



## OPEN ACCESS

## EDITED BY

Ji-Chuan Kang,  
Guizhou University,  
China

## REVIEWED BY

Victor Manuel Bandala,  
Instituto de Ecología (INECOL), Mexico

Qiang Li,  
Chengdu University,  
China

## \*CORRESPONDENCE

Yu-Cheng Dai  
✉ yuchengdai@bjfu.edu.cn  
Ying-Da Wu  
✉ wydbjfu@163.com

<sup>1</sup>These authors have contributed equally to this work and share first authorship

## SPECIALTY SECTION

This article was submitted to  
Evolutionary and Genomic Microbiology,  
a section of the journal  
Frontiers in Microbiology

RECEIVED 19 November 2022

ACCEPTED 19 January 2023

PUBLISHED 13 February 2023

## CITATION

Zhou H-M, Liu S, Deng X-J, Liu H-G, Xing R, Dai Y-C and Wu Y-D (2023) Two new species of *Antrodia* (Polyporales, Basidiomycota) in western China. *Front. Microbiol.* 14:1102575.  
doi: 10.3389/fmicb.2023.1102575

## COPYRIGHT

© 2023 Zhou, Liu, Deng, Liu, Xing, Dai and Wu. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](#). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

# Two new species of *Antrodia* (Polyporales, Basidiomycota) in western China

Hong-Min Zhou<sup>1†</sup>, Shun Liu<sup>1†</sup>, Xiao-Juan Deng<sup>2</sup>, Hong-Gao Liu<sup>3</sup>, Rui Xing<sup>4</sup>, Yu-Cheng Dai<sup>1\*</sup> and Ying-Da Wu<sup>1,5\*</sup>

<sup>1</sup>Institute of Microbiology, School of Ecology and Nature Conservation, Beijing Forestry University, Beijing, China, <sup>2</sup>College of Biological Science and Engineering, North Minzu University, Yinchuan, China, <sup>3</sup>Faculty of Agronomy and Life Sciences, Zhaotong University, Zhaotong, China, <sup>4</sup>Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, China, <sup>5</sup>China Fire and Rescue Institute, Beijing, China

Two new species of *Antrodia*, *A. aridula* and *A. variispora*, are described from western China. Phylogeny based on a six-gene dataset (ITS+nLSU+nSSU+mtSSU+TEF1+RPB2) demonstrates that samples of the two species form two independent lineages within the clade of *Antrodia* s.s. and are different in morphology from the existing species of *Antrodia*. *Antrodia aridula* is characterized by its annual and resupinate basidiocarps with angular to irregular pores of 2–3 mm each and oblong ellipsoid to cylindrical basidiospores measuring 9–12×4.2–5.3 µm, growing on gymnosperm wood in a dry environment. *Antrodia variispora* is characterized by its annual and resupinate basidiocarps with sinuous or dentate pores with a size of 1–1.5 mm each and oblong ellipsoid, fusiform, pyriform, or cylindrical basidiospores measuring 11.5–16×4.5–5.5 µm, growing on the wood of *Picea*. The differences between the new species and morphologically similar species are discussed in this article.

## KEYWORDS

fomitopsidaceae, multigene, taxonomy, wood-inhabiting fungi, phylogeny

## Introduction

*Antrodia* P. Karst. is one of the major groups of fungi causing brown rot, mostly on gymnosperm wood in the Northern Hemisphere ([Gilbertson and Ryvarden, 1986](#); [Núñez and Ryvarden, 2001](#); [Ryvarden and Melo, 2017](#); [Wu et al., 2022](#)), and traditionally, the members of the genus are characterized by annual to perennial, leathery, mostly light colored, resupinate to effused-reflexed or distinctly pileate basidiocarps; a dimitic hyphal structure or a few species with a monomitic hyphal system; generative hyphae with clamp connections; skeletal hyphae negative in Melzer's reagent; some species with amyloid skeletal hyphae; and hyaline, thin-walled basidiospores which are negative in Melzer's reagent and cotton blue ([Spirin et al., 2013](#); [Liu et al., 2022](#)). Recent studies demonstrated that this genus is polyphyletic including 12 small and monophyletic genera ([Ortiz-Santana et al., 2013](#); [Spirin et al., 2013](#); [Runnel et al., 2019](#); [Liu et al., 2022](#)), and *Antrodia* s. str. has been delimited as the species grouped around *Antrodia serpens* (Fr.) P. Karst. within the antrodia clade of Polyporales ([Hibbett and Donoghue, 2001](#); [Spirin et al., 2013](#)).

During an investigation on polypores in western China, five resupinate, cream to buff specimens were collected from Qinghai Province and Inner Mongolia Autonomous Region, western China. Macromorphology and the ecology of brown rot on gymnosperm wood showed that they belong to *Antrodia* s.l., and further morphological examination and phylogenetic analysis indicated that they represent two undescribed species of *Antrodia* s. str. Thus, we describe them as two new species in the present article.

TABLE 1 PCR primers used in this study.

| Gene  | Primer   | Primer sequences (5'-3')         | References                 |
|-------|----------|----------------------------------|----------------------------|
| ITS   | ITS5     | GGA AGT AAA AGT CGT AAC AAG G    | White et al. (1990)        |
|       | ITS4     | TCC TCC GCT TAT TGATAT GC        | White et al. (1990)        |
| nLSU  | LR0R     | ACC CGC TGA ACT TAA GC           | Vilgalys and Hester (1990) |
|       | LR7      | TAC TAC CAC CAA GAT CT           | Vilgalys and Hester (1990) |
| nSSU  | MS1      | CAG CAG TCA AGA ATATTA GTC AAT G | White et al. (1990)        |
|       | MS2      | GCG GAT TAT CGA ATT AAATAA C     | White et al. (1990)        |
| mtSSU | MS1      | CAG CAG TCA AGA ATATTA GTC AAT G | White et al. (1990)        |
|       | MS2      | GCG GAT TAT CGA ATT AAATAA C     | White et al. (1990)        |
| TEF   | 983F     | GCY CCY GGH CAY CGT GAY TTY AT   | Rehner and Buckley (2005)  |
|       | 1567R    | ACH GTR CCR ATA CCA CCR ATC TT   | Rehner and Buckley (2005)  |
| RPB2  | RPB2-5F  | GAY GAY MGW GAT CAY TTY GG       | Liu et al. (1999)          |
|       | RPB2-7cR | ATG GGY AAR CAA GCY ATG GG       | Liu et al. (1999)          |

## Materials and methods

### Morphological studies

All studied specimens are deposited in the herbarium of the Institute of Microbiology, Beijing Forestry University (BJFC). Morphological descriptions are based on field notes and microscopic examinations of voucher specimens. Special color terms are based on Anonymous (1969) and Petersen (1996). Microscopic structures refer to Spirin et al. (2013), Chen and Cui (2015), and Liu et al. (2022).

### DNA extraction, amplification, and sequencing

Acetyl trimethylammonium bromide rapid plant genome extraction kit (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to obtain DNA templates from dried specimens and perform the polymerase chain reaction (PCR) according to the manufacturer's instructions with some modifications (Chen and Dai, 2021; Liu et al., 2022). The primers of ITS, including nLSU, nSSU, mtSSU, TEF1, and RPB2, for amplifying the DNA regions are mentioned in Table 1. The PCR procedure for ITS, mtSSU, TEF1, and RPB2 follows Liu et al. (2022). All newly generated sequences have been submitted to GenBank and are listed in Table 2.

### Phylogenetic analysis

A total of 98 samples of *Antrodia* and related taxa were used for phylogenetic analysis in this study (Table 2). *Oligoporus rennyi* (Berk. & Broome) Donk and *Postia lactea* (Fr.) P. Karst. were selected as outgroups for phylogenetic analysis following Liu et al. (2022), based on the combined datasets of the internal transcribed spacer (ITS) region, the large subunit nuclear ribosomal RNA gene (nLSU), the small subunit nuclear ribosomal RNA gene (nSSU), the small subunit mitochondrial rRNA gene sequences (mtSSU), the translation elongation factor 1- $\alpha$  gene (TEF1), and the second subunit of RNA polymerase II (RPB2). Sequences were aligned with MAFFT v. 7 online<sup>1</sup> adjusting the direction of nucleotide sequences

according to the first sequence (accurate enough for most cases), selecting the G-INS-i iterative refinement method (Katoh et al., 2017). The aligned sequences were deposited at TreeBase (submission ID 29874).<sup>2</sup>

The analyses of maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) refer to Liu et al. (2022).

## Results

### Phylogeny

The concatenated dataset included 98 ITS sequences, 90 nLSU sequences, 67 nSSU sequences, 64 mtSSU sequences, 70 TEF1 sequences, and 66 RPB2 sequences representing 54 taxa. There are 4,608 characters in the dataset, including 3,044 were constant, 144 were variable and parsimony-uninformative, and 1,420 were parsimony-informative. MP analysis yields a tree (TL = 8,189, CI = 0.323, RI = 0.700, RC = 0.226, HI = 0.677). “GTR + I + G” was the best model for the BI analysis, lset nst = 6, rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). The average standard deviation of split frequencies in the BI analysis was 0.008957. Branches that received bootstrap support for MP (MP-BS), ML (ML-BS), and BI (BPP) greater than or equal to 50% (MP-BS and ML-BS) and 0.95 (BPP) are considered as significantly supported, respectively.

The current phylogeny placed all samples of *Antrodia* in a high supported clade (Figure 1). Two new species *Antrodia aridula* and *A. variispora* formed two well-supported lineages, respectively (100% MP 100% ML 1.00 BI and 99% MP 100% ML 1.00 BI). The two new species clustered with *Antrodia macra* (Sommerf.) Niemelä formed a well-supported subclade (96% MP 98% ML 1.00 BI).

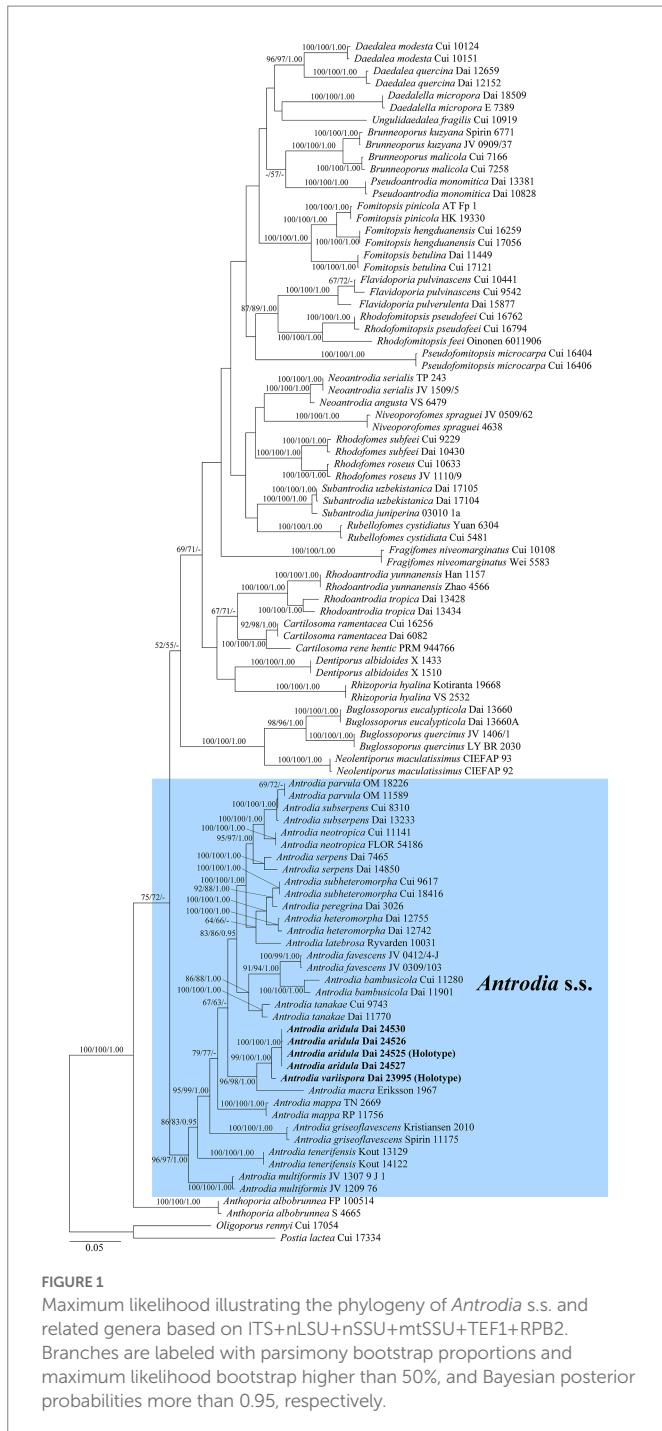
### Taxonomy

***Antrodia aridula*** Y.C. Dai, H.M. Zhou, Y.D. Wu & Shun Liu, sp. nov. Figures 2, 3.

MycoBank number: 846495.

<sup>1</sup> <https://mafft.cbrc.jp/alignment/server/>

<sup>2</sup> <http://purl.org/phylo/treebase>



**FIGURE 2**  
Basidiocarps of *Antrodia aridula* (holotype, Dai 24525). Scale bar: 2cm.

lacerate. Subiculum cream, hard corky, paler contrast with tubes, up to 0.1-mm thick. Tubes concolorous with pores, hard corky, up to 0.4-mm long.

Hyphal structure: Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae IKI-, CB-; tissue unchanged in KOH.

Subiculum: Generative hyphae hyaline, thin-to slightly thick-walled, rarely branched, 2–3 µm in diam; skeletal hyphae dominant, hyaline, thick-walled with a narrow lumen to subsolid, rarely branched, 2–5 µm in diam.

Tubes: Generative hyphae frequent, hyaline, thin-to slightly thick-walled, rarely branched, 2–3 µm in diam; skeletal hyphae dominant, hyaline, thick-walled with a narrow lumen to subsolid, rarely branched, interwoven, 3–4 µm in diam. Cystidia absent; cystidioles present, fusoid, thin-walled, 21–26×5–7 µm. Basidia clavate, with a basal clamp connection and four sterigmata, 23–30×9–10 µm; basidioles in shape similar to basidia, but smaller.

Spores: Basidiospores oblong ellipsoid to cylindrical, gently arcuate and tapering toward the apiculus, hyaline, thin-walled, smooth, sometimes within a few small guttules, IKI-, CB-, (8.5–)9–12(–12.8)×(4–)4.2–5.3(–5.6) µm, L=10.31 µm, W=4.7 µm, Q=2.14–2.22 (n=90/3).

Additional specimens examined (paratypes): China. Inner Mongolia Autonomous Region, Alxa Left Banner, Helanshan Nature Reserve, elev. 2270 m, N 38.865282, E 105.899814, on fallen trunk of *Picea crassifolia*, 17 September 2022, Dai 24525 (BJFC).

Holotype: China. Inner Mongolia Autonomous Region, Alxa Left Banner, Helanshan Nature Reserve, elev. 2270 m, N 38.865282, E 105.899814, on fallen trunk of *Picea crassifolia*, 17 September 2022, Dai 24525 (BJFC).

Etymology: *Aridula* (Lat.): Referring to the species that prefer to the dry environment in Helan Mts. around the desert area of the Inner Mongolia Autonomous Region.

Basidiocarps: Annual, resupinate, tightly attached on wood, leathery when fresh, hard corky when dry, up to 5 cm long, 2 cm wide, and 0.5-mm thick at the center. Pore surface cream when fresh, becoming cream to buff when dry; sterile margin thinning out, white, up to 1 mm wide; pores angular to irregular, 2–3 per mm; dissepiments thin,

Notes: *Antrodia aridula* is characterized by its annual and resupinate basidiocarps with angular to irregular pores of 2–3 per mm, a dimitic hyphal structure, the presence of fusoid cystidioles,

TABLE 2 Taxa information and GenBank accession numbers of the sequences used in this study.

| Species name                       | Sample no.       | Locality       | ITS      | nLSU     | nSSU     | mtSSU    | TEF1     | RPB2     |
|------------------------------------|------------------|----------------|----------|----------|----------|----------|----------|----------|
| <i>Anthoporia albobrunnea</i>      | FP 100514        | Unknown        | EU232215 | EU232299 | EU232257 | —        | —        | —        |
| <i>Anthoporia albobrunnea</i>      | S 4665           | Russia         | KY948808 | KY948880 | —        | —        | —        | —        |
| <i>Antrodia aridula</i>            | Dai 24525        | China          | OP854667 | OP856750 | OP856745 | OP856741 | OP851386 | OP851381 |
| <i>Antrodia aridula</i>            | Dai 24526        | China          | OP854668 | OP856751 | OP856746 | OP856742 | OP851387 | OP851382 |
| <i>Antrodia aridula</i>            | Dai 24527        | China          | OP854669 | OP856752 | OP856747 | OP856743 | OP851388 | OP851383 |
| <i>Antrodia aridula</i>            | Dai 24530        | China          | OP854670 | OP856753 | OP856748 | —        | —        | OP851384 |
| <i>Antrodia bambusicola</i>        | Cui 11280        | China          | MG787579 | MG787620 | MG787726 | MG787667 | MG787845 | MG787792 |
| <i>Antrodia bambusicola</i>        | Dai 11901        | China          | MG787580 | MG787621 | MG787727 | MG787668 | MG787846 | MG787793 |
| <i>Antrodia favescens</i>          | JV 0309/103      | USA            | KC543127 | MG787622 | MG787729 | MG787669 | KC543178 | MG787794 |
| <i>Antrodia favescens</i>          | JV 0412/4-J      | USA            | KC543129 | KC543129 | MG787730 | MG787670 | KC543179 | MG787795 |
| <i>Antrodia griseoflavescens</i>   | Spirin 11175     | Russia         | MK119762 | MK119762 | —        | —        | —        | —        |
| <i>Antrodia griseoflavescens</i>   | Kristiansen 2010 | Norway         | MK119763 | MK119763 | —        | —        | —        | —        |
| <i>Antrodia heteromorpha</i>       | Dai 12755        | USA            | KP715306 | KP715322 | KR605908 | KR606009 | KP715336 | KR610828 |
| <i>Antrodia heteromorpha</i>       | Dai 12742        | USA            | KP715319 | ON417199 | MG787728 | MG787671 | MG787847 | KT895887 |
| <i>Antrodia latebrosa</i>          | Ryvarden 10031   | Tanzania       | MK119769 | MK119769 | —        | —        | —        | —        |
| <i>Antrodia macra</i>              | Eriksson 1967    | Unknown        | KR605810 | KR605749 | KR605909 | —        | KR610739 | MG787796 |
| <i>Antrodia mappa</i>              | RP 11756         | Finland        | KC543113 | KC543113 | —        | —        | —        | —        |
| <i>Antrodia mappa</i>              | TN 2669          | Canada         | KC543130 | KC543130 | —        | —        | —        | —        |
| <i>Antrodia multiformis</i>        | JV 1209/76       | USA            | KT381618 | KT381618 | —        | —        | —        | —        |
| <i>Antrodia multiformis</i>        | JV 1307 9-J-1    | USA            | KT381619 | KT381619 | —        | —        | —        | —        |
| <i>Antrodia neotropica</i>         | Cui 11141        | China          | MG787581 | MG787623 | —        | MG787673 | MG787848 | MG787797 |
| <i>Antrodia neotropica</i>         | FLOR 54186       | Brazil         | KT970445 | KT970454 | —        | —        | —        | —        |
| <i>Antrodia parvula</i>            | OM 18226         | Indonesia      | MK119764 | MK119764 | —        | —        | —        | —        |
| <i>Antrodia parvula</i>            | OM 11589         | Indonesia      | MK119766 | MK119766 | —        | —        | —        | —        |
| <i>Antrodia peregrina</i>          | Dai 3026         | China          | MK119767 | MK119767 | —        | —        | —        | —        |
| <i>Antrodia serpens</i>            | Dai 7465         | Luxemburg      | KR605813 | KR605752 | KR605913 | KR606013 | KR610742 | KR610832 |
| <i>Antrodia serpens</i>            | Dai 14850        | Poland         | MG787582 | MG787624 | MG787731 | MG787674 | MG787849 | MG787798 |
| <i>Antrodia subheteromorpha</i>    | Cui 9617         | China          | MG787583 | MG787625 | MG787735 | MG787675 | MG787850 | MG787799 |
| <i>Antrodia subheteromorpha</i>    | Cui 18416        | China          | MW377257 | MW377338 | MW377416 | MW382052 | MW337088 | MW337025 |
| <i>Antrodia subserpens</i>         | Cui 8310         | China          | KP715310 | KP715326 | MG787732 | MG787677 | KP715340 | KT895888 |
| <i>Antrodia subserpens</i>         | Dai 13233        | China          | KP715309 | KP715325 | MG787734 | MH055437 | KP715339 | KT895889 |
| <i>Antrodia tanakae</i>            | Cui 9743         | China          | KR605814 | KR605753 | KR605914 | KR606014 | KR610743 | KR610833 |
| <i>Antrodia tanakae</i>            | Dai 11770        | China          | KR605815 | KR605754 | KR605915 | KR606015 | KR610744 | KR610834 |
| <i>Antrodia tenerifensis</i>       | Kout 13129       | Spain          | KY446066 | KY446066 | —        | —        | —        | —        |
| <i>Antrodia tenerifensis</i>       | Kout 1412/2      | Spain          | KY446065 | KY446065 | —        | —        | —        | —        |
| <i>Antrodia variispora</i>         | Dai 23995        | China          | OP854671 | OP856749 | OP856744 | —        | —        | OP851385 |
| <i>Brunneoporus kuzyana</i>        | JV 0909/37       | Czech Republic | KU866267 | MG787628 | MG787738 | MG787680 | KU866221 | MG787803 |
| <i>Brunneoporus kuzyana</i>        | Spirin 6771      | Russia         | KU866265 | MG787629 | MG787739 | MG787681 | KU866218 | MG787804 |
| <i>Brunneoporus malicola</i>       | Cui 7258         | China          | MG787586 | MG787631 | MG787741 | MG787683 | MG787853 | MG787806 |
| <i>Brunneoporus malicola</i>       | Cui 7166         | China          | MG787585 | MG787630 | MG787740 | MG787682 | MG787852 | MG787805 |
| <i>Buglossoporus eucalypticola</i> | Dai 13660        | China          | KR605808 | KR605747 | KR605906 | KR606007 | KR610736 | KR610825 |
| <i>Buglossoporus eucalypticola</i> | Dai 13660A       | China          | KR605809 | KR605748 | KR605907 | KR606008 | KR610737 | KR610826 |
| <i>Buglossoporus quercinus</i>     | JV 1406/1        | Czech Republic | KR605801 | KR605740 | KR605899 | KR606002 | KR610730 | KR610820 |
| <i>Buglossoporus quercinus</i>     | LY BR 2030       | France         | KR605799 | KR605738 | KR605897 | KR606000 | KR610728 | KR610818 |
| <i>Cartilosoma ramentacea</i>      | Cui 16256        | China          | OK045506 | OK045512 | OK045494 | OK045500 | OK076960 | OK076904 |

(Continued)

TABLE 2 (Continued)

| Species name                        | Sample no.      | Locality       | ITS      | nLSU     | nSSU     | mtSSU    | TEF1     | RPB2     |
|-------------------------------------|-----------------|----------------|----------|----------|----------|----------|----------|----------|
| <i>Cartilosoma ramentacea</i>       | Dai 6082        | China          | MG787595 | MG787640 | MG787750 | MG787692 | MG787860 | MG787813 |
| <i>Cartilosoma rene-hentic</i>      | PRM 944766      | Czech Republic | MK558725 | —        | —        | —        | —        | —        |
| <i>Daedalea modesta</i>             | Cui 10151       | China          | KP171205 | KP171227 | KR605883 | KR605986 | KR610716 | KR610806 |
| <i>Daedalea modesta</i>             | Cui 10124       | China          | KR605791 | KR605730 | KR605882 | KR605985 | KR610715 | KR610805 |
| <i>Daedalea quercina</i>            | Dai 12152       | Czech Republic | KP171207 | KP171229 | KR605886 | KR605989 | KR610717 | KR610809 |
| <i>Daedalea quercina</i>            | Dai 12659       | Finland        | KP171208 | KP171230 | KR605887 | KR605990 | KR610719 | KR610810 |
| <i>Daedalella micropora</i>         | Dai 18509       | Malaysia       | MW377286 | MW377365 | MW377444 | MW382073 | MW337113 | MW337049 |
| <i>Daedalella micropora</i>         | E 7389          | Indonesia      | AJ542527 | —        | —        | —        | —        | —        |
| <i>Dentiporus albidooides</i>       | X 1433          | Italy          | KC543147 | KC543147 | —        | —        | —        | —        |
| <i>Dentiporus albidooides</i>       | X 1510          | France         | KC543168 | —        | —        | —        | —        | —        |
| <i>Flavidoporia pulvulenta</i>      | Dai 15877       | China          | MG787588 | —        | MG787745 | MG787687 | MG787855 | MG787810 |
| <i>Flavidoporia pulvinascens</i>    | Cui 10441       | China          | MG787590 | MG787636 | ON417019 | MG787688 | MG787857 | MG787811 |
| <i>Flavidoporia pulvinascens</i>    | Cui 9542        | China          | MG787589 | MG787635 | MG787746 | ON417078 | MG787856 | ON424764 |
| <i>Fomitopsis betulina</i>          | Cui 17121       | China          | OL621853 | OL621242 | OL621779 | OL621753 | OL588982 | OL588969 |
| <i>Fomitopsis betulina</i>          | Dai 11449       | China          | KR605798 | KR605737 | KR605895 | KR605998 | KR610726 | KR610816 |
| <i>Fomitopsis hengduanensis</i>     | Cui 16259       | China          | MN148232 | OL621247 | OL621782 | OL621758 | MN161747 | MN158175 |
| <i>Fomitopsis hengduanensis</i>     | Cui 17056       | China          | MN148233 | OL621248 | OL621783 | OL621759 | MN161748 | MN158176 |
| <i>Fomitopsis pinicola</i>          | AT Fp 1         | Sweden         | MK208852 | —        | —        | —        | MK236359 | MK236362 |
| <i>Fomitopsis pinicola</i>          | HK 19330        | Russia         | KF169655 | —        | —        | —        | KF178380 | KF169724 |
| <i>Fragifomes niveomarginatus</i>   | Cui 10108       | China          | KR605778 | KR605717 | KR605851 | KR605955 | KR610684 | KR610776 |
| <i>Fragifomes niveomarginatus</i>   | Wei 5583        | China          | HQ693994 | KC507175 | KR605852 | KR605956 | KR610685 | ON424771 |
| <i>Neoantrodia angusta</i>          | VS 6479         | Russia         | KT995127 | KT995149 | MG787756 | MG787696 | KU052718 | MG787818 |
| <i>Neoantrodia serialis</i>         | JV 1509/5       | Czech Republic | KT995120 | KT995143 | —        | —        | KU052726 | —        |
| <i>Neoantrodia serialis</i>         | TP 243          | Finland        | KT995121 | KT995144 | —        | —        | KU052725 | —        |
| <i>Neolentiporus maculatissimus</i> | CIEFAP 93       | Argentina      | JX090122 | —        | —        | —        | —        | —        |
| <i>Neolentiporus maculatissimus</i> | CIEFAP 92       | Argentina      | JX090121 | —        | —        | —        | —        | —        |
| <i>Niveoporofomes spraguei</i>      | JV 0509/62      | USA            | KR605786 | KR605725 | KR605864 | KR605968 | KR610697 | KR610788 |
| <i>Niveoporofomes spraguei</i>      | 4638            | France         | KR605784 | KR605723 | KR605862 | KR605966 | KR610696 | KR610786 |
| <i>Oligoporus rennyi</i>            | Cui 17054       | China          | OK045508 | OK045514 | OK045496 | OK045502 | OK076962 | OK076934 |
| <i>Postia lacteal</i>               | Cui 17334       | China          | OM039287 | OM039187 | OM039254 | OM039222 | OM037810 | OM037782 |
| <i>Pseudoantrodia monomitica</i>    | Dai 13381       | China          | MG787602 | ON417234 | MG787768 | —        | MG787866 | MG787822 |
| <i>Pseudoantrodia monomitica</i>    | Dai 10828       | China          | MG787601 | MG787648 | MG787767 | —        | MG787865 | ON424803 |
| <i>Pseudofomitopsis microcarpa</i>  | Cui 16404       | Vietnam        | MW377316 | MW377394 | MW377473 | MW382097 | MW337139 | —        |
| <i>Pseudofomitopsis microcarpa</i>  | Cui 16406       | Vietnam        | MW377317 | MW377395 | MW377474 | MW382098 | ON424865 | —        |
| <i>Rhizophoria hyalina</i>          | VS 2532         | Russia         | JQ700267 | JQ700267 | —        | —        | —        | —        |
| <i>Rhizophoria hyalina</i>          | Kotiranta-19668 | Russia         | JQ700284 | JQ700284 | —        | —        | —        | —        |
| <i>Rhodoantrodia tropica</i>        | Dai 13428       | China          | MG787605 | MG787652 | MG787778 | MG787708 | MG787867 | MG787823 |
| <i>Rhodoantrodia tropica</i>        | Dai 13434       | China          | MG817481 | MG817479 | MG787779 | MG787709 | —        | MG787824 |
| <i>Rhodoantrodia yunnanensis</i>    | Han 1157        | China          | MT497886 | MT497884 | —        | —        | —        | —        |
| <i>Rhodoantrodia yunnanensis</i>    | Zhao 4566       | China          | MT497887 | MT497885 | —        | —        | —        | —        |
| <i>Rhodofomes roseus</i>            | Cui 10633       | China          | KR605782 | KR605721 | KR605860 | KR605964 | KR610693 | KR610784 |
| <i>Rhodofomes roseus</i>            | JV 1110/9       | Czech Republic | KR605783 | KR605722 | KR605861 | KR605965 | KR610694 | KR610785 |
| <i>Rhodofomes subfeei</i>           | Cui 9229        | China          | KR605789 | KR605728 | KR605869 | ON417098 | KR610701 | KR610793 |
| <i>Rhodofomes subfeei</i>           | Dai 10430       | China          | KR605788 | KR605727 | KR605868 | KR605972 | KR610702 | KR610792 |
| <i>Rhodofomitopsis feei</i>         | Oinonen 6011906 | Brazil         | KC844851 | KC844856 | KR605837 | KR605943 | KR610671 | KR610767 |

(Continued)

TABLE 2 (Continued)

| Species name                      | Sample no. | Locality   | ITS      | nLSU     | nSSU     | mtSSU    | TEF1     | RPB2     |
|-----------------------------------|------------|------------|----------|----------|----------|----------|----------|----------|
| <i>Rhodofomitopsis pseudofeei</i> | Cui 16794  | Australia  | MK461952 | MK461956 | MK461964 | MK461960 | MK463986 | MK463984 |
| <i>Rhodofomitopsis pseudofeei</i> | Cui 16762  | Australia  | MK461951 | MK461955 | MK461963 | MK461959 | MK463985 | MK463983 |
| <i>Rubellofomes cystidiata</i>    | Cui 5481   | China      | KF937288 | KF937291 | KR605832 | KR605938 | KR610667 | KR610765 |
| <i>Rubellofomes cystidiatus</i>   | Yuan 6304  | China      | KR605769 | KR605708 | KR605833 | KR605939 | KR610668 | —        |
| <i>Subantrodia juniperina</i>     | 03010/1a   | USA        | MG787606 | MG787653 | MG787782 | MG787712 | MG787873 | MG787831 |
| <i>Subantrodia uzbekistanica</i>  | Dai 17104  | Uzbekistan | KX958182 | KX958186 | —        | ON417103 | ON424883 | —        |
| <i>Subantrodia uzbekistanica</i>  | Dai 17105  | Uzbekistan | KX958183 | KX958187 | —        | ON417104 | ON424884 | —        |
| <i>Ungulidaedalea fragilis</i>    | Cui 10919  | China      | KF937286 | KF937290 | KR605840 | KR605946 | KR610674 | KR610770 |

New sequences are shown in bold.

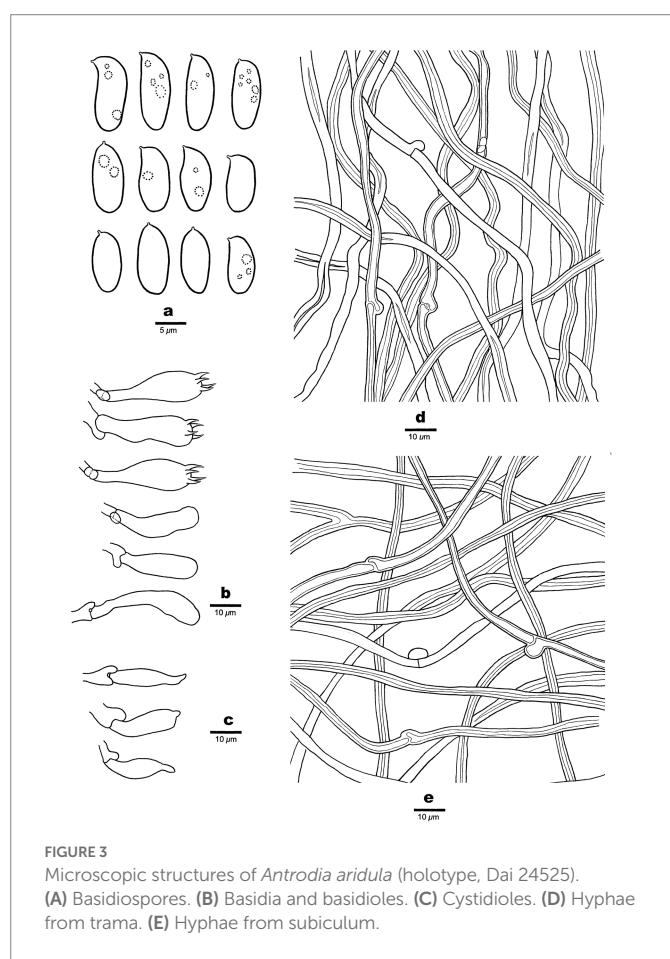


FIGURE 3

Microscopic structures of *Antrodia aridula* (holotype, Dai 24525). (A) Basidiospores. (B) Basidia and basidioles. (C) Cystidioles. (D) Hyphae from trama. (E) Hyphae from subiculum.

basidiospores oblong ellipsoid to cylindrical, gently arcuate and tapering toward the apiculus,  $9-12 \times 4.2-5.3 \mu\text{m}$ , and growing on gymnosperm wood in a dry environment of West China. *Antrodia aridula* and *Cartilosoma ramentaceum* (Berk. & Broome) Teixeira ( $\equiv$  *Antrodia ramentacea* (Berk. & Broome) Donk) have similar pores and growing on the wood of *Pinus*, but the latter differs from the former by gelatinous basidiocarps, smaller basidiospores ( $6.2-8.1 \times 2.1-2.7 \mu\text{m}$  vs.  $9-12 \times 4.2-5.3 \mu\text{m}$ ) and wider geographical distribution (Niemelä, 2005). *Cartilosoma* is different from *Antrodia* by completely resupinate and soft basidiocarps when fresh, and gelatinous hymenophore (Liu et al., 2022). *Antrodia aridula* is similar to *A. macra* (Sommerf.) Niemelä in macromorphology, and both



FIGURE 4  
Basidiocarp of *Antrodia variispora* (holotype, Dai 23995). Scale bar: 2cm.

species are closely related (Figure 1), but the latter species has smaller basidiospores ( $7.4-11 \times 3-4.3 \mu\text{m}$  vs.  $9-12 \times 4.2-5.3 \mu\text{m}$ , Niemelä, 2005), and growing on *Salix* and *Populus* only (Ryvarden and Melo, 2017). *Antrodia aridula* is also closely related to *Antrodia variispora* (Figure 1), but the latter species has bigger and variable basidiospores ( $9-12 \times 4.2-5.3 \mu\text{m}$  vs.  $11.5-16 \times 4.5-5.5 \mu\text{m}$ ).

Ecologically, *Antrodia aridula* grows on fresh fallen gymnosperm trunks and branches in a dry environment, indicating a pioneer decayer in the coniferous forests of western China.

*Antrodia variispora* Y.C. Dai, H.M. Zhou, Y.D. Wu & Shun Liu, sp. nov. Figures 4, 5.

Mycobank number: 846496.

Holotype: China. Qinghai Province, Nangqian County, Baizha Forest Park, elev. 4090 m, N 31.855040, E 96.467402, on stump of *Picea likiangensis* var. *balfouriana*, 7 August 2022, Dai 23995 (BJFC).

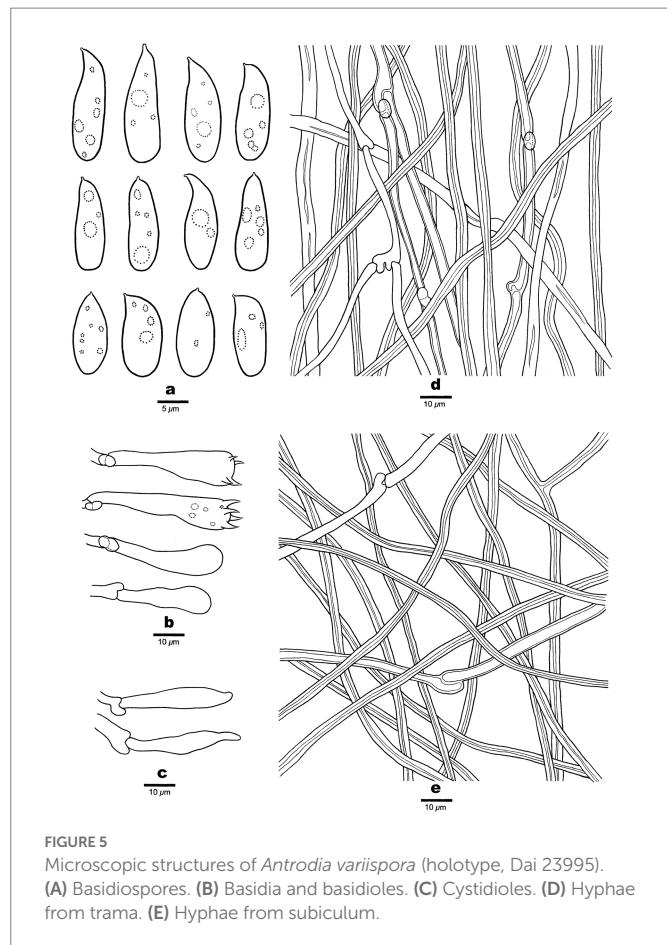


FIGURE 5

Microscopic structures of *Antrodia variispora* (holotype, Dai 23995). (A) Basidiospores. (B) Basidia and basidioles. (C) Cystidioles. (D) Hyphae from trama. (E) Hyphae from subiculum.

**Etymology:** *Variispora* (Lat.): Referring to the species having variable basidiospores.

**Basidiocarp:** Annual, resupinate, tightly attached to wood, leathery when fresh, hard corky to rigid when dry, up to 16 cm long, 6 cm wide, and 1.3-mm thick at the center. Pore surface cream when fresh, becoming cinnamon-buff when dry; sterile margin very narrow to almost lacking; pores sinuous or dentate, (0.5–)1–1.5(–2) per mm; dissepiments thin, lacerate. Subiculum cream, hard corky, paler contrast with tubes, up to 0.3-mm thick. Tubes concolorous with pores, rigid, up to 1-mm long.

**Hyphal structure:** Hyphal system dimitic; generative hyphae with clamp connections; skeletal hyphae IKI–, CB–; tissue unchanged in KOH.

**Subiculum:** Generative hyphae infrequent, hyaline, thin-to slightly thick-walled, rarely branched, 2–4 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a narrow lumen to subsolid, rarely branched, interwoven, 2.5–4 μm in diam.

**Tubes:** Generative hyphae frequent, hyaline, thin-to slightly thick-walled, frequently branched, 2.5–4 μm in diam; skeletal hyphae dominant, hyaline, thick-walled with a narrow lumen to subsolid, occasionally branched, interwoven, 3–5 μm in diam. Cystidia absent; cystidioles present, fusoid, thin-walled, 22–41 × 4.5–5 μm. Basidia clavate to pyriform, with a basal clamp connection and four sterigmata, 24–35 × 7–10 μm; basidioles in shape similar to basidia, but smaller.

**Spores:** Basidiospores variable, oblong ellipsoid, fusiform, pyriform or cylindrical, gently arcuate and tapering toward the

apiculus, hyaline, thin-walled, smooth, usually within a few small guttules, IKI–, CB–, (11–)11.5–16(–18.5) × 4.5–5.5(–5.8) μm, L = 13.47 μm, W = 5.12 μm, Q = 2.63 (n = 30/1).

**Notes:** *Antrodia variispora* is characterized annual and resupinate basidiocarps with sinuous or dentate pores of 1–1.5 per mm, a dimitic hyphal structure, the presence of fusoid cystidioles, basidiospores variable, oblong ellipsoid, fusiform, pyriform or cylindrical, 11.5–16 × 4.5–5.5 μm, and growing on the wood of *Picea* in West China. *Antrodia variispora* is similar to *Adustoporia sinuosa* (Fr.) Audet (≡ *Antrodia sinuosa* (Fr.) P. Karst.) in macromorphology, but the latter species has distinctly smaller basidia (11–15 × 4–5 μm vs. 24–35 × 7–10 μm, Ryvarden and Gilbertson, 1993) and smaller basidiospores (4.9–6 × 1.4–1.8 μm vs. 11.5–16 × 4.5–5.5 μm, Niemelä, 2005). *Adustoporia* differs from *Antrodia* s. str. by pale brown pore surface when fresh, smaller basidia (15–22 × 4–5 μm), smaller basidiospores (4–6 × 1–2 μm, Audet, 2017b). *Antrodia variispora* and *Dentiporus albidooides* (A. David & Dequatre) Audet (≡ *Antrodia albidooides* A. David & Dequatre) have similar pore and basidiospore dimensions (Ryvarden and Melo, 2017), but the latter species has skeletocystidia, uniformed cylindrical basidiospores, and growing on angiosperm wood in Mediterranean area (Ryvarden and Melo, 2017). In addition, phylogenetically both species are distantly related (Figure 1). The genus *Dentiporus* differs from *Antrodia* s. str by often resupinate basidiocarps usually with rose pink tinted pore surface and round to irlpicoid pores (Audet, 2017a). *Antrodia variispora* is closely related to *A. macra* (Figure 1), but *A. macra* has regularly cylindrical to oblong ellipsoid basidiospores which are smaller than those in *Antrodia variispora* (7.4–11 × 3–4.3 μm vs. 11.5–16 × 4.5–5.5 μm, Niemelä, 2005).

Ecologically, *Antrodia variispora* grows on a large stump of *Picea likiangensis* var. *balfouriana* in a virgin forest, and we tried to find more samples in a similar environment of the same forest, and unfortunately, we did not find the second sample. Thus, *Antrodia variispora* seems to be a rare species in old growth forests.

## Discussion

Adding the two new species from China, the definition of *Antrodia* s. str. is modified as follows: Basidiocarps annual, resupinate to effused-reflexed, soft corky to leathery when fresh, become corky to hard corky or rigid when dry; pileal surface glabrous or matted, white, cream to brownish gray; pore surface white to cream when fresh, buff to pale brown upon drying; pores round, angular, sinuous or dentate; subiculum or context cream, corky; hyphal system dimitic with clamped generative hyphae; skeletal hyphae IKI–, CB–; cystidia absent; fusoid cystidioles present or absent; basidiospores long (6.5–16 μm), oblong ellipsoid, cylindrical, fusiform or pyriform, hyaline, thin-walled, smooth, IKI–, CB–; causing a brown rot.

## Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article.

## Author contributions

Y-CD coordinated the project and designed the experimental plan. H-MZ, Y-CD, and SL analyzed the data. Y-CD, X-JD, and H-GL collected the samples from the field. H-MZ and Y-CD wrote the original draft. H-MZ, Y-CD, Y-DW, and SL reviewed and edited the manuscript. Y-CD acquired funding. All authors contributed to the article and approved the submitted version.

## Funding

The research was supported by the National Natural Science Foundation of China (Project Nos. 32161143013, 31870007). We are grateful to Zhan-Bo Liu was a companion on the field trips.

## References

- Anonymous (1969). *Flora of British Fungi. Colour Identification Chart*. London: Her Majesty's Stationery Office.
- Audet, S. (2017a). New genera and new combinations in Antrodia s. l. or Polyporus s.l., or new families in the Polyporales. *Mushrooms Nomencl.* 3:1.
- Audet, S. (2017b). New genera and new combinations in Antrodia s.l. or Polyporus s.l., or new families in the Polyporales. *Mushrooms Nomencl.* 11:1.
- Chen, Y. Y., and Cui, B. K. (2015). Phylogenetic analysis and taxonomy of the Antrodia heteromorpha complex in China. *Mycoscience* 57, 1–10. doi: 10.1016/j.myc.2015.07.003
- Chen, J. J., and Dai, Y. C. (2021). Two new species of Physipsorinus (Polyporales, Basidiomycota) from Yunnan, Southwest China. *Mycol. Prog.* 20, 1–10. doi: 10.1007/s11557-020-01647-8
- Gilbertson, R. L., and Ryvarden, L. (1986). *North American polypores I. Abortiporus-Lindneria*. Oslo: Fungiflora, 1–433.
- Hibbett, D. S., and Donoghue, M. J. (2001). Analysis of character correlations among wood decay mechanisms, mating systems, and substrate ranges in Homobasidiomycetes. *Syst. Biol.* 50, 215–242. doi: 10.1080/10635150151125879
- Katoh, K., Rozewicki, J., and Yamada, K. D. (2017). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Brief. Bioinform.* 20, 1160–1166. doi: 10.1093/bib/bbx108
- Liu, S., Chen, Y. Y., Sun, Y. F., He, X. L., Song, C. G., Si, J., et al. (2022). Systematic classification and phylogenetic relationships of the brown-rot fungi within the Polyporales. *Fungal Divers.* doi: 10.1007/s13225-022-00511-2
- Liu, Y. J., Whelen, S., and Hall, B. D. (1999). Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Mol. Biol. Evol.* 16, 1799–1808. doi: 10.1093/oxfordjournals.molbev.a026092
- Niemelä, T. (2005). Polypores, lignicolous fungi. *Norrlinia* 13, 1–320.
- Núñez, M., and Ryvarden, L. (2001). East Asian polypores 2. Polyporaceae s. lato. *Synop. Fungorum* 14, 170–522.
- Ortiz-Santana, B., Lindner, D. L., Miettinen, O., Justo, A., and Hibbett, D. S. (2013). A phylogenetic overview of the Antrodia clade (Basidiomycota, Polyporales). *Mycologia* 105, 1391–1411. doi: 10.3852/13-051
- Petersen, J. H. (1996). *The Danish mycological Society's colour-chart*. Greve: Foreningen til Svampeskundskabens Fremme.
- Rehner, S. A., and Buckley, E. (2005). A Beauveria phylogeny inferred from nuclear ITS and EF1- $\alpha$  sequences: evidence for cryptic diversification and links to Cordyceps teleomorphs. *Mycologia* 97, 84–98. doi: 10.3852/mycologia.97.1.84
- Runnel, K., Spirin, V., Miettinen, O., Vlasák, J., Dai, Y. C., Ryvarden, L., et al. (2019). Morphological plasticity in brown-rot fungi: Antrodia is redefined to encompass both poroid and corticioid species. *Mycologia* 111, 871–883. doi: 10.1080/00275514.2019.1640532
- Ryvarden, L., and Gilbertson, R. L. (1993). European polypores. Part 1. *Synop. Fungorum* 6, 1–387.
- Ryvarden, L., and Melo, I. (2017). Poroid fungi of Europe, 2nd edition. *Synop. Fungorum* 37, 1–431.
- Spirin, V., Vlasák, J., Niemelä, T., and Miettinen, O. (2013). What is Antrodia sensu stricto? *Mycologia* 105, 1555–1576. doi: 10.3852/13-039
- Vilgalys, R., and Hester, M. (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. *J. Bacteriol.* 172, 4238–4246. doi: 10.1128/jb.172.8.4238-4246.1990
- White, T. J., Bruns, T., Lee, S., and Taylor, J. (1990). "Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics" in *PCR Protocols: A Guide to Methods and Applications*. eds. M. A. Innis, D. H. Gelfand, J. J. Sninsky and T. J. White (New York, NY: Academic Press), 315–322.
- Wu, F., Man, X. W., Tohtirjap, A., and Dai, Y. C. (2022). A comparison of polypore fungi and species composition in forest ecosystems of China, North America, and Europe. *For. Ecosyst.* 9:100051. doi: 10.1016/j.fecs.2022.100051

## 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.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.