park, on fallen trunk of *Picea*, 16 September 2014, Cui 12088 (BJFC, paratype); Yunnan Province, Weixi
County, Laojunshan Nature Reserve, on fallen trunk of *Picea*, 21 September 2011, Cui 10446 (BJFC, paratype).

*Cyanosporus subhirsutus*. CHINA. Fujian Province, Yongqing County, Huboliao Nature Reserve, on fallen angiosperm branch, 26 October 2013, Cui 11330 (BJFC, paratype); Guizhou Province, Jiangkou County, Fanjingshan Nature Reserve, on fallen trunk of *Pterocarya*, 21 November 2014, Dai 14892 (BJFC, holotype); Yunnan Province, Pu’er, Taiyanghe National Forest Park, on fallen angiosperm trunk, 8 July 2013, Cui 11019 (BJFC, paratype).

*Cyanosporus subcaesius*. FINLAND. Helsinki, Arabia, on angiosperm stump, 23 November 1996, Dai 2345 (IFP); Vantaa, on fallen trunk of *Pruus*, 4 October 1997, Dai 2725 (IFP).

*Cyanosporus tricolor*. CHINA. Sichuan Province, Luding County, Hailuogou Forest Park, on fallen trunk of *Abies*, 20 October 2012, Cui 10790 (BJFC, paratype), on fallen trunk of *Picea*, 20 October 2012, Cui 10780 (BJFC, paratype); Xizang (Tibet), Motuo County, on fallen branch of *Abies*, 20 September 2014, Cui 12233 (BJFC, holotype).

*Cyanosporus unguulatus*. CHINA. Sichuan Province, Minning County, Lingshansi Park, on fallen branch of *Castanopsis*, 17 September 2012, Dai 12897 (BJFC, holotype); Luding County, Hailuogou Forest Park, on fallen trunk of *Abies*, 20 October 2012, Cui 10778 (BJFC, paratype).

**DISCUSSION**

The genus *Cyanosporus*, usually with blue-tinted basidiocarps, is easy to recognize, but identification to species level is difficult as morphological features are quite similar among the species. The main morphological characters of the species in *Cyanosporus* are provided in Table 2.

In our current phylogenetic analyses, the genus *Cyanosporus* is supported as an independent genus; 31 species grouped phylogenetically and clusters with other brown-rot fungal genera, such as *Amaropostia* (Ryvarden) V. Papp, *B.K. Cui, L.L. Shen & Y.C. Dai, Amyloycystis Bondartsev & Singer ex Singer, Calciopostia B.K. Cui, L.L. Shen & Y.C. Dai, Cystidiopostia B.K. Cui, L.L. Shen & Y.C. Dai, Fusciopostia B.K. Cui, L.L. Shen & Y.C. Dai, Oligoporus Bref., Ostina Donk, Postia Fr. and Spongiporus Murrill, which is similar to previous studies (Ortiz-Santana et al., 2013; Ryvarden and Melo, 2014; Han et al., 2016; Shen et al., 2019).

The nomenclatural and taxonomic history of the *Postia caesia* complex was critically reviewed by Papp (2014), the generic name of the *P. caesia* complex have been changed many times, Papp proposed *Cyanosporus* as a subgenus of *Postia* to contain the *P. caesia* complex. Miettinen et al. (2018) revised the species concept of the *Postia caesia* complex based on morphology and two gene markers (ITS and TEF) and discussed that TEF sequences are more reliable for molecular identification of the *P. caesia* complex than ITS sequences. They also indicated that host tree is important for species identification of the *P. caesia* complex; their study raised the species number of the *Postia caesia* complex from 10 to 24, but their study did not focus on the taxonomic status of the *P. caesia* complex of *Postia sensu lato*.

Previously, species identification of the *Postia caesia* complex was only based on morphological characters and host trees in China. Samples grown on angiosperm woods were usually identified as *Postia alni* Niemelä & Vampola and those on gymnosperm woods as *Postia caesia*; only two species were recorded from China before Dai (2012). Shen et al. (2019) carried out a comprehensive phylogenetic and taxonomic study of *Postia* and related genera based on morphological characters and the combined seven-gene (*ITS + nLSU + nSSU + mtSSU + RPB1 + RPB2 + TEF*) sequences, *Cyanosporus* was confirmed as an independent genus of *Postia sensu lato* and 12 species belonging to the *P. caesia* complex were recognized in *Cyanosporus*, which was distant from *Postia s.s.*.

In the current study, the novel species were supported by phylogenetic analyses based on *ITS + TEF* sequences, *ITS + nLSU + TEF* sequences and *ITS + nLSU + nSSU + mtSSU + RPB1 + RPB2 + TEF* sequences, respectively, but for the ITS sequences, several species have very similar base pairs and could not be separated by ITS sequences. The suitable DNA barcoding gene is the TEF gene for species identification of *Cyanosporus*, this result is consistent with a previous study by Miettinen et al. (2018). Our study expanded the number of *Cyanosporus* species to 31 around the world including 19 species from China. Our study indicated that more cryptic species could be discovered by combined evidence of morphological characters, molecular data, host trees and distribution areas in species complexes. However, several species of the *Postia caesia* complex, such as, *P. africana* (Ryvarden) V. Papp, *P. amyloidea* (Corner) V. Papp, *P. atrostrigosa* (Cooke) Rajchenb. and *P. caesioides* (Pat.) V. Papp, are not included in the current phylogenetic analysis due to the lack of DNA sequences. Although the morphological characters of these species fit well with *Cyanosporus*, we did not transfer them to *Cyanosporus* in the current study. A fully resolved phylogeny for *Cyanosporus* and its related genera requires evolutionary information from more samples and more conserved gene markers.

In addition, some species with yellow basidiocarps, such as *C. auricoma*, *C. caesioides*, and *C. lutecaesius*, and some species with white to cream colored basidiocarps, such as *C. bubalinus* and *C. nothofigicola*, are grouped together within *Cyanosporus*; this expanded the concept of the genus to include taxa without blue-tinted basidiocarps. More novel species might be discovered from different regions in future studies.

**DATA AVAILABILITY STATEMENT**

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: http://purl.org/phylo/treebase, 27274.
AUTHOR CONTRIBUTIONS

B-KC and SL designed the experiments. SL, L-LS, GG, and B-KC prepared the samples. SL, YW, and T-MX conducted the molecular experiments and analyzed the data. SL, GG, and B-KC drafted the manuscript. All the authors approved the manuscript.

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

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NOMENCLATURE

AR: Argentina; BI: Bayesian inference; BJFC: Herbarium of the Institute of Microbiology, Beijing Forestry University; BGI: Beijing Genomics Institute; BPP: Bayesian posterior probabilities; BT: Bootstrap; CB: Cotton Blue; CB+: cyanophilous; CB–: acyanophilous; GB: Great Britain; GTR + I + G: General time reversible + proportion invariant + gamma; CTAB: Cetyl trimethylammonium bromide; IFP: Herbarium of the Institute of Applied Ecology, Chinese Academy of Sciences; IKI: Melzer's reagent, IKI–: neither amyloid nor dextrinoid; ILD: Incongruence length difference test; ITS: Internal transcribed spacer; KOH: 5% potassium hydroxide; L: mean spore length (arithmetic average of all spores); ML: Maximum likelihood; MP: Maximum parsimony; MPT: Most Parsimonious Tree; mtSSU: Mitochondrial small subunit rRNA; n (a/b): number of spores (a) measured from given number (b) of specimens; nLSU: Nuclear large subunit rDNA; nSSU: Nuclear small subunit rRNA; Q: variation in the L/W ratios between the specimens studied; RPB1: DNA-directed RNA polymerase II subunit 1; RPB2: DNA-directed RNA polymerase II subunit 2; TL: Tree length; W: mean spore width (arithmetic average of all spores); CI: Consistency Index; RI: Retention Index; RC: Rescaled Consistency Index; HI: Homoplasy Index; TEF: Translation elongation factor 1-α.