Species Diversity, Molecular Phylogeny, and Ecological Habits of Fomitopsis (Polyporales, Basidiomycota)

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Fomitopsis is a worldwide brown-rot fungal genus of Polyporales, which grows on different gymnosperm and angiosperm trees and has important ecological functions and economic values. In this study, species diversity, phylogenetic relationships, and ecological habits of Fomitopsis were investigated. A total of 195 specimens from 24 countries representing 29 species of Fomitopsis were studied. Based on the morphological characters and phylogenetic evidence of DNA sequences including 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 translation elongation factor 1-α gene (TEF), and the second subunit of RNA polymerase II (RPB2), 30 species are accepted in Fomitopsis, including four new species: F. resupinata, F. srilankensis, F. submeliae and F. yimengensis. Illustrated descriptions of the novel species and the geographical locations of the Fomitopsis species are provided.

Keywords: brown-rot fungi, distribution areas, multi-gene phylogeny, new species, polypore

INTRODUCTION

Fomitopsis P. Karst. was established by Karsten (1881) and typified by F. pinicola (Sw.) P. Karst. It is the type genus of Fomitopsidaceae Jülich. Species in Fomitopsis causes a brown rot and plays an important role in degradation and reduction of forest ecosystems (Wei and Dai, 2004). Some species of Fomitopsis are forest pathogens, such as, F. nivosa (Berk.) Gilb. & Ryvarden and

Abbreviations: 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; CBñ, acyanophilous; GTR + I + G, general time reversible + proportion invariant + gamma; IKI, Melzer's reagent; IKIñ, 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; RPR2, 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.
F. pinicola (Dai, 2012); and some species are medicinal fungi, such as, F. betulina (Bull.) B.K. Cui, M.L. Han & Y.C. Dai has the function of antibacteria, antitumor, and antioxidant (Dai et al., 2009; Zhao et al., 2014); F. pinicola has the function of dispelling wind-evil and dampness, and has antitumor, antifungal, antioxidant, immunomodulation, and neuroprotective activities (Dai et al., 2009; Guler et al., 2009; Bao et al., 2015; Sun et al., 2016; Guo and Wolf, 2018).

Fomitopsis is a widely distributed brown-rot fungal genus and many studies have been focused on this genus since its establishment. Previously, some new species of Fomitopsis were described only based on morphological characteristics (Bondartsev and Singer, 1941; Cunningham, 1950; Sasaki, 1954; Ito, 1955; Reid, 1963; Ryvarden, 1972, 1984, 1988; Gilbertson and Ryvarden, 1985; Buchanan and Ryvarden, 1988; Corner, 1989; Zhao and Zhang, 1991; Reng and Zhang, 1992; Masuka and Ryvarden, 1993; Ryvarden and Gilbertson, 1993; Roy and De, 1996; Hattori, 2003; Aime et al., 2007; Stokland and Ryvarden, 2008). According to the 10th edition of the Dictionary of Fungi (Kirk et al., 2008), 32 species are accepted in Fomitopsis and a considerable number of these species lack molecular data.

With the progress of molecular biology technology, DNA sequencing and phylogenetic techniques have been used in the systematic study of Fomitopsis. Some phylogenetic studies showed that Fomitopsis clustered with other brown-rot fungal genera and embedded in the antrodia clade (Hibbett and Donoghue, 2001; Hibbett and Thorn, 2001; Binder et al., 2005). Subsequently, phylogenetic analyses indicated that Fomitopsis is polyphyletic and the taxonomic position of Fomitopsis is still problematic (Kim et al., 2005, 2007; Justo and Hibbett, 2011; Ortiz-Santana et al., 2013). Recently, taxonomic and phylogenetic studies on Fomitopsis have been carried out and several new species have been described (Li et al., 2013; Han et al., 2014, 2016; Han and Cui, 2015; Soares et al., 2017; Haight et al., 2019; Liu et al., 2019, 2021a; Zhou et al., 2021). Han et al. (2016) investigated phylogenetic relationships of Fomitopsis and its related genera and reported that species previously placed in Fomitopsis were divided into seven lineages: Fomitopsis s. s., Fragifomes B.K. Cui, M.L. Han & Y.C. Dai, Niveoporofomes B.K. Cui, M.L. Han & Y.C. Dai, Rhodofoves Kotl. & Pouzar, Rhodofomitopsis B.K. Cui, M.L. Han & Y.C. Dai, Rubellofomes B.K. Cui, M.L. Han & Y.C. Dai, and Ungulidaedalei B.K. Cui, M.L. Han & Y.C. Dai.

To date, 127 taxa of Fomitopsis have been recorded in the database of Index Fungorum and 138 taxa of Fomitopsis have been recorded in the database of MycoBank, however, it includes a large number of synonymous taxa and invalid published names. In the current study, phylogenetic analysis of Fomitopsis was carried out based on the combined sequence dataset of ITS + nLSU + mtSSU + nSSU + RPB2 + TEF rRNA and/or rDNA gene regions. Combining with morphological characters and molecular evidence, four new species, F. resupinata, F. srilankensis, F. submeliae, and F. yimengensis have been discovered.

**MATERIALS AND METHODS**

**Morphological Studies**

The examined specimens were deposited at 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). Morphological descriptions and abbreviations used in this study followed Cui et al. (2019) and Shen et al. (2019).

**DNA Extraction and Sequencing**

The procedures for DNA extraction and polymerase chain reaction (PCR) used in this study were the same as described by Han et al. (2016) and Liu et al. (2019, 2022). The ITS regions were amplified with the primer pairs ITS4 and ITS5, the nLSU regions were amplified with the primer pairs LR0R and LR7, the nSSU regions were amplified with the primer pairs NS1 and NS4, the mtSSU regions were amplified with the primer pairs MS1 and MS2, the RPB2 gene was amplified with the primer pairs fRPB2-f5F and bRPB2-7.1R, and the TEF gene was amplified with the primer pairs EFI-983F and EFI-1567R (White et al., 1990; Matheny, 2005; Rehner and Buckley, 2005).

The PCR cycling schedules for different DNA sequences of ITS, nLSU, nSSU, mtSSU, RPB2, and TEF genes used in this study followed those used in Liu et al. (2019); Shen et al. (2019), Zhu et al. (2019), and Ji et al. (2022) with some modifications. The PCR products were purified and sequenced at Beijing Genomics Institute, China, with the same primers. All newly generated sequences were submitted to GenBank and are listed in Table 1.

**Phylogenetic Analyses**

Sequences were aligned with additional sequences downloaded from GenBank (Table 1) using BioEdit (Hall, 1999) and ClustalX (Thompson et al., 1997). Alignment was manually adjusted to allow maximum alignment and to minimize gaps. Sequence alignment was deposited at TreeBase (submission ID 29193). The sequences of Laetiporus sulphureus (Bull.) Murrill and L. zonatus B.K. Cui & J. Song, obtained from GenBank, were used as outgroups for the phylogenetic analyses of Fomitopsis.

Phylogenetic analyses approaches used in this study followed Sun et al. (2020) and Liu et al. (2021b). The congruences of the 6-genes (ITS, nLSU, nSSU, mtSSU, 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 1,000 homogeneity replicates. Maximum parsimony (MP) analysis was performed in PAUP* version 4.0b10 (Swofford, 2002). Clade robustness was assessed using a bootstrap (BT) analysis with 1,000 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. Maximum Likelihood (ML) analysis was performed in RAxML v.7.2.8 with a GTR + G + I model (Stamatakis, 2006). Bayesian inference

1http://www.treebase.org
| Species name                  | Sample no. | Locality          | GenBank accessions                              |
|------------------------------|------------|-------------------|-------------------------------------------------|
| **Antrodia heteromorpha**    | Dai 12755  | United States     | KP715306 KP715322 KP606009 KP605908 KP610828    |
| **Antrodia serpens**         | Dai 14850  | Poland             | MG787582 MG787624 MG787674 MG787731 MG787798    |
| **Antrodia subserpens**      | Cui 8310   | China              | KP715310 KP715326 MG787677 MG787732 KT895888    |
| **Antrodia tanakae**         | Cui 9743   | China              | KR605814 KR605753 KP606014 KR605914 KP610833    |
| **Brunneoporus cyclopis**    | Miettinen   | Indonesia          | KU866249 MG787672 MG787679 MG787737 MG787802    |
| **Brunneoporus kuzyana**     | JI 0909/37 | Czech Republic     | KU866267 MG787628 MG787690 MG787738 MG787803    |
| **Brunneoporus malicola**    | Cui 7258   | China              | MG787586 MG787631 MG787683 MG787741 MG787806    |
| **B. tenuis**                | Dai 13660  | Indonesia          | KG605808 KG605747 KG606007 KG605906 KG610825    |
| **Daedalea circularis**      | Cui 10125  | China              | KG780411 KP717220 KG605978 KG605875 KG610799    |
| **Daedalea modesta**         | Cui 10124  | China              | KG605791 KG605730 KG605985 KG605882 KG610805    |
| **Daedalea quercina**        | Dai 12659  | Finland            | KP717208 KP717230 KP605990 KG605887 KG610810    |
| **Daedalea radiata**         | Cui 8575   | China              | KP717210 KP717233 KG605991 KG605888 KG610811    |
| **Flavidoporia mellita**     | VS 3315    | Russia             | KC543140 – – – – – –                            |
| **Flavidoporia pulverula**   | LY BR 3450 | France             | JQ700280 JQ700280 – – – – – –                    |
| **Flavidoporia pulvinascens**| X 1372     | Finland            | JQ700280 JQ700280 – – – – – –                    |
| **Fomitopsis abieticola**    | Cui 10521  | China              | MG787586 MG787631 MG787683 MG787741 MG787806    |
| **Fomitopsis abieticola**    | Dai 12755  | United States      | KP715306 KP715322 KP606009 KP605908 KP610828    |
| **Fomitopsis abieticola**    | Cui 10532  | China              | MG787586 MG787631 MG787683 MG787741 MG787806    |
| **Fomitopsis bambusae**      | Cui 10521  | China              | MG787586 MG787631 MG787683 MG787741 MG787806    |
| **Fomitopsis bambusae**      | Dai 13660  | Indonesia          | KG605808 KG605747 KG606007 KG605906 KG610825    |
| **Fomitopsis betulina**      | Cui 10125  | China              | KG780411 KP717220 KG605978 KG605875 KG610799    |
| **Fomitopsis betulina**      | Dai 11449  | China              | KG605791 KG605730 KG605985 KG605882 KG610805    |
| **Fomitopsis bondartsevae**  | X 1207     | China              | JQ700277 JQ700277 – – – – – –                    |
| **Fomitopsis bondartsevae**  | X 1059     | China              | JQ700277 JQ700277 – – – – – –                    |
| **Fomitopsis cana**          | Cui 10125  | China              | MG787586 MG787631 MG787683 MG787741 MG787806    |
| **Fomitopsis cana**          | Dai 13660  | Indonesia          | KG605808 KG605747 KG606007 KG605906 KG610825    |
| **Fomitopsis caribensis**    | Cui 10521  | China              | MG787586 MG787631 MG787683 MG787741 MG787806    |
| **Fomitopsis caribensis**    | Dai 13660  | Indonesia          | KG605808 KG605747 KG606007 KG605906 KG610825    |
| **Fomitopsis durescens**     | Overholts  | United States      | KF397293 KF397295 KF396594 KF396835 – – – – – – |
| **Fomitopsis durescens**     | O 10796    | Venezuela          | KF397292 KF397294 KF396594 KF396835 – – – – – – |
| **Fomitopsis eucalypticola** | Cui 16594  | Australia          | KG605260 KG605110 KG606118 KG606126 KG604767    |
| **Fomitopsis eucalypticola** | Cui 16598  | Australia          | KG605260 KG605110 KG606118 KG606126 KG604767    |
| **Fomitopsis ginkgonis**     | Cui 17170  | China              | MG605263 MG605114 MG606122 MG606130 MG604807    |
| **Fomitopsis ginkgonis**     | Cui 17171  | China              | MG605264 MG605115 MG606123 MG606131 MG604808    |
| **Fomitopsis hengduanensis** | Cui 16259  | China              | MG605263 MG605114 MG606122 MG606130 MG604807    |
| **Fomitopsis hengduanensis** | Cui 17056  | China              | MG605263 MG605114 MG606122 MG606130 MG604807    |
| **Fomitopsis ibericana**     | Dai 6614   | China              | MG787591 MG787637 MG787689 MG787747 MG787812    |
| **Fomitopsis ibericana**     | O 10811    | Italy              | KF605772 KR605711 – – – – – – – – – – – – – – – – |
| **Fomitopsis kesiyae**       | Cui 18437  | Vietnam            | MN148232 OL61249 OL612756 OL612782 MN158175     |
| **Fomitopsis kesiyae**       | Cui 16466  | Vietnam            | MN148232 OL61249 OL612756 OL612782 MN158175     |
| **Fomitopsis massoniana**    | Cui 11304  | China              | MN148232 OL6125 OL612756 OL612782 MN158176      |
| **Fomitopsis massoniana**    | Cui 11299  | China              | MN148232 OL6125 OL612756 OL612782 MN158176      |
| **Fomitopsis meliae**        | Roberts GA | United Kingdom     | KR605775 KR605714 KR605953 KR605848 – – – – – – |
| **Fomitopsis meliae**        | Ryvarden   | Unknown            | KR605775 KR605714 KR605953 KR605848 KR610775    |
| **Fomitopsis mounceae**      | DR-366     | United States      | KF169624 – – – – – – – – – – – – – – – – – – – – |
| **Fomitopsis mounceae**      | JAG-06-19  | United States      | KF169626 – – – – – – – – – – – – – – – – – – – – |
| **Fomitopsis novas**         | Man 9      | Brazil             | MF589766 MF590166 – – – – – – – – – – – – – – – |
| **Fomitopsis novas**         | JI 0609/52-X | China           | KR605779 KR605714 KR605957 KR605835 KR610777     |
| **Fomitopsis ochracea**      | ss 5       | Canada             | KF169609 – – – – – – – – – – – – – – – – – – –– |
| **Fomitopsis ochracea**      | ss 7       | Canada             | KF169610 – – – – – – – – – – – – – – – – – – –– |
TABLE 1 | (Continued)

| Species name                        | Sample no.          | Locality     | GenBank accessions |
|-------------------------------------|---------------------|--------------|-------------------|
|                                     |                     |              | ITS               |
| Fomitopsis ostreiformis            | Cui 18217           | Malaysia     | OL621855          |
|                                     |                     |              | OL621244*         |
| Fomitopsis ostreiformis            | IRET 22             | Gabon        | KY449363          |
| Fomitopsis ostreiformis            | LDMCY 21            | India        | KY111252          |
| Fomitopsis palustris               | Cui 7597            | China        | KP171213           |
|                                     |                     |              | KP171236          |
| Fomitopsis palustris               | Cui 7615            | China        | KP605780           |
|                                     |                     |              | KP605719           |
| Fomitopsis pinicola                | LT 319              | Estonia      | KF169652          |
| Fomitopsis pinicola                | AT Fp 1             | Sweden       | MK028585           |
| Fomitopsis resupinata              | Cui 6697            | China        | OL621842*         |
| Fomitopsis resupinata              | Dai 10819 holotype  | China        | OL621843*         |
|                                     | Fomitopsis roseolaiba | AS 1496     | KT189139          |
|                                     | Fomitopsis schrenkii | JEH-144     | KF169621          |
|                                     |                     | United States|                  |
| Fomitopsis srilankensis            | Dai 19528 holotype  | Sri Lanka    | OL621844*         |
| Fomitopsis srilankensis            | Dai 19539           | Sri Lanka    | OL621845*         |
| Fomitopsis submeliae               | Dai 10035           | China        | KF605774           |
|                                     |                     |              | KF605713           |
| Fomitopsis submeliae               | Dai 18324           | Vietnam      | OL621846*         |
|                                     |                     |              | OL621235*         |
| Fomitopsis submeliae               | Dai 9719            | China        | OL621847*         |
|                                     |                     |              | OL621236*         |
| Fomitopsis submeliae               | Dai 18559 holotype  | Malaysia     | OL621848*         |
| Fomitopsis submeliae               | Cui 6305            | China        | OL621849*         |
|                                     |                     |              | OL621238*         |
| Fomitopsis subpinicola             | Cui 9836 holotype   | China        | MN148249           |
|                                     |                     |              | OL621253*         |
| Fomitopsis subpinicola             | Dai 11206           | China        | MN148252           |
|                                     |                     |              | OL621254*         |
| Fomitopsis subtropica              | Dai 18566           | Brazil       | KT189139          |
|                                     |                     |              | KT189140          |
| Fomitopsis schrenkii               | JEH-150 holotype    | United States| KF169622          |
|                                     |                     |              |                  |
| Fomitopsis seriale               | Dai 1509/5          | Czech Republic| KT995120          |
|                                     |                     |              |                  |
| Fomitopsis serrata                | Dai 7626            | China        | KP605812           |
|                                     |                     |              | KP605750           |
| Fomitopsis subserialis             | Cui 9706            | China        | KF605811           |
|                                     |                     |              | KP605750           |
| Niveoporofomes spraguei            | 4638                | France       | KF605784           |
|                                     |                     |              | KP605723           |
| Niveoporofomes spraguei            | JV 0509/62          | United States| KF605786           |
|                                     |                     |              | KF605725           |
| Rhodofomes cajanderi              | Cui 9888            | China        | KC507156           |
|                                     |                     |              | KC507166           |
| Rhodofomes incarnates             | Cui 10348           | China        | KC844848           |
|                                     |                     |              | KC844853           |
| Rhodofomes rosea                  | Cui 10520           | China        | KC507162           |
|                                     |                     |              | KC507172           |
| Rhodofomes subaelei               | Dai 11877           | China        | KC507160           |
|                                     |                     |              | KC507170           |
| Rhodofomites feei                 | Ryvarden 37603      | Venezuela    | KC844850           |
|                                     |                     |              | KC844855           |
| Rhodofomites ilicogniglua         | Schigel 5193        | Australia    | KF605773           |
|                                     |                     |              | KF605712           |
| Rhodofomites monomitic             | Dai 16894           | China        | KY421733           |
|                                     |                     |              | KY421735           |
| Rubefoimes cystidatius             | Cui 5481            | China        | KF937288           |
|                                     |                     |              | KF937291           |
| Rubefoimes cystidatius             | Yuan 6304           | China        | KF605769           |
|                                     |                     |              | KF605708           |
| Rubefoimes minitupirus             | Rajchenberg 10661   | Argentina    | KF605777           |
|                                     |                     |              | KF605716           |
| Subantarctis juniperina            | G0310/1a            | United States| MG787606           |
|                                     |                     |              | MG787653           |
| Subantarctis uzbekistanica        | Dai 17104           | Uzbekistan   | KX068182           |
|                                     |                     |              | KX068186           |
| Subantarctis uzbekistanica        | Dai 17105           | Uzbekistan   | KX068183           |
|                                     |                     |              | KX068187           |
| Unguldaedalia fragilis            | Cui 10919           | China        | KF937286           |
|                                     |                     |              | KF937290           |

*Newly generated sequences for this study. New species are shown in bold.
(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). The branch support was evaluated with a bootstrapping method of 1,000 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 combined 6-gene sequences dataset for phylogenetic analyses had an aligned length of 4,626 characters including gaps (610 characters for ITS, 1,346 characters for nLSU, 526 characters for mtSSU, 1,009 characters for nSSU, 648 characters for RPB2, 487 characters for TEF), of which 3,113 characters were constant, 240 were variable and parsimony-uninformative, and 1,273 were parsimony-informative. MP analysis yielded 12 equally parsimonious trees (TL = 6,756, CI = 0.366, RI = 0.722, RC = 0.264, HI = 0.634). The best model for the concatenate sequence dataset estimated and applied in the Bayesian inference was GTR + I + G with equal frequency of nucleotides, lset nst = 6 rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). Bayesian analysis resulted in a concordant topology with an average standard deviation of split frequencies = 0.008762. ML analysis resulted in a similar topology as MP and Bayesian analyses, and only the ML topology is shown in Figure 1. The phylogenetic trees inferred from ITS + nLSU + nSSU + mtSSU + RPB2 + TEF gene sequences were obtained from 103 fungal samples representing 65 taxa of Fomitopsis and its related genera within the antrodia clade. Also, 64 samples representing 30 taxa of Fomitopsis clustered together and separated from other genera.

Taxonomy

**Fomitopsis resupinata** B.K. Cui & Shun Liu, sp. nov. (Figures 2A, 3).

MycoBank: MB 842873.

**Diagnosis** — *Fomitopsis resupinata* is characterized by its resupinate basidiomata with cream to buff pore surface when fresh, becoming pinkish buff to honey-yellow upon drying and cylindrical to slightly allantoid basidiospores (7.2–9 × 2.7–3.3 μm).

**Holotype** — CHINA. Hainan Province, Changjiang County, Bawangling Nature Reserve, on fallen trunk of Mangifera indica, 9 May 2009, Dai 10819 (BJFC 010395).

**Etymology** — “resupinata” (Lat.): refers to the resupinate basidiomata.

**Fruiting body** — Basidiomata annual, resupinate, not easily separated from substrate, without odor or taste when fresh, becoming corky and light in weight upon drying; up to 9 cm long, 8.4 cm wide, and 8 mm thick at center. Pore surface cream to buff when fresh, becoming pinkish buff to honey-yellow upon drying; pores round to angular, 4–6 per mm; dissepiments slightly thick, entire. Context very thin, corky, cream to buff, up to 3 mm thick. Tubes concolorous with pore surface, corky, up to 5 mm long. Tissues unchanged in KOH.

**Hyphal structure** — Hyphal system dimitic; generative hyphae bearing clamp connections; skeletal hyphae IKI–, CB–.

http://tree.bio.ed.ac.uk/software/figtree/
**Context** — Generative hyphae infrequent, hyaline, thin-walled, rarely branched, 2–3.4 μm in diam; skeletal hyphae dominant, yellowish brown to cinnamon brown, thick-walled with a narrow lumen to subsolid, unbranched, straight, interwoven, 3.2–5.5 μm in diam.

**Tubes** — Generative hyphae infrequent, hyaline, thin-walled, rarely branched, 1.9–3 μm in diam; skeletal hyphae dominant, yellowish brown to cinnamon brown, thick-walled with a wide to narrow lumen, unbranched, more or less straight, interwoven, 2–5 μm in diam. Cystidia absent; cystidioles occasionally present, fusoid, hyaline, thin-walled, 13.2–22 × 3.2–4.3 μm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 13.5–17.4 × 4.8–6.2 μm; basidioles dominant, similar to basidia but smaller.

**Spores** — Basidiospores cylindrical to slightly allantoid, hyaline, thin-walled, smooth, IKI−, CB−, (7–)7.2–9(–9.5) × (2.6–)2.7–3.3(–3.5) μm, L = 8.14 μm, W = 2.93 μm, Q = 2.46–3.52 (n = 60/2).

**Type of rot** — Brown rot.

**Notes** — Phylogenetically, *Fomitopsis resupinata* was closely related to *F. durescens* (Overh. ex J. Lowe) Gilb. & Ryvarden, *F. nivosa* and *F. ostreiformis* (Berk.) T. Hatt (*Figure 1*). They share similar sized pores, but *F. durescens* differs in its pileate basidiomata with a white to cream pore surface when fresh, ochraceous when dry, smaller and narrower cylindrical basidiospores (6–8 × 1.5–2.5 μm; Gilbertson and Ryvarden, 1986); *F. nivosa* differs by having pileate basidiomata with a cream to pale sordid brown or tan pore surface, and has a...
distribution in Asia, North America, and South America (Núñez and Ryvarden, 2001; Han et al., 2016); *F. ostreiformis* differs in its effused reflexed to pileate basidiomata, soft when fresh, hard when dry, a trimitic hyphal system, smaller and cylindrical basidiospores (4.2–5.6 × 1.4–2.6 μm; De, 1981). *Fomitopsis bambusae* Y.C. Dai, Meng Zhou & Yuan Yuan and *F. cana* B.K. Cui, Hai J. Li & M.L. Han also distribute in Hainan Province of China, but *F. bambusae* differs by having bluish-gray to pale mouse-gray pore surface when fresh, becoming mouse-gray to dark gray when dry, smaller pores (6–9 per mm), smaller and cylindrical to oblong ellipsoid basidiospores (4.2–6.1 × 2–2.3 μm), and grows on bamboo (Zhou et al., 2021); *F. cana* differs by having cream to straw colored pore surface when young which becoming mouse-gray to dark gray with age, a trimitic hyphal system, smaller and cylindrical to oblong-ellipsoid basidiospores (5–6.2 × 2.1–3 μm; Li et al., 2013).

Additional specimen (paratype) examined — CHINA. Hainan Province, Wanning County, on fallen angiosperm trunk, 14 May 2009, *Cui* 6697 (BJFC 004551).
**Fomitopsis srilankensis** B.K. Cui & Shun Liu, sp. nov. (Figures 2B,C, 4).

MycoBank: MB 842874.

**Diagnosis** — *Fomitopsis srilankensis* is characterized by its resupinate to effused-reflexed or pileate basidiomata with pale mouse-gray to honey-yellow pileal surface when dry, buff to cinnamon-buff pore surface when dry, and cylindrical basidiospores (5.5–6.6 × 1.9–2.5 µm).

**Holotype** — Sri Lanka. Wadduwa, South Bolgoda Lake, on angiosperm stump, February 28, 2018, Dai 19539 (BJFC 031218).

**Etymology** — “srilankensis” (Lat.): refers to the species occurrence in Sri Lanka.

**Fruiting body** — Basidiomata annual, resupinate to effused-reflexed or pileate, without odor or taste, becoming corky and light in weight upon drying. Pilei applanate, semicircular to elongated, projecting up to 2.5 cm, 1.3 cm wide, and 7 mm thick at
base; resupinate part up to 8.6 cm long, 2.8 cm wide and 1.8 mm thick at center. Pileal surface pale mouse-gray to honey-yellow when dry, glabrous, sulcate, azonate; margin obtuse, concolorous with the pileal surface. Pore surface buff to cinnamon-buff when dry; pores round to angular, 5ñ8 per mm; dissepiements thick, entire. Context cream to pinkish buff, corky, up to 4 mm thick. Tubes concolorous with pore surface, corky, up to 3 mm long. Tissues unchanged in KOH.

FIGURE 5 | Microscopic structures of Fomitopsis submeliae (Holotype, Dai 18569). (A) Basidiospores. (B) Basidia and basidioles. (C) Cystidioles. (D) Hyphae from trama. (E) Hyphae from context. Drawings by: Shun Liu.
**Hyphal structure** — Hyphal system dimitic; generative hyphae bearing clamp connections; skeletal hyphae IKI−, CB−.

**Context** — Generative hyphae infrequent, hyaline, thin-walled, rarely branched, 2–3.4 μm in diam; skeletal hyphae dominant, yellowish brown to cinnamon brown, thick-walled with a wide to narrow lumen, occasionally branched, more or less straight, interwoven, 2.4–5.8 μm in diam.

**Tubes** — Generative hyphae infrequent, hyaline, thin-walled, occasionally branched, 1.9–3 μm in diam; skeletal hyphae dominant, yellowish brown to cinnamon brown, thick-walled with a wide to narrow lumen, occasionally branched, more or less straight, interwoven, 2–5 μm in diam. Cystidia absent; cystidioles occasionally present, fusoid, hyaline, thin-walled, 10.5–15.5 × 2.4–3.2 μm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 8.9–15.8 × 4.8–6.2 μm; basidioles dominant, similar to basidia but smaller.

**Spores** — Basidiospores cylindrical, hyaline, thin-walled, smooth, IKI−, CB−, (5.3–)5.5–6.6(−6.7) × (1.7–)1.9−2.5 μm, L = 6.11 μm, W = 2.16 μm, Q = 2.52–2.96 (n = 60/2).

**Type of rot** — Brown rot.

**Notes** — In the phylogenetic tree, *Fomitopsis srilankensis* grouped together with *F. cana*, *F. meliae* (Underw.) Gilb. and *F. submeliae* (Figure 1). Morphologically, they share similar sized pores, but *F. cana* differs in having pale mouse-gray to dark gray pileal surface, cream to straw colored pore surface when young and turning mouse-gray to dark gray with age, a trimitic hyphal system and wider basidiospores (5–6.2 × 2.1–3 μm; Li et al., 2013); *F. meliae* differs in having pileate basidiomata, glabrous to minutely tomentose pileal surface, ochraceous pore surface and larger basidiospores (6–8 × 2.5–3 μm; Gilbertson, 1981; Núñez and Ryvarden, 2001); *F. submeliae* differs from *F. srilankensis* by its cream pileal surface when fresh, becoming buff to buff yellow when dry, cream to pinkish buff pore surface when fresh, becoming cream to clay-buff when dry and small basidiospores (4–5 × 1.9–2.4 μm).

Additional specimen (paratype) examined — Sri Lanka. Wadduwa, South Bolgoda Lake, on fallen angiosperm trunk, February 28, 2018, Dai 19528 (BJFC IFP 031207).

**Fomitopsis submeliae** B.K. Cui & Shun Liu, sp. nov. (Figures 2D, 5).

**MycoBank:** MB 842875.

**Diagnosis** — *Fomitopsis submeliae* is characterized by its effused-reflexed basidiomata with several small imbricate pilei protruding from a large resupinate part, pale mouse-gray to grayish brown pileal surface when dry, cream to clay-buff pore surface when dry, and cylindrical to oblong-ellipsoid basidiospores (4–5 × 1.9–2.4 μm).

**Holotype** — MALAYSIA. Kuala Lumpur, Forest Eco-Park, on fallen angiosperm trunk, 14 April 2018, Dai 18559 (BJFC 0026848).

**Etymology** — “*submeliae*” (Lat.): refers to the new species resembling *Fomitopsis meliae* in morphology.

**Fruiting body** — Basidiomata annual, effused-reflexed with several small imbricate pilei protruding from a large resupinate part, inseparable from the substrate, corky, without odor or taste when fresh, corky to fragile and light in weight when dry. Single pilei up to 2 cm, 3.8 cm wide, and 6 mm thick at base; resupinate part up to 12 cm long, 4.5 cm wide, and 2.4 mm thick at center. Pileal surface cream when fresh, becoming buff to buff yellow when dry, rough, azonate; margin cream to buff, acute, incurved. Pore surface cream to pinkish buff when fresh, becoming cream to clay-buff when dry; pores round to angular, 4–7 per mm; dissepiments thick, entire to slightly lacerate. Context cream to buff, corky, up to 4 mm thick. Tubes concolorous with pore surface, corky to fragile, up to 2 mm long. Tissues unchanged in KOH.

**Hyphal structure** — Hyphal system dimitic; generative hyphae bearing clamp connections; skeletal hyphae IKI−, CB−.

**Context** — Generative hyphae infrequent, hyaline, thin-walled, rarely branched, 2–3.5 μm in diam; skeletal hyphae dominant, hyaline to pale yellowish, thick-walled with a wide to narrow lumen, rarely branched, more or less straight, interwoven, 2.6–6.4 μm in diam.

**Tubes** — Generative hyphae infrequent, hyaline, thin-walled, occasionally branched, 1.8–3 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a wide to narrow lumen, rarely branched, more or less straight, interwoven, 2–5 μm in diam. Cystidia absent; cystidioles occasionally present, fusoid, hyaline, thin-walled, 14.5–18 × 3.2–5 μm. Basidia clavate, bearing four sterigmata and a basal clamp connection, 15.8–21.5 × 4.8–6.5 μm; basidioles dominant, similar to basidia but smaller.

**Spores** — Basidiospores cylindrical to oblong-ellipsoid, hyaline, thin-walled, smooth, IKI−, CB−, (3.8–)4–5(–5.2) × 1.9–2.4(–2.6) μm, L = 4.49 μm, W = 2.11 μm, Q = 1.92–2.42 (n = 90/3).

**Type of rot** — Brown rot.

**Notes** — Five samples of *Fomitopsis submeliae* from China, Malaysia, and Vietnam formed a highly supported subgroup (99% ML, 100% MP, 1.00 BPP), and then grouped with *F. cana*, *F. meliae* and *F. srilankensis* (Figure 1). Morphologically, *F. cana* differs by having effused-reflexed and grayish basidiomata, pale mouse-gray to dark gray pileal surface, a trimitic hyphal system and larger basidiospores (5–6.2 × 2.1–3 μm; Li et al., 2013); *F. meliae* differs in having pileate basidiomata with an ochraceous pore surface and larger basidiospores (6–8 × 2.5–3 μm; Gilbertson, 1981; Núñez and Ryvarden, 2001); *F. srilankensis* differs in its pale mouse-gray to honey-yellow pileal surface, buff to cinnamon-buff pore surface when dry and larger basidiospores (5.5–6.6 × 1.9–2.5 μm). *Fomitopsis subtropica* B.K. Cui & Hai J. Li also distributes in China, Malaysia, and Vietnam, but *F. subtropica* differs from *F. submeliae* by having smaller pores (6–9 per mm) and smaller basidiospores (3.2–4 × 1.8–2.1 μm), a trimitic hyphal system (Li et al., 2013); in addition, it is distant from *F. submeliae* in the phylogenetic analyses (Figure 1).

Additional specimens (paratypes) examined — CHINA. Hainan Province, Baoting County, Tropical Garden, on fallen angiosperm trunk, May 27, 2008, Dai 9719 (IFP 007971); Qionghzhong County, Limushan Forest Park, on fallen angiosperm trunk, 24 May 2008, Dai 9544 (BJFC 007830); on rotten angiosperm wood, May 24, 2008, Dai 9535 (BJFC 010339); Dai 9543 (BJFC 010338); on angiosperm wood, May 24, 2008, Dai 9525 (BJFC 007818). VIETNAM. Hochiminh, Botanic Garden, on angiosperm stump, October 12, 2017, Dai 18324 (BJFC 025847).
**Fomitopsis yimengensis** B.K. Cui & Shun Liu, sp. nov. (Figures 2E,F, 6).

MycoBank: MB 842876.

**Diagnosis** — *Fomitopsis yimengensis* is characterized by its pileate, solitary or imbricate basidiomata with pinkish buff, clay-buff to grayish-brown pileal surface, cream to pale cinnamon pore surface, thin-walled to slightly thick-walled generative hyphae in context, cylindrical basidiospores (6–7.2 × 2–3 μm).

**Holotype** — **CHINA**. Shandong Province, Mengyin County, on stump of *Pinus* sp., July 28, 2007, *Cui 5027* (BJFC 003068).

**Etymology** — “yimengensis” (Lat.): refers to the species distributed in Yimeng Mountains.

**Basidiomata** — Basidiomata annual, pileate, solitary or imbricate, without odor or taste when fresh, becoming hard corky and light in weight when dry. Pilei semicircular to flabelliform, projecting up to 2.8 cm long, 5.7 cm wide, and 1.7 cm thick.
at base. Pileal surface pinkish buff, clay-buff to grayish-brown, glabrous or with irregular warts, azonate; margin obtuse, cream to honey-yellow. Pore surface cream to pale cinnamon; pores round, 4–6 per mm; dissepiments thick, entire. Context cream to buff-yellow, corky, up to 1.2 cm thick. Tubes concolorous with pore surface, hard corky, up to 5 mm long. Tissues unchanged in KOH.

Hyphal structure — Hyphal system dimitic; generative hyphae bearing clamp connections; skeletal hyphae IKI-, CB-.

Context — Generative hyphae infrequent, hyaline, thin-walled, to slightly thick-walled, occasionally branched, 2.2–4 µm in diam; skeletal hyphae dominant, yellowish brown to cinnamon brown, thick-walled with a wide to narrow lumen, occasionally branched, straight, 2.2–6.2 µm in diam.

Tubes — Generative hyphae infrequent, hyaline, thin-walled, occasionally branched, 1.9–3.3 µm in diam; skeletal hyphae dominant, hyaline to pale yellowish, thick-walled with a wide to narrow lumen, rarely branched, more or less straight, 1.9–4 µm in diam. Cystidia absent, but fusoid cystidioles occasionally present, hyaline, thin-walled, 13.8–18 × 2.8–4.2 µm. Basidia clavate, with a basal clamp connection and four sterigmata, 15.5–18 × 4.9–6.5 µm; basidioles dominant, similar to basidia but smaller.

Spores — Basidiospores cylindrical, hyaline, thin-walled, smooth, IKI-, CB-, 6–7.2 × 2–3(–3.1) µm, L = 6.64 µm, W = 2.71 µm, Q = 2.13–2.78 (n = 90/3).

Type of rot — Brown rot.

Notes — Three samples of *F. yimengensis* were successfully sequenced and formed a well-supported lineage (93% ML, 97% MP, 1.00 BPP) and then grouped with *F. caribensis* B.K. Cui & Shun Liu and *F. palustris* (Berk. & M.A. Curtis) Gilb. & Ryvarden (*Figure 1*). Morphologically, *F. caribensis* differs by having cream to pinkish buff pore surface when dry, round to angular and smaller pores (6–9 per mm), growth on angiosperm trees and distribution in the Caribbean regions (Liu et al., 2019); *F. palustris* differs in having malodorous fresh fruiting bodies, larger pores (2–4 per mm) and basidia (24–28 × 6–7 µm), and growth on angiosperm trees (Núñez and Ryvarden, 2001). *Fomitopsis yimengensis* and *F. bondartsevae* (Spirin) A.M.S. Soares & Gibertoni have similar basidiospores, but *F. bondartsevae* differs from *F. yimengensis* by having effused reflexed to plicate basidiomata, larger pores (2–3 per mm), a trimitic hyphal system and growth on *Tilia cordata* (Spirin, 2002). *Fomitopsis iberca* Melo & Ryvarden also grows on *Pinus* sp., but it differs from *F. yimengensis* by having larger pores (3–4 per mm), a trimitic hyphal system, larger cystidioles (20–27 × 4–5–5 µm), and has a distribution in Europe (Melo and Ryvarden, 1989).

Additional specimens (paratypes) examined — CHINA. Shandong Province, Mengyin County, Dongchamning, on stump of *Pinus* sp., July 28, 2007, Cui 5031 (BJFC 003072); Mengyin County, Mengshan Forest Park, on fallen trunk of *Pinus* sp., August 6, 2007, Cui 5111 (BJFC 003152).

**DISCUSSION**

In our current phylogenetic analyses, 30 species of *Fomitopsis* grouped together and formed a highly supported lineage (100% ML, 100% MP, 1.00 BPP; *Figure 1*). *Fomitopsis bondartsevae*, *F. caribensis*, *F. daurescens*, *F. ginkgonis* B.K. Cui & Shun Liu, *F. hemitephra* (Berk.) G. Cunn., *F. iberca*, *F. nivoasa*, *F. ostreiformis*, *F. palustris* and the two new species from China, viz., *F. resupinata*, *F. yimengensis* grouped together with high support (100% ML, 100% MP, 1.00 BPP; *Figure 1*); *F. cana*, *F. meliae* and the two new species, viz., *F. srilankensis*, *F. submeliae* formed a highly supported group (100% ML, 100% MP, 1.00 BPP; *Figure 1*); *F. roseoalba* A.M.S. Soares, Ryvarden & Gibertoni and *F. subtropica* formed a highly supported group (100% ML, 100% MP, 1.00 BPP; *Figure 1*); 10 species of the *F. pinicola* complex grouped together and formed a well-supported lineage (100% ML, 100% MP, 1.00 BPP) and related to *F. betulina* (*Figure 1*); *F. bambusae*, *F. eucalypticola* B.K. Cui & Shun Liu formed separate lineages, respectively (*Figure 1*).

In addition, the current phylogenetic analyses also showed that *Fomitopsis* and other related brown-rot fungal genera clustered together within the antrodia clade, which are consistent with previous studies (Ortiz-Santana et al., 2013; Han et al., 2016; Liu et al., 2019, 2021a; Zhou et al., 2021).

*Fomitopsis* is a genus with important ecological functions and economic values. Since the establishment of the *Fomitopsis*, many new species and combinations had been described or proposed, and some *Fomitopsis* species have been removed to other genera. The taxonomic concept of *Fomitopsis* has been a subject of debate for a long time. Some species which previously belong to *Fomitopsis* are suggested to be excluded from the genus, such as, *F. concava* (Cooke) G. Cunn. (Cunningham, 1950), *F. maire* (G. Cunn.) P. K. Buchanan & Ryvarden (Buchanan and Ryvarden, 1988), and *F. zuluensis* (Wakef.) Ryvarden (Ryvarden, 1972). Although molecular data are not available for these species, their thick-walled basidiospores are quite different from the typical features of *Fomitopsis*. *Fomitopsis sanmingensis* is treated as a synonym of *F. pseudopetchii* (Lloyd) Ryvarden (Ryvarden, 1972). Although some species lack molecular data, the morphological descriptions are consistent with the *Fomitopsis* and remain in *Fomitopsis* according to previous studies, viz., *F. epileucina* (Pilát) Ryvarden & Gilb. (Ryvarden and Gilbertson, 1993), *F. minuta* Aime & Ryvarden (Ryvarden, 1972), *F. pseudopetchii* (Lloyd) Ryvarden (Ryvarden, 1972), *F. scortea* (Corner) T. Hatt. (Hattori, 2003), *F. singularis* (Corner) T. Hatt. (Hattori, 2003) and *F. subvinosa* (Corner) T. Hatt. & Sotome (Hattori and Sotome, 2013).

**Pilatoporus** Kottl. & Pouzar was established by Kotlába and Pouzar (1990) and typified by *P. palustris* (Berk. & M.A. Curtis) Kottl. & Pouzar based on the presence of pseudoskeletal hyphae with conspicuous clamp connections. Zmitrovich (2018) transferred *Fomitopsis cana*, *F. daurescens*, *F. hemitephra*, *F. ostreiformis* and *F. subtropica* to *Pilatoporus*. However, there are no significant differences that can be found between *Pilatoporus* and *Fomitopsis* in morphology, and they grouped together in phylogeny (*Figure 1*). Thus, *Pilatoporus* is not supported as an independent genus and is considered as a synonym of *Fomitopsis* as previous studies show (Kim et al., 2005, 2007; Han et al., 2016).

During the investigations of *Fomitopsis*, the information of distribution areas and host trees were also obtained (Table 2), and
### TABLE 2 | The main ecological habits of *Fomitopsis* with an emphasis on distribution areas, host trees, and fruiting body types.

| Species                  | Type locality | Distribution in the world | Distribution in China | Geographical elements | Host | Fruiting body types | References                     |
|--------------------------|---------------|---------------------------|-----------------------|-----------------------|------|---------------------|--------------------------------|
| *Fomitopsis abieticola*  | China         | Asia (China)              | Yunnan (plateau humid climate) | Endemic to China      | Gymnosperm (Abies) | Pileate             | Liu et al., 2021a               |
| *Fomitopsis bambusae*    | China         | Asia (China)              | Hainan (tropical monsoon climate) | Endemic to China      | Angiosperm (bamboo) | Resupinate to effused-reflexed or pileate | Zhou et al., 2021               |
| *Fomitopsis betulina*    | Norway        | Asia (China, Japan, Korea), Europe (Austria, Belgium, Czech Republic, Finland, Germany, Italy, Lithuania, Norway, Russia, Switzerland, United Kingdom), North America (Canada, United States) | Beijing, Heilongjiang, Inner Mongolia, Jilin, Shaanxi, Sichuan, Xizang, Xinjiang, Yunnan (temperate to subtropical) | Cosmopolitan | Angiosperm (Betula) | Pileate | Ryvarden and Melo, 2014; present study |
| *Fomitopsis bondartsevae*| Russia        | Asia (China, Europe (Russia)) | East Asia-Europe | Angiosperm (Prunus, Tilia) | Pileate to effused-reflexed | Soares et al., 2017 |
| *Fomitopsis cana*        | China         | Asia (China)              | Hainan (tropical monsoon climate) | Endemic to China      | Angiosperm (Delonix) | Resupinate to effused-reflexed or pileate | Li et al., 2013 |
| *Fomitopsis caribensis*  | Puerto Rico   | North America (Puerto Rico) | North America | Angiosperm (undetermined) | Pileate | Liu et al., 2019 |
| *Fomitopsis durescens*   | United States | North America (United States), South America (Venezuela) | North America-South America | Angiosperm (Fagus) | Pileate | Gilbertson and Ryvarden, 1986 |
| *Fomitopsis eucalypticola* | Australia     | Oceania (Australia)       | Oceania | Angiosperm (Eucalyptus) | Pileate to effused-reflexed | Liu et al., 2019 |
| *Fomitopsis ginkgonis*   | China         | Asia (China)              | Hubei (subtropical) | Endemic to China      | Gymnosperm (Ginkgo) | Pileate | Liu et al., 2019 |
| *Fomitopsis hemitephra*  | New Zealand   | Oceania (Australia, New Zealand, Samoa) | Oceania | Angiosperm (Nothofagus) | Pileate | Cunningham, 1965 |
| *Fomitopsis hengduanensis* | China         | Asia (China)              | Yunnan (temperate to plateau continental climate) | Endemic to China      | Gymnosperm (Picea) | Pileate | Liu et al., 2021a |
| *Fomitopsis iberica*     | Portugal      | Asia (China), Europe (Austria, France, Italy, Portugal) | Beijing (temperate continental monsoon climate) | Europe | Angiosperm (Betula, Broussonetia, Prunus), Gymnosperm (Pinus) | Pileate | Melo and Ryvarden, 1989; present study |
| *Fomitopsis kesiyae*     | Vietnam       | Asia (Vietnam)            | | | | | Liu et al., 2021a |
| *Fomitopsis massoniana*  | China         | Asia (China)              | Fujian, Guandong (subtropical) | Endemic to China      | Gymnosperm (Pinus) | Effused-reflexed to pileate | Liu et al., 2021a |
| *Fomitopsis meliae*      | United States | Europe (United Kingdom), North America (United States) | Europe-North America | Angiosperm (Prunus persica) | Pileate | Gilbertson, 1981 |
| *Fomitopsis mounceae*    | Canada        | North America (Canada, United States) | North America | Angiosperm (Betula, Populus), Gymnosperm (Abies, Picea, Tsuga) | Pileate | Haight et al., 2019 |
| *Fomitopsis nivosa*      | Brazil        | Asia (China, Japan), South America (Brazil), North America (Guatemala, United States) | Guangxi, Sichuan (alpine plateau to subtropical) | Cosmopolitan | Angiosperm (Betula, Cinnamomum, Plum, Populus, Prunus) | Pileate | Gilbertson and Ryvarden, 1986 |

(Continued)
the geographical locations of the *Fomitopsis* species distributed in the world and in China are indicated on the map, respectively (Figures 7, 8). The species of *Fomitopsis* have a wide range of distribution (distributed in Asia, Europe, North America, Oceania, South America; Table 2) and host type (grows on many different gymnosperm and angiosperm trees; Table 2). With regard to the geographical distribution, we found that 20 species of *Fomitopsis* are distributed in Asia, five in Europe, 10 in North America, three in South America and two in Oceania (Figure 7 and Table 2). Among the 20 species of *Fomitopsis* distributed in Asia, 17 are distributed in China, and 10 species are endemic to China (Figure 8 and Table 2). When analyzing the host type of the species of *Fomitopsis*, we found that all the species of *F. pinicola* complex can grow on gymnosperm trees.

### TABLE 2 (Continued)

| Species            | Type locality | Distribution in the world | Distribution in China | Geographical elements | Host | Fruiting body types | References |
|--------------------|---------------|---------------------------|-----------------------|-----------------------|------|---------------------|------------|
| *Fomitopsis ochracea* | Canada        | North America (Canada, United States) | North America | Angiosperm (Betula, Populus), Gymnosperm (Abies, Picea, Tsuga) | Pileate | Stokland and Ryvarden, 2008; Haight et al., 2019 |
| *Fomitopsis ostreiformis* | Philippines | Asia (Indonesia, Malaysia, Philippines, Thailand) | Southeast Asia | Angiosperm (Cocos) | Effused-reflexed to pileate | De, 1981; Hattori, 2003; Present study |
| *Fomitopsis palustris* | United States | Asia (China), North America (United States) | China, Hubei, Sichuan (temperate to subtropical) | East Asia-North America | Angiosperm (Algitarum, Ligustrum, Mangifera, Prunus, Tilia) | Effused-reflexed to pileate | Corner, 1989; Hattori, 2003; present study |
| *Fomitopsis pinicola* | Sweden        | Europe (Belgium, Czech Republic, Estonia, Finland, France, Italy, Poland, Russia, Sweden) | North America | Angiosperm (undetermined), Gymnosperm (Picea, Pinus) | Pileate | Ryvarden and Melo, 2014; Haight et al., 2019; Present study |
| *Fomitopsis resupinata* | China         | Asia (China) | Hainan (tropical monsoon climate) | Endemic to China | Angiosperm (undetermined) | Resupinate | Present study |
| *Fomitopsis roseoalba* | Brazil        | North America (United States), South America (Venezuela) | South America | Angiosperm (undetermined) | Pileate, resupinate to effused-reflexed | Tibpromma et al., 2017 |
| *Fomitopsis schrenkii* | United States | North America (United States) | North America | Angiosperm (undetermined), Gymnosperm (Abies, Picea, Pinus, Pseudotsuga) | Pileate | Haight et al., 2019 |
| *Fomitopsis srilankensis* | Sri Lanka | Asia (Sri Lanka) | South Asia | Angiosperm (undetermined) | Resupinate to effused-reflexed or pileate | Present study |
| *Fomitopsis submeliae* | China         | Asia (China, Malaysia, Vietnam) | East Asia | Angiosperm (undetermined) | Resupinate to effused-reflexed or pileate | Present study |
| *Fomitopsis subpinicola* | China         | Asia (China) | Heilongjiang, Inner Mongolia, Jilin (boreal to temperate) | Endemic to China | Gymnosperm (Pinus) | Pileate | Liu et al., 2021a |
| *Fomitopsis subtropica* | China         | Asia (China, Malaysia, Singapore, Vietnam) | East Asia | Angiosperm (Castanoposis) | Resupinate to effused-reflexed or pileate | Li et al., 2013; present study |
| *Fomitopsis tianshanensis* | China         | Asia (China) | Xinjiang (alpine plateau to continental climate) | Endemic to China | Gymnosperm (Picea) | Effused-reflexed to pileate | Liu et al., 2021a |
| *Fomitopsis yimengensis* | China         | Asia (China) | Shandong (temperate) | Endemic to China | Gymnosperm (Pinus) | Pileate | Present study |

New species are shown in bold.
However, of the remaining species, only *F. ginkgonis*, *F. iberica* and *F. yimengensis* can grow on gymnosperm trees (Figure 1 and Table 2). Furthermore, some species of *Fomitopsis* have limited distribution areas and host specialization. In East Asia, *F. abieticola* is distributed in southwestern China and grows on *Abies* sp. (Liu et al., 2021a); *F. bambusae* is distributed in Hainan Province of China and grows on bamboo (Zhou et al., 2021); *F. cana* is distributed in Hainan Province of China and grows on *Delonix* sp. or other angiosperm wood (Zhou et al., 2021); *F. cana* is distributed in Hainan Province of China and grows on bamboo (Zhou et al., 2021); *F. ginkgonis* is distributed in subtropical areas of Hubei Province of China and grows on *Ginkgo* sp. (Liu et al., 2019); *F. hengduanensis* is distributed in high altitude areas of the Hengduan Mountains of southwestern China and grows mostly on *Picea* sp. and other gymnosperm wood (Liu et al., 2021a); *F. kesiyae* is distributed in subtropical areas of southeastern China and grows mainly on *Pinus* sp. and other gymnosperm wood (Liu et al., 2021a); *F. massoniana* is distributed in tropical areas of Vietnam and grows only on *Pinus kesiya* (Liu et al., 2021a); *F. massoniana* is distributed in subtropical areas of northeastern China and grows mainly on *Pinus koraiensis* and occasionally on other gymnosperm or angiosperm wood (Liu et al., 2021a); *F. tianshanensis* is distributed in Tianshan Mountains of northwestern China and only grows on *Picea schrenkiana* (Liu et al., 2021a); *F. yimengensis* is distributed in Shandong Province of China and grows on *Pinus* sp. In North America, *F. caribensis* is distributed in the Caribbean regions and grows on angiosperm wood (Liu et al., 2019). In Oceania, *Fomitopsis eucalypticola* is distributed in Australia and grows on *Eucalyptus* sp. (Liu et al., 2019).

Fruiting body is one of the most significant morphological structures of fungi, which can protect developing reproductive organs and promote spore diffusion (Nagy et al., 2017). Previous studies have shown that the evolution of fruiting body types of higher taxonomic level (at or above the order level) in Basidiomycota have a trend from resupinate to pileate-stipitate (Hibbett and Binder, 2002; Hibbett, 2004; Nagy et al., 2017; Varga et al., 2019), however, few studies have explored the evolution of fruiting body types of specific families or genera. According to our observation of the fruiting body types of the species of *Fomitopsis*, we found that the species of *Fomitopsis* mainly with pileate or effused-reflexed basidiomata, and only *F. resupinata* produces completely resupinate basidiomata in the genus (Figure 1 and Table 2). The fruiting body types of *Fomitopsis* are similar to those of some genera of Fomitopsidaceae, such as...
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**Figure 8** | The geographical locations of the *Fomitopsis* species distributed in China.

*Buglossoporus* Kotl. & Pouzar, *Daedalea* Pers. and *Rhodofomes* (Han et al., 2016). We may draw a preliminary hypothesis that the ancestral of the *Fomitopsis* originated in Eurasia, with a pileate basidiomata and growth on gymnosperm trees. The current research cannot accurately reveal the ecological, morphological, and biogeographical evolution of *Fomitopsis*, which needs further study.

**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: https://www.ncbi.nlm.nih.gov/genbank/, OL621842, OL621843, OL621844, OL621845, OL621846, OL621847, OL621848, OL621849, OL621850, OL621851, OL621852, OL621231, OL621232, OL621233, OL621234, OL621235, OL621236, OL621237, OL621238, OL621239, OL621240, OL621241, OL621245, OL621746, OL621747, OL621748, OL621749, OL621750, OL621751, OL621752, OL621839, OL621840, OL621841, OL621768, OL621769, OL621770, OL621771, OL621772, OL621773, OL621774, OL621775, OL621776, OL621777, OL621778, OL588960, OL588961, OL588962, OL588963, OL588964, OL588965, OL588966, OL588967, OL588968, OL588971, OL588972, OL588973, OL588974, OL588975, OL588976, OL588977, OL588978, OL588979, OL588980, and OL588981.

**Author Contributions**

B-KC designed the experiment. SL, D-MW, and B-KC prepared the samples and drafted the manuscript. SL, C-GS, T-MX, and XJ conducted the molecular experiments and analyzed
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