Taxonomy and Phylogeny Reveal Two New Potential Edible Ectomycorrhizal Mushrooms of *Thelephora* from East Asia

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**Abstract:** The ectomycorrhizal basidiomycetes genus *Thelephora* has been understudied in subtropical ecosystems. Many species of *Thelephora* are important edible and medicinal fungi, with substantial economic value. Two new *Thelephora* species, *T. grandinioides* and *T. wuliangshanensis* spp. nov. are proposed here based on a combination of morphological features and molecular evidence. *Thelephora grandinioides* is characterized by laterally stipitate basidiocarps with a grandinioid hymenial surface, a mononitic hyphal system with clamped generative hyphae, and the presence of tubular and septated cystidia and subglobose to globose basidiospores measuring as 5.3–7.4 × 4–6.5 µm. *Thelephora wuliangshanensis* is characterized by infundibuliform basidiocarps, radially black striate on the pileus, a smooth, umber to coffee hymenial surface, a mononitic hyphal system with thick-walled generative hyphae, and basidiospores that turn greenish grey to buff in 5% KOH. Phylogenetic analyses of rDNA internal transcribed spacer region (ITS) and nuclear large subunit region (nrLSU) showed that the two new *Thelephora* are phylogenetically distinct: *T. grandinioides* is sister to *T. aurantiotincta* and *T. sikkimensis*, while *T. wuliangshanensis* is sister to a clade comprising *T. austrosinensis* and *T. aurantiotincta* with high support as well.

**Keywords:** corticioid fungi; macro fungi; molecular phylogeny; Thelephoraceae; *Thelephora grandinioides; Thelephora wuliangshanensis*; Yunnan Province

1. Introduction

*Thelephora* Ehrh. ex Willd., the genus type of Thelephoraceae Chevall. is one of the most important taxa in basidiomycetes [1–5]. They are widely distributed worldwide, especially in the northern temperate and tropical regions [1–5]. *Thelephora* is a fairly well-studied ectomycorrhizal basidiomycetes genus with basidiocarps of various shape; the entire genus forms ectomycorrhizal relationships with diverse plants and significant contribution to plant health and ecosystem stability [4,6–12]. As mycorrhiza-formers, *Thelephora* play a very important role in pioneer microhabitats of coniferous forests [13,14]. Acting as white rot fungi, they also can decompose dead wood [14,15].

Some species of *Thelephora* are economically important edible and medicinal mushrooms. *Thelephora ganbajun* M. Zang is one of the most popular edible fungi in China...
and some East Asian countries [14–21]. *Thelephora* is typified by *T. terrestris* Ehrh. ex Willd. [22], and the genus is characterized by its diverse forms of basidiomycetes as stereoid, clavarioid, cantharelloid, spathulate, pleurodally pileate to resupinate; hymenophore smooth to slightly wrinkled and often cyanescent in KOH; pileus surface glabrous to strigose, even or faintly ribbed or papillose; hymenium continuous, usually on inferior side, sometimes amphigenous in some species; hyphal system monomitic with clamped generative hyphae; basidia 4-spored; basidiospores subhyaline to brownish, ornamented, typically muricate, verruculose or echinulate, even or slightly rough-walled in a few species, and inamyloid [1,3,12,22]. As of 2008, fifty species of *Thelephora* have been accepted [23], and some new species have been reported in recent years [4,5,14,24–27].

Index Fungorum [28] shows 871 specific and infraspecific names in *Thelephora*. However, to date, 62 species of *Thelephora* have been accepted [3–5,14,23–27].

*Thelephora* share similar characteristics with *Tomentella* Pers. ex Pat. especially in the form, size, and type of spore ornamentations [3,29,30]. Based on phylogenetic analyses using rDNA internal transcribed spacer region (ITS) sequences showed that the species of *Thelephora* mixed with *Tomentella*, revealing that both genera are closely related, but it is well-known that the phylogenetic analyses of ITS loci are insufficient to resolve phylogenetic relationships among closely related taxa [4,5,31,32]. Based on ITS and nrLSU analyses, Vizzini et al. [25] showed that *Thelephora* and *Tomentella* species do not separate to two monophyletic groups but they are intermixed and form a well-supported monophyletic clade (*Thelephora*/Tomentella clade). Back to traditional method, the most important characteristic for distinguishing *Thelephora* and *Tomentella* is the form of the basidiocarps (resupinate in *Tomentella*; erect, with varied forms, to partially resupinate in *Thelephora*) [24,29,33]. Das et al. [26] proposed that other features such as the hymenophore surface needed to be observed to determine whether it could act as a more informative characteristic than the highly variable stipitate/resupinate configuration of basidiocarps. Phylogenetic analyses of combined ITS and nrLSU dataset in Basidiomycota revealed that *Thelephora* is sister to *Tomentella* nested in Thelephoraceae while the limits between both genera are not yet clear [5,26,34]. While ITS and nrLSU sequences alone cannot resolve phylogenetic relationships in this complex group of species [5,34], Vizzini et al. [25] mentioned that in the future *Thelephora* and *Tomentella* will be considered as one genus merging *Tomentella* into *Thelephora*.

With this work we intend to identify two *Thelephora* species found in southern China based on morphology and phylogeny, and provide full descriptions, color photographs, a detailed comparison of two new species with closely related taxa and a phylogenetic tree to show the placement of two new species.

### 2. Materials and methods

#### 2.1. Specimens Collection and Herbarium Specimen Preparation

Four samples of *Thelephora* were collected in Yunnan (Figure 1A–C) viz. CLZhao 3406 (Holotype) from the Wuliangshan National Nature Reserve, Huangcaoling, Jingdong County, Puer, at latitude 24°18′ N and longitude 101°05′ E, at 2113 m above sea level, 1 October 2017; CLZhao 3408 from the Xieqipo Forest Park, Zhenyuan County, Puer, at latitude 24°18′ N and longitude 101°05′ E, at 1350 m above sea level, 1 October 2017; CLZhao 4107 (Holotype) from the Wuliangshan National Nature Reserve, Huangcaoling, Jingdong County, Puer, at latitude 24°23′ N and longitude 100°45′ E, at 2313 m above sea level, 5 October 2017; CLZhao 21020 from the Wuliangshan National Nature Reserve, Huangcaoling, Jingdong County, Puer, at latitude 23°57′ N and longitude 100°57′ E, 8 October 2020. The fruiting bodies were observed growing on the ground of pine-broadleaved mixed forest. Photographs of the fruiting bodies were taken in the field, macromorphological characteristics were recorded and then the fruiting bodies were collected. The collected fruiting bodies were dried in an electric food dehydrator at 40 °C, then sealed and stored in an envelope bag. They were then transported to mycology
laboratory of Southwest Forestry University, Kunming where microscopic morphology and phylogeny were studied.

Figure 1. The localities of new Thelephora species. (A) Jingdong county and Zhenyuan county in Yunnan province. (B) The locality of Thelephora wuliangshanensis strain (Holotype: CLZhao 4107) in Jingdong county. (C) The locality of T. wuliangshanensis (CLZhao 21020) and T. grandinioides (Holotype: CLZhao 3406; CLZhao 3408) in Zhenyuan county. Source: Map data ©2021 Google.

2.2. Morphology

The specimens studied are deposited at the herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, China. Macromorphological descriptions were based on field notes and photos captured in the field and lab. Color terminology followed Petersen [35]. Micromorphological data were obtained from the dried specimens, and were observed under a light microscope following Dai [36]. The following abbreviations were used: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB– = acyanophilous, IKI = Melzer’s reagent, IKI– = both inamyloid and indextrinoid, L = mean spore length (arithmetic average for all spores), W = mean spore width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied, n = a/b (number of spores (a) measured from given number (b) of specimens).
2.3. Molecular Phylogeny

A conventional cetyl trimethylammonium bromide (CTAB) plant genome rapid extraction kit (DN14, Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to obtain genomic DNA from dried specimens, according to the manufacturer’s instructions [37]. Amplification reactions were performed in a 30 μL reaction volume composed of 15 μL 2 × FastTaq Premix (a mixture of FastTaq TM DNA Polymerase, buffer, dNTP Mixture, and stabilizer) (Beijing Qingke Biological Technology Co., Ltd., Beijing, China), 1 μL of each of the reverse and forward primers (Beijing Kinco Biotechnology Co., Ltd., Kunming Branch, China), 8.5 μL double distilled water (ddH2O), and 1–1.2 μL DNA. ITS region was amplified with primer pair ITS5 and ITS4 [38]. The nrLSU was amplified with primer pairs LR0R and LR7 [39]. PCR procedure for ITS followed: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and a final extension of 72 °C for 10 min. For the nrLSU regions, PCR amplification conditions were used as follows: initial denaturation of 1 min at 94 °C, followed by 35 cycles of denaturation at 94 °C for 30 s, 1 min of annealing at 48 °C, 90 s extension at 72 °C, and a final extension of 10 min at 72 °C. PCR products were purified and sequenced at Kunming Tsingke Biological Technology Limited Company, Kunming, Yunnan Province, China. All newly generated sequences were deposited in NCBI GenBank/UNITE (Table 1). Sequences were aligned in MAFFT 7 (https://mafft.cbrc.jp/alignment/server/, accessed on 3 December 2021) using G-INS-i strategy for ITS combined dataset, and manually adjusted in BioEdit [40]. Aligned dataset was deposited in TreeBase (submission ID 28432). Odontia fibrosa (Berk. and M.A. Curtis) Kõljalg and O. ferruginea Pers. were selected as outgroup for phylogenetic analyses of combined dataset [25,26].

Table 1. Names, vouchers, location, and corresponding GenBank/UNITE accession numbers of taxa used in this study.

| Taxon Names          | Voucher | Location                  | GenBank/UNITE Accession Number |
|----------------------|---------|---------------------------|---------------------------------|
|                      |         |                           | ITS    | nrLSU   | Reference |
| Odontia ferruginea   | UK18    | Estonia                   | UDB000285 | UDB018691 | [25]      |
| O. fibrosa           | SS38    | Sweden                    | MH310788 | UDB018463 | [25,26]  |
| Thelephora albomarginata | KHL8457 | Sweden                    | –      | UDB018707 | [5]       |
| T. americana         | UAMH 9578 | Chile                  | AY219838 | –        | [41]      |
| T. anthocephala      | UBC F28410 | Canada                 | KP454019 | KP454019 | [26]      |
| T. anthocephala      | TAA165304 | Estonia                | AF272927 | UDB018693 | [27]      |
| T. atra              | UK50    | Russia                    | –      | UDB018697 | UNITE     |
| T. aurantiotincta    | 115437  | –                         | –      | TU115437 | UNITE     |
| T. aurantiotincta    | 520625MF420 | China               | MZ057686 | –        | GenBank   |
| T. aurantiotincta    | 346–518 | Japan                     | AB509809 | –        | GenBank   |
| T. austrosinensis    | GDGM 48867 T | China            | MF593265 | MF593265 | [5]       |
| T. austrosinensis    | GDGM 48891 | China             | MF593266 | MF593266 | [5]       |
| T. austrosinensis    | GDGM 48899 | China             | MF593267 | MF593267 | [5]       |
| T. caryophyllea      | ELarsson89-09 | Sweden         | MK602776 | MK602776 | [42]      |
| T. caryophyllea      | TAAM172626 | Estonia    | –      | UDB018694 | [5]       |
| T. caryophyllea      | TL-6566  | Denmark                  | AJ889980 | –        | [27]      |
| T. caryophyllea      | GO-2010-163 | Mexico          | KC152242 | –        | [26]      |
| T. caryophyllea      | TAAM172626 | Estonia      | UDB018694 | –        | [5]       |
| T. dominicana        | JBSD126510 T | Dominican Republic | KX216400 | KX216400 | [25]      |
| T. ganbajun          | Gb151    | China                    | EU696873 | –        | [9]       |
| T. ganbajun          | Gb152    | China                    | EU696874 | –        | [9]       |
| T. ganbajun          | HMAS 276818 | China            | –      | LC164937 | GenBank   |
| T. ganbajun          | ZRL20151295 | China          | –      | KY418908 | [43]      |
| T. grandinioides     | CLZhao 3406 T | China      | MZ400673 | MZ400675 | Present study |
T. grandinioides | CLZhao 3408 | China | MZ400674 | MZ400676 | Present study
---|---|---|---|---|---
T. iqbalii | MH810 T | Pakistan | JX241471 | – | [27]
T. japonica | 420526MF0417 | China | – | MG712350 | GenBank
T. palmata | JMP0085 | USA | EU819443 | – | [44]
T. palmata | LW 84 | – | – | AF291265 | [45]
T. palmata | TAA149550 | Swedish | AF272919 | – | [44]
T. palmata | Telpa31/38 | – | – | AJ406477 | [5]
T. aff. palmata | 350–421 | Japan | AB509755 | – | [27]
T. penicillata | 0465 | China | MT325773 | – | [26]
T. penicillata | LTT8 | USA | U83484 | – | [46]
T. penicillata | TAAM169453 | Estonia | – | UDB018695 | [5]
T. pseudoterrestris | TAA159625 | Estonia | AF272907 | – | [27]
T. pseudoterrestris | UK34 | – | UDB000209 | – | [25]
T. pseudoversatilis | 11H2-1 | Mexico | KU530339 | – | [26]
T. pseudoversatilis | FCME 26152 T | Mexico | KJ462486 | – | [4]
T. pseudoversatilis | FCME 26232 | Mexico | JX075890 | JX514167 | [4]
T. regularis | UBC F33227 | Canada | MG953966 | – | [26]
T. regularis | JMT17371 | USA | U83485 | – | [46]
T. aff. regularis | GO-2010-125 | Mexico | KC152240 | – | [26]
T. aff. regularis | GO-2010-134 | Mexico | KC152241 | – | [26]
T. sikkimensis | KD 16-003 | India | MF684017 | – | [26]
T. sikkimensis | KD 16-042 | India | MF684018 | – | [26]
T. subtiliaca | UP161 | Sweden | EF493288 | – | [27]
T. terrestris | CBS 703.85 | Netherlands | – | MH873600 | [47]
T. terrestris | Hilszczanska D. 1-IBL | Poland | FJ532478 | – | [4]
T. terrestris | P17_M2_772 | Poland | KM409440 | – | [26]
T. terrestris | UK14 | Estonia | – | DB018696 | [5]
T. versatilis | MEXU:27094 | Mexico | KC595628 | – | [4]
T. versatilis | UNAM:FCME26141 T | Mexico | NR154492 | – | [4]
T. vialis | Thv1 | – | – | AJ406478 | [28]

T. wuliangshanensis | CLZhao 4107 T | China | MZ400671 | MZ400677 | Present study
T. wuliangshanensis | CLZhao 21020 | China | MZ400672 | MZ400678 | Present study

Maximum parsimony (MP) analysis was applied to the ITS and nrLSU dataset followed Zhao and Wu [37]. Tree construction procedure was performed in PAUP* version 4.0b10 [48]. All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using bootstrap analysis with 1000 replicates [49]. Descriptive tree statistics: tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each Maximum Parsimonious Tree generated. Datamatrix was also analyzed using Maximum Likelihood (ML) approach with RAxML-HPC2 through the Cipres Science Gateway (www.phylo.org, accessed on 3 December 2021) [50]. Branch support for ML analysis was determined by 1000 bootstrap replicates.

MrModeltest 2.3 [51] was used to determine the best-fit evolution model for the data set for Bayesian inference (BI). BI was calculated with MrBayes 3.1.2 [52]. Four Markov chains were run for 2 runs from random starting trees for 160 thousand generations for ITS. The first one-fourth of all generations was discarded as burn-in. The majority rule consensus tree of all remaining trees was calculated. Branches were considered as
significantly supported if they received maximum likelihood bootstrap value > 60%, maximum parsimony bootstrap value > 50%, or Bayesian posterior probabilities > 0.90.

2.4. Pairwise Homoplasy Test

The Genealogical concordance phylogenetic species recognition analysis (GCPSR) is a tool used to check significant recombinant events. The data were analyzed using SplitsTree 4 with the pairwise homoplasy \( \Phi_w \) PH test to determine the recombination level within closely related species [53–55]. One-locus dataset (ITS and nrLSU) with closely related species were used for the analyses. PH test results lower than 0.05 (\( \Phi_w < 0.05 \)) indicates a significant recombination is present in the dataset. The relationships between closely related taxa were visualized by constructing split graphs from the concatenated datasets, using the LogDet transformation and splits decomposition options.

3. Results

3.1. Molecular Phylogeny

ITS+nrLSU dataset (Figure 2) included 14 sequences representing 9 species, ITS dataset (Figure 3) included 42 sequences representing 23 species, and the nrLSU dataset (Figure 4) consisted of 27 sequences representing 18 species. The ITS+nrLSU dataset had an aligned length of 1887 characters, of which 1514 characters are constant, 123 are variable and parsimony-uninformative, and 250 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious trees (TL = 616, CI = 0.7403, HI = 0.2597, RI = 0.7217, RC = 0.5343). Best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR + I + G (\{set nst = 6, rates = invgamma; preset statefreqpr = dirichlet (1, 1, 1, 1)\}). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.006269. Estimated base frequencies; \( A = 0.249341, C = 0.218571, G = 0.275562, T = 0.256526 \); substitution rates \( AC = 1.282736, AG = 4.546435, AT = 0.637878, CG = 0.715981, CT = 11.556530, GT = 1.000000 \); proportion of invariant sites \( I = 0.502830 \); distribution shape parameter \( \alpha = 0.545315 \). The ITS dataset had an aligned length of 727 characters, of which 355 characters are constant, 87 are variable and parsimony-uninformative, and 285 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious trees (TL = 1026, CI = 0.5312, HI = 0.4688, RI = 0.7579, RC = 0.4026). Best model for the ITS dataset estimated and applied in the Bayesian analysis was GTR + I + G (\{set nst = 6, rates = invgamma; preset statefreqpr = dirichlet (1, 1, 1, 1)\}). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.009479. Estimated base frequencies; \( A = 0.219763, C = 0.258778, G = 0.243142, T = 0.278317 \); substitution rates \( AC = 1.165884, AG = 5.728342, AT = 0.893563, CG = 0.776446, CT = 8.106172, GT = 1.000000 \); proportion of invariant sites \( I = 0.125398 \); distribution shape parameter \( \alpha = 0.548666 \). The nrLSU dataset had an aligned length of 1393 characters, of which 1203 characters are constant, 63 are variable and parsimony-uninformative, and 127 are parsimony-informative. Maximum parsimony analysis yielded 1 equally parsimonious trees (TL = 360, CI = 0.5611, HI = 0.4389, RI = 0.5741, RC = 0.3221). Best model for the nrLSU dataset estimated and applied in the Bayesian analysis was GTR + I + G (\{set nst = 6, rates = invgamma; preset statefreqpr = dirichlet (1, 1, 1, 1)\}). Bayesian analysis and ML analysis resulted in a similar topology to MP analysis with an average standard deviation of split frequencies = 0.009402. Estimated base frequencies; \( A = 0.263240, C = 0.200643, G = 0.293575, T = 0.242542 \); substitution rates \( AC = 1.213148, AG = 7.899379, AT = 0.709533, CG = 0.649904, CT = 18.992697, GT = 1.000000 \); proportion of invariant sites \( I = 0.629441 \); distribution shape parameter \( \alpha = 0.755239 \).

The phylogram inferred from ITS+nrLSU, ITS, and nrLSU sequences (Figures 2–4) demonstrated that our specimens formed two isolated branches within Telephora while \( T. grandinioideis \) is sister to \( T. aurantiotincta \) Corner, and \( T. sikkimensis \) K. Das, Hembrom
and Kuhar, and *T. wuliangshanensis* are sister to a clade comprising *T. austrosinensis* T.H. Li and T. Li and *T. aurantiotincta*.

**Figure 2.** Maximum parsimony strict consensus tree based on the ITS+nrLSU sequences. Bootstrap support values for maximum likelihood (ML) equal to or higher than 60%, Bayesian Probability (PP) equal to or higher than 0.90, and maximum parsimony (MP) bootstrap proportions equal to or higher than 50% are mentioned above the branches (MP/ML/PP). Strains of the newly described species are depicted in blue.

**Figure 3.** Maximum parsimony consensus tree based on the ITS sequences. Bootstrap support values for maximum likelihood (ML) equal to or higher than 60%, Bayesian Probability (PP) equal to or higher than 0.90, and maximum parsimony (MP) bootstrap proportions equal to or higher than 50% are mentioned above the branches (MP/ML/PP). Strains of the newly described species are depicted in blue.
Figure 4. Maximum parsimony strict consensus tree based on the nrLSU sequences. Bootstrap support values for maximum likelihood (ML) equal to or higher than 60%, Bayesian Probability (PP) equal to or higher than 0.90, and maximum parsimony (MP) bootstrap proportions equal to or higher than 50% are mentioned above the branches (MP/ML/PP). Strains of the newly described species are depicted in blue.

Application of PHI test to the ITS and nrLSU tree-locus sequences revealed no recombination level within phylogenetically related species. No significant recombination events were observed between *Thelephora grandinioide* and *T. wuliangshanensis* and phylogenetically closely related species viz. *T. austrosinensis*, *T. ganbajan*, and *T. sikkimensis* (Figures 5 and 6). The test results of ITS sequence dataset show $\Phi_w = 0.8271$ ($\Phi_w > 0.05$) no recombination is present in the two new species with *T. aurantiotincta*, *T. austrosinensis*, *T. dominicana* Angelini, Losi and Vizzini, *T. ganbajan*, *T. pseudoterrestris* Corner, *T. sikkimensis* and *T. vialis* (Figure 5). The test results of nrLSU sequence dataset show $\Phi_w = 0.9964$ ($\Phi_w > 0.05$) no recombination is present in the two new species with *T. aurantiotincta*, *T. austrosinensis*, *T. dominicana*, *T. ganbajan*, *T. pseudoterrestris* and *T. vialis* (Figure 6).

Figure 5. Split graphs showing the results of PHI test for the ITS data of *Thelephora grandinioide* and *T. wuliangshanensis* and closely related taxa using LogDet transformation and splits decomposition.
PHI test results $\Phi_w \leq 0.05$ indicate that there is significant recombination within the dataset. New taxa are in red while, closely related species to new species are in other colors.

**Figure 6.** Split graphs showing the results of PHI test for the nrLSU data of *Thelephora grandinioides* and *T. wuliangshanensis* and closely related taxa using LogDet transformation and splits decomposition. PHI test results $\Phi_w \leq 0.05$ indicate that there is significant recombination within the dataset. New taxa are in red while, closely related species to new species are in other colors.

3.2. **Taxonomy**

*Thelephora grandinioides* C.L. Zhao and X.F. Liu, sp. nov. Figures 7A and 8.

MycoBank no.: MB840633.

**Holotype**—China, Yunnan Province, Puer, Zhenyuan County, Xieqipo Park, on the ground of pine-broadleaved mixed forest, 101°05′E, 24°18′N, 2113 m a.s.l., 1 October 2017, CLZhao 3406 (SWFC 00003406).

**Etymology**—*grandinioides* (Lat.): referring to the grandinoid hymenophore of the type specimens.

Basidiocarps—Annual, laterally stipitate, gregarious. Pilei medium-sized, coriaceous, infundibuliform, up to 9 cm long, 7 cm wide, 1.5 mm thick; fawn to isabelline when fresh, greyish brown on drying; proliferous from a central common base, rosulate, usually with several to many laterally confluent spathulate to flabelliform or valves, uplifted; the surface radially striate; margin thin, wavy. Hymenial surface grandinoid, olivaceous buff to clay-buff when fresh, clay-buff to slightly greyish brown on drying. Stipe cylindrical, up to 4 cm long, up to 1.5 cm in diameter. Context fleshy tough to leathery in fresh condition, corky to leathery in dried condition, up to 1 mm thick at the thickest portion of pileus, thinner at margin and thicker toward the base, pinkish buff to buff. Aculei, 6–8 per mm, 0.1–0.2 mm long, greyish brown. Odor mild when fresh, somewhat smelly when dried, or with the beef jerky flavor.

**Hyphal system**—Monomitic, generative hyphae with clamps, colorless, thick-walled, frequently branched, interwoven, 3–6.5 µm in diameter; IKI–, CB–; tissues turn to greenish grey to buff in KOH.
Hymenium—Cystidia of two types: (1) tubular cystidia, thick-walled, 35–60 × 5–7.5 μm; (2) septated cystidia, numerous, thick-walled, 40–75 × 6–8.5 μm; basidia cylindrical to clavate, slightly constricted in the middle to somewhat sinuous, with 4 sterig mata and a basal clamp, 27–62 × 5–7.5 μm, basidioles dominant, cylindrical, but slightly smaller than basidia.

Basidiospores—Subglobose to globose, nodulose to verrucose or ridged, echinulis 0.5–1 μm, fuscous vinaceous, thick-walled, with guttatae or not, IKI−, CB−, greenish grey to buff in 5% KOH, (5–)5.3–7.4(–7.8) × (3.8–)4–6.5(–7) μm (including ornamentations), L = 6.29 μm, W = 5.31 μm, Q = 1.18–1.21 (n = 60/2).

Additional specimens examined—China, Yunnan Province, Puer, Zhenyuan County, Xieqipo Forest Park, 101°05′ E, 24°18′ N, 1350 m a.s.l., on the ground of pine-broadleaved mixed forest, leg. C.L. Zhao, 1 October 2017, CLZhao 3408 (SWFC 00003408).

Notes—Thelephora grandinioides is phylogenetically closely related to T. aurantiotincta, T. dominicana, T. sikkimensis, while T. wuliangshanensis is sister to a clade comprising T. aurantiotincta and T. austrosinensis. The nucleotide differences of phylogenetically similar species to T. grandinioides are shown in Table 2. However, morphologically T. aurantiotincta differs from T. grandinioides by the larger basidiospores (6.5–9 × 5.5–6.5 μm vs. 5.3–7.4 × 4–6.5 μm) and shorter basidia (43–55 × 6.5–8 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4). In addition, the results of BLAST queries in NCBI based on ITS and nrLSU separately are shown in Table 3.

Morphologically, T. grandinioides is similar to T. aurantiotincta, T. fuscella Ces. ex Lloyd, T. gelatinoides Lloyd, T. griseozonata Cooke, T. intybacea Pers., T. japonica Yasuda and T. terrestris by having a grandinoid or odontoid hymenial surface. However, T.
aurantiotincta differs from T. grandinioides by larger basidiospores (6.5–9 × 5.5–6.5 μm vs. 5.3–7.4 × 4–6.5 μm) and shorter basidia (43–55 × 6.5–8 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4); T. fuscella differs in its shorter basidia (35–45 × 6–7 μm vs. 27–62 × 5–7.5 μm) with 2–4 sterigmata [3] (Table 4); T. gelatinoides differs in having larger basidiospores (7–9.5 × 6–9 μm vs. 5.3–7.4 × 4–6.5 μm) and basidia (45–70 × 8–10 vs. 27–62 × 5–7.5 μm) [3] (Table 4); T. griseozonata separates from T. grandinioides by having larger basidiospores (8–12 × 5–8 μm vs. 5.3–7.4 × 4–6.5 μm) [3] (Table 4); T. intybacea differs from T. grandinioides by having larger basidiospores (8–12 × 6–9 μm vs. 5.3–7.4 × 4–6.5 μm) and basidia (45–90 × 9–12 vs. 27–62 × 5–7.5 μm) with 2–4 sterigmata [3] (Table 4); T. japonica differs from T. grandinioides by having larger basidiospores (7–10 × 6–8 μm vs. 5.3–7.4 × 4–6.5 μm) and smaller basidia (40–55 × 8–10 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4); T. terrestris differs from T. grandinioides by having larger basidiospores (8–12 × 6–9 μm vs. 5.3–7.4 × 4–6.5 μm) and basidia (40–90 × 8–12 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4).

Table 2. The nucleotide differences of phylogenetically similar species to Thelephora grandinioides and T. sikkimensis.

| Species | Thelephora grandinioides | Thelephora wulianghshanensis |
|---------|--------------------------|-----------------------------|
| Specimens | CLZhao 3406 | CLZhao 4107 | CLZhao 21020 |
| Gene | ITS (bp) | nrLSU (bp) | ITS (bp) | nrLSU (bp) | ITS (bp) | nrLSU (bp) |
| T. aurantiotincta 115437 | NA | 13 | NA | 13 | 24 | NA |
| T. aurantiotincta 346–518 | 1 | NA | 1 | 42 | NA | 40 |
| T. aurantiotincta 520625MF420 | 8 | NA | 8 | 78 | NA | 76 |
| T. austrosinensis GDGM 48891 | 89 | 28 | 89 | 28 | 36 | 17 |
| T. austrosinensis GDGM 48867 | 89 | 29 | 89 | 29 | 37 | 18 |
| T. austrosinensis GDGM 48899 | 87 | 30 | 87 | 30 | 35 | 18 |
| T. dominicana JBSD126510 | 84 | 32 | 83 | 32 | 27 | 26 |
| T. ganbajun Gb151 | 98 | NA | 98 | NA | 53 | NA |
| T. ganbajun Gb152 | 85 | NA | 85 | NA | 78 | NA |
| T. ganbajun HMAS 276818 | NA | 29 | NA | 29 | 18 | NA |
| T. ganbajun ZRL20151295 | NA | 27 | NA | 27 | 18 | NA |
| T. pseudoterrestris UK34 | 87 | NA | 87 | NA | 48 | NA |
| T. pseudoterrestris TAA159625 | 64 | NA | 64 | NA | 48 | NA |
| T. sikkimensis KD1603 | 45 | NA | 45 | NA | 76 | NA |
| T. sikkimensis KD1642 | 43 | NA | 43 | NA | 77 | NA |
| T. vialis Thv1 | NA | 26 | NA | 26 | 20 | NA |

Table 3. The top ten species results of Blast search of Thelephora grandinioides and T. sikkimensis sequences.

| Species | Max Score | Total Score | Query Cover | E Value | Identi | Species | Max Score | Total Score | Query Cover | E Value | Identi |
|---------|-----------|-------------|-------------|---------|--------|---------|-----------|-------------|-------------|---------|--------|
| T. aurantiotincta | 1109 | 1109 | 94% | 0.0 | 98.87% | T. ganbajun | 1011 | 1011 | 97% | 0.0 | 95.32% |
| T. sikkimensis | 907 | 907 | 96% | 0.0 | 92.36% | T. ganbajun | 1005 | 1005 | 97% | 0.0 | 95.16% |
| T. sikkimensis | 872 | 872 | 91% | 0.0 | 92.61% | T. ganbajun | 1000 | 1000 | 97% | 0.0 | 95.01% |
| To. lateritica | 806 | 806 | 98% | 0.0 | 89.12% | T. ganbajun | 1000 | 1000 | 97% | 0.0 | 95.01% |
Table 4. Comparison of Basidiospore, Basidia, Cystidia, Host, Substrate, Location and corresponding references of *Thelelphora* species. The characteristics of newly generated taxa are shown in black bold.

| Species          | Basidiospore (µm) | Basidia (µm) | Cystidia Sterigmata (µm) | Host/Substrate | Location | Reference |
|------------------|-------------------|--------------|--------------------------|----------------|----------|-----------|
| *Thelelphora*    |                   |              |                          |                |          |           |
| *altibolibrunea* | 8.5–10.5(–11) × 6–8.5 | 55–80 × 11–13 | 4                        | On the ground; Acer rubrum L., *Amelanchier canadensis* (L.) Medik., *Amelanchier* sp., *Carpinus caroliniana* Walter | Canada, USA | [3,56–58] |
| *alta*           | 7.6–8.5 × 6–7     |              |                          | On the ground | Borneo, Brunei Darussalam, Indonesia, Malaysia | [3,58,59] |
| *anthocephala*   | (7–)8–10(–11) × (5–)6–8.5 | 40–80 × 7–11 | 2–4                      | On the ground in woods; *Fagus* sp., *Quercus* sp. | Austria, China, Denmark, Italy, Netherlands, North Temperate, Norway, Russia, Spain, Slovenia, Sweden, USA, UK | [3,58,60–62] |
| *arbascula*      | 6–7 × 5.5–6       |              |                          | On the ground in forest | India, Mexico, Papua New Guinea; Ukraine | [3,63] |
| *atra*           | 9–13 × 8–11       | 50–100 × 9–12 | 2–3                      | On the ground | Spain, Poland | [3,64,65] |
| *atrocitina*     | 8–13 × 6.5–9      | 45–75 × 8–13 | 2–4                      | On the ground in woods (Abies sp., Carpinus sp., Fagus sp., Quercus sp.) | Austria, Belgium, Brazilian, Czechoslovakia, France, Germany, Netherlands, Spain | [3,66] |
| *aurantiotaicta* | 6.5–9 × 5.5–6.5   | 43–55 × 6.5–8 | 4                        | on the ground in humus in mountain forest | China, Malaysia | [3,67] |
| *austrisinensis* | (5.2–)5.7–6.3(–6.7) × (4.6–)5.0–5.4(–5.8) | 15–24 × 5–7 | 4                        |                          | China | [5] |
| Species          | Range       | Habitat                                      | Locations                                      |
|------------------|-------------|----------------------------------------------|------------------------------------------------|
| T. bresadela     | 5–7         | On the ground in woods                       | Hungary, Czechoslovakia [3]                   |
| T. brunneoviolacea | 7.5–11 × 6–8.5 | 2–4 On the ground in the forest              | Congo [3]                                      |
| T. caespitans    | 7–8 × 5–6   | On the ground                               | Canada, USA [3]                               |
| T. carophyllea   | 5–10 × 5–8  | On sandy ground in coniferous woods; Betula nigra L., Larix occidentalis Nutt., Pinus silvestris L., Salix sitchensis Sanson ex Bong. | Canada, China, Georgia, India, Mexico, North temperate, Poland, Russia, Spain, USA [3,20,60,62,64,67] |
| T. corborea      | 8–11 × 6–8.3| 2–4 On the ground in dry forest              | Congo [3]                                      |
| T. cercicornis   | 7–8.5 × 6.5–7.5 | On the ground                               | Bahamas, Mexico, USA [3,68]                   |
| T. cercina       | 6–7.5 × 5–6 | On the ground                               | China [3]                                      |
| T. congesta      | 8.5–11 × 5.5–8.3 | 30–40 × 7–8 4 On the ground                 | Australia [3]                                 |
| T. crassitexta   | 9–11 × 6–9  | 65–100 × 10–12 2–4 On the wood              | Borneo [3]                                     |
| T. cuticularis   | 7.5–12.5 × 6–9 | On mossy bark at the base of trees and on fallen twigs; Juniperus virginiana L. | UK, USA [3,56,57]                            |
| T. cylindrica    | 8–11 × 6.5–9 | 80–110 × 11–14 4 On the ground in the forest | Japan, Java, Sumatra, [3]                     |
| T. dactylites    | 6.5–8 × 5–7 | 4 On the ground                               | China [3]                                      |
| T. dentosa       | 7–9 × 6.5–8 | 18–46 × 8–13 4 19–36 × 4.5–7.5 On dead twigs and leaves | Brazil, Cuban, Hait, Indian, Jamaica, Mexico [3,66,69] |
| T. dominicana    | 8–9.6 × 7.2–8.8 | (30–)50–60 × 10–12 4 On deciduous forest litter; | Dominican Republic, Mexico [14,25]           |
| T. erebia        | 9–12 × 7–10 | 45–60 × 10–12 2 On the ground in the forest | Malaysia [3]                                  |
| T. fragilis      | 6–7 × 4–5   | 14–28 × 5–7 2–4 On the ground in the forest | Malaysia, Philippines [3]                     |
| T. fuscoide      | 7–9 × 6–8   | On the ground in the forest                  | India, Malaysia, Pakistan, USA [3]            |
| T. fuscella      | 6–8 × 4.5–6 | 35–45 × 6–7 2–4 On the ground; Symbiotic with plants | China, Europe, India, Japan, Malaysia, Nepal, North America, Singapore [3,11,70] |
| T. ganbajou      | 7–12 × 6–8  | 25–35 × 9–12 4 52–80 × 7–14 In the root of Pinus yunnanensis Fr. and Pinus kesjya var. langbianensis | China [5,18,21]                               |
| T. gelatinoidae  | 7–9.5 × 6–9 | 45–70 × 8–10 4 On the ground in the forest  | China, India, Malaysia [3]                    |
| T. gelidioides   | 6–8 × 4.5–6 | On the ground in the forest                  | Singapore [3]                                  |
| T. grandinioidea | (5–)35.3–7.4(–7.8) × (3.8–)4–6.5(–7) 27–62 × 5–7.5 4 35–60 × 5–7.5 On the ground of pine-broadleaved mixed forest | China Present study                            |
| T. grisezonata   | 8–12 × 5–8  | On sandy ground in pine woods (Pinus sp.)     | Germany, Puerto Rico, New Zealand, USA, Virgin Islands [3,56] |
| T. intyacea      | 8–12 × 6–9  | 45–90 × 9–12 2–4 In pine woods; Cedrus de- | European, New Zealand, North [3,56]           |
| Species       | Habitats                                                                 | Hosts                                                                 | References |
|--------------|--------------------------------------------------------------------------|----------------------------------------------------------------------|------------|
| *T. investiens* | 8.5–10 × 7–9.5 | On the ground in forest | Malaysia [3] |
| *T. japonica*  | (6–)7–10 × (5.5–)6–8 | 40–55 × 8–10 | 2–4 | On the ground, often encrusting small living plants; Ectomycorrhizal, humicolous, gregarious in mixed forest of *Populus nigra* L. and *Salix alba* L. | China, India, Japan [3,12] |
| *T. lutoso*    | 5–6 × 3.5–4 | On the ground in roads and in woods | USA [3,56] |
| *T. luzonensis* | 5–6.5 × 4.7–5.7 | 2–3 | On ground in hill dipterocarp forest | Philippines, USA [3] |
| *T. magnifica* | 9–12 × 7–9 | 60–75 × 8–10 | 2–3–4 | On mossy ground | Brunei, Malaysia [3,71] |
| *T. magnispora* | 11–12 × 9–11 | 50–70 × 10–11 | 4 | In woods | Indian, Jamaica, USA [3,72] |
| *T. mollissima* | 8.5–10.7 × 6–7.7 | | | | European, China [3,60] |
| *T. multipartita* | 6–8.5(–)9 × 4.7–7 | | | On the ground in frondose woods; *Quercus* sp. | Canada, China, Japan, USA, Venezuela [3,56,60] |
| *T. nigrescens* | 6–9 × 5–8 | 30–50 × 7–10 | 4, rarely 2–4 | On the ground | Brunei Darussalam, China, Indonesia, Japan, Philippines [3,58] |
| *T. palmata*    | 8–12 × 7–9 | 70–100 × 9–12 | 2–4 | On the ground in coniferous woods; *Pinus* sp.; *Quercus humboldtii* Bonpl. | Colombia, France, North temperate, Russia, Sweden, UK, USA [3,56] |
| *T. paraguayensis* | 6.5–8.5 × 4.5–7 | 4 | On the ground in woods | Brazil, Columbia; Paraguay [3,58] |
| *T. pendens*    | 8–10 × 7–8 | 40–50 × 10–12 | 4 | Rotten wood in the forest | Malaysia [3] |
| *T. penicillata* | 7–10 × 5–8 | 30–75 × 7–11 | | On the ground and crusted leaves, branches, grass; *Quercus coccifera* L. | Canada, China, Galapagos Islands [3,60], India, Russia, UK |
| *T. phyllophoroides* | 5–7.5 × 4.5–5.5 | | | On the ground | Japan [3] |
| *T. pseudoterrestris* | 9–11.5 × 7–9 | 50–60 × 12–14 | | On the ground in the forest, leaves | Malaysia [3] |
| *T. pseudoversatilis* | (6–)7–8(–)8.5 × (5–)5.5–6(–)7 | 47–55 × 9–12 | 4 | Sub-perennial tropical forest | Mexico [4] |
| *T. ranarioides* | 7–12.5 × 5–8.5 | 46–70 × 5–12 | 2–4, rarely 6–8 | 50–150 × 5–12 | On the ground under *Cassiopea equisetifolia* L. | Australia, Borneo, Java, Malaysia [3] |
| *T. regularis*  | 6–8 × 4.5–6.5 | 35.2–102.4 × 6.4–9.6 | 4 | In moss in wet places and in humus; Ectomycorrhizal, humicolous, scattered | Canada, India, under *Salix exigua* J.F.Gmel., *S. alba* L. and *Populus nigra* L. | [3,12,56] |
| *T. scissilis*  | 6–8.5 × 5–7 | 4 | On the ground in oak forest | Borneo, India, Indonesia | [3] |
| *T. sikkimensis* | 6–(7.3)–8.8 × 5–(6.26)–7 | 35–65 × 7–9 | 4 | 30–50 × 3–10 | On the ground of *Cassiopea equisetifolia* | India [26] |
| *T. spiculosa*  | 8–12 × 7.5–9 | 60–70 × 9–12 | | Encrusting coniferous needles of *Pinus* sp. | France, Japan, Sweden, UK [3,57] |
| *T. tenuis* | 7–8 × 6–7 | | | On sandy ground | China, Russia [3] |
| *T. terrestris* | 8–12 × 6–9 | 40–90 × 8–12 | 2–4 | On the ground in coniferous, on roots, syumps and seedlings; *Picea abies* L.; *Picea sitchensis* (Bong.) Carr. | Australia, Bavaria, Brazil, China, Europe, Germany, India, Jamaica, Japan, Mexico, New Zealand, North America [3,21,60,64,67,68,72] |
| Species               | Size (mm) | Location/Notes                                      |
|----------------------|-----------|----------------------------------------------------|
| *T. versatilis*      | 6–7(8.5) × 4(5–6(6.5) | Deciduous and sub-perennial tropical forest, Mexico [4] |
|                       | 30–86 × 7(8–11)              | On the ground in forest in Mexico, China, India, Japan, North America, USA [3,12,56,60,73] |
| *T. vialis*          | 4.5–7(–8) × 4.5–6(–6.5) 26.4–64.0 × 5.6–10.4 | Denmark, Estonia, France, Germany, North temperate, Norway, Spain, Russia, Sweden, UK, USA [14] |
|                       | 40–65 × 7.5–12                | Colonizes all kinds of wood debris, China, Present study |
| *T. wakefieldiae*    | 40–65 × 7.5–12                | Colonizes all kinds of wood debris, China, Present study |
|                       | 40–65 × 7.5–124               | China, Present study |
| *T. wulangshanensis* | 5(–5.5)–8(–7.1) × (3.7)–4.5–7(–7.6) | 30–60 × 5–9.5 4 28–55 × 3–7.5 On the ground of pine-broadleaved mixed forest, China, Present study |
| *T. zeylanica*       | 8–12 × 4.8.5                     | On the ground, Ceylon, [3] |

Thelephora grandinioides morphologically resembles *T. ganbajun* and *T. ramarioides* D.A. Reid due to the presence of cystidia. However, *T. ganbajun* differs from *T. grandinioides* by its larger basidiospores (7–12 × 6–8 μm vs. 5.3–7.4 × 4–6.5 μm), shorter basidia (25–35 × 9–12 μm vs. 27–62 × 5–7.5 μm), and larger cystidia (52–80 × 7–14 μm vs. 35–60 × 5–7.5 μm) [17] (Table 4); *T. ramarioides* differs from *T. grandinioides* by its larger basidiospores (7–12.5 × 5–8.5 μm vs. 5.3–7.4 × 4–6.5 μm) and smaller basidia (46–70 × 5–12 μm vs. 27–62 × 5–7.5 μm) [3] (Table 4).
Figure 8. Microscopic structures of Thelephora grandinoides (holotype CLZhao 3406). (A) A section of hymenium; (B) A section of hymenium; (C) A section of hymenium; (D) A section of hymenium; (E) Generative hyphae with clamps; (F) Basidia; (G) Basidioles; (H) Tubular cystidia; (I) Septated cystidia; (J) Basidiospores. Bars: (A) = 50 µm, (B–I) = 20 µm.

Thelephora wuliangshanensis C.L. Zhao and X.F. Liu, sp. nov. Figures 7B and 9.

MycoBank no.: MB840634.

Holotype—China, Yunnan Province, Puer, Jingdong County, Huangcaoling, Wuliangshan National Nature Reserve, 100°45' E, 24°23' N, 2313 m a.s.l., on the ground of pine-broadleaved mixed forest, leg. C.L. Zhao, 5 October 2017, CLZhao 4107 (SWFC 00004107).

Etymology—wuliangshanensis (Lat.): referring to the provenance (Wuliangshan) of the type specimens.

Basidiocarps—Annual, laterally stipitate, gregarious. Pilei small to medium-sized, coriaceous, infundibuliform, up to 5.5 cm long, 4.5 cm wide, 1 mm thick; buff to salmon when fresh, pinkish buff to cinnamon-buff on drying; proliferous from a central common base, usually with several to many laterally confluent spathulate to flabelliform, uplifted; the surface radially black striate; margin thin, serrulate. Hymenial surface smooth, umb to coffee when fresh, coffee on drying. Stipe cylindrical, up to 2 cm long, up to 5 mm in diameter. Context fleshy tough in fresh condition, leathery in dried condition, up to 0.7 mm thick at the thickest portion of pileus, thinner at margin and thicker towards the base, pinkish buff. Odor mild when fresh, somewhat with the beef jerky flavor.
**Hyphal system**—Monomitic, generative hyphae with clamps, colorless, thick-walled, frequently branched, interwoven, 2.5–6 µm in diameter; IKI−, CB−; tissues turn to greenish grey in KOH.

**Hymenium**—Cystidia tubular, thick-walled, 28–55 × 3–7.5 µm; basidia barrel-shaped to slightly clavate, with 4 sterigmata and a basal clamp, 30–60 × 5–9.5 µm, basidioles dominant, clavate, but slightly smaller than basidia.

**Basidiospores**—Subglobose to globose, nodulose to verrucose, echinulis 0.5–1 µm, umber purple, thick-walled, with guttatae or not, IKI−, CB−, greenish grey to buff in 5% KOH, (5–)5.2–8.7 (–9.3) × (3.7–)4.5–7.2 (–7.6) µm (including ornamentations), L = 7 µm, W = 5.66 µm, Q = 1.23–1.25 (n = 60/2).

**Additional specimens examined**—China, Yunnan Province, Puer, Zhenyuan County, Huangcaoling, Wuliangshan National Nature Reserve, 100°57′ E, 23°57′ N, on the ground of pine-broadleaved mixed forest, 8 October 2020 CLZhao 21020 (SWFC 00021020).

**Notes**—Thelephora wuliangshanensis is sister to a clade comprising T. aurantiotincta and T. austrosinensis in phylogeny; and the nucleotide differences of phylogenetically similar species to T. sikkimensis are shown in Table 2. Thelephora sikkimensis differs from T. grandinioides by its shorter cystidia (30–50 µm vs. 35–60 µm) and hairy basidiocarp surface [26] (Table 4). Thelephora aurantiotincta separates from T. wuliangshanensis by smaller basidia (43–55 × 6.5–8 µm vs. 30–60 × 5–9.5 µm) [3] (Table 4); while T. austrosinensis differs from T. wuliangshanensis by its smaller basidiospores (5.7–6.3 × 5.0–5.4 µm vs. 5.2–8.7 × 4.5–7.2 µm) and basidia (15–24 × 5–7 µm vs. 30–60 × 5–9.5 µm) [27] (Table 4). In addition, the results of BLAST queries in NCBI based on ITS and nrLSU separately are shown in Table 3.
Figure 9. Microscopic structures of *Thelephora wuliangshanensis* (Holotype CLZhao 4107). (A) A section of hymenium; (B) A section of hymenium; (C) A section of hymenium; (D) A section of hymenium; (E) Generative hyphae with clamps; (F) Basidia; (G) Basidioles; (H) Cystidia; (I) Basidiospores. Bars: (A–I) = 20 µm.

4. Discussion

In the present study, two new species, *Thelephora grandinioides* and *T. wuliangshanensis* are described based on phylogenetic analyses and morphological characteristics. In addition, the PHI test (Figures 5 and 6) was carried out to confirm there is no recombination present in the two new species compared with closely related taxa.

*Thelephora*, a genus with diverse basidiocarp forms, are widely distributed worldwide [3,26,28]. Basidia form is an important characteristic of intraspecific identification in *Thelephora*, and most species of *Thelephora* have 4-spored basidia, there are 2-spored (*T. crebia*), 2–3-spored (*T. atra* and *T. luzonensis*), 2–4-spored (*T. anthocephala*, *T. atrocintra*, *T. bruneoviolacea*, *T. caryophyllea*, *T. ciberea*, *T. crassitexta*, *T. fragilis*, *T.
fuscella, T. intybea, T. japonica, T. magnifica, T. nigrescens, T. palmata, and T. terrestris) and sometimes there are 6–8-spored (T. ramaroioides) [3–5,21] (Table 4).

Thelephora is closely related to Tomentella both in morphology and phylogeny [5,10,14,25,29,74]. Molecular phylogenetic analyses of previous studies showed that the taxa of Thelephora and Tomentella are non-monophyletic groups, and they are intermixed in molecular phylogeny [4,5,25,29,31,33]. Traditionally, the form of basidiocarps is the most important characteristic in distinguishing Thelephora and Tomentella, which are resupinate in Tomentella, but erect, with varied forms, to partially resupinate in Thelephora [3,14,24,25,29,34,74]. The variations in basidiocarp form may also complicate the characteristics of taxa [75,76], and the results of the morphological investigations and molecular phylogenetic analyses suggested that basidiocarp reduction happened several times independently across the evolution of thelephoroid fungi [14,25]. Taxa with reduced basidiocarps should be taken into account in the diagnoses of genera for which the initial descriptions did not cover a real spectrum of polymorphism and trends of morphological rationalization in connection with colonization of specific habitats [14,25,76]. According to molecular data, only one genus may be recognized, and Tomentella will be merged into Thelephora [25].

In the habitat and distribution, thelephoroid fungi have a circumglobal distribution, ranging from polar deserts [9] to tropical forests [3], but their peak diversity is observed within the boreal zone of the planet [14,33]. Most of the species in this group have ectomycorrhizal associations [77,78], but it is also capable of destroying wood debris as white rot producers [14,15]. The species of Thelephora are a widely distributed group found on six continents except Antarctica [3,5,14,17,26], mainly distributed across Europe in Austria, Bavaria, Belgium, Denmark, Estonia, France, Georgia, Germany, Italy, Netherlands, Norway, Poland, Russia, Slovenia, Spain, Sweden, UK and Ukraine [3,5,28,58,59,62,65,66,76]; additionally, the most-common substrata are hardwood and conifer [3,5]. It is also distributed in Asia (Borneo, China, Japan, India, Malaysia, Nepal, Pakistan, Philippines, Sri Lanka, and Singapore) [3,5,56–58,60,67,70,71], North America (Bahamas, Canada, Cuba, Dominican Republic, Haiti, Jamaica, Mexico, and USA) [3,5,14,25,56–58,62,63,69], South America (Uruguay) [3], Oceania (Australia and Papua New Guinea) [3], and Africa (Congo and Southern Africa) [3,5,56] seen in Table 4. Twenty-one species of Thelephora have been reported from China (including our two new species), in which T. ganbajun and T. vialis Schwein. are the two most commonly reported taxa, and the former is one of the most popular edible fungi in Southwest China [5,17–20,60,61,67–79]. The diversity of Thelephora in China is still not well-known, especially in the subtropical and tropical regions and many recently described taxa of thelephoroid fungi are from these areas [5,67]. Thelephora grandinioides and T. wuliangshanensis are also from subtropics. According to our statistics, twenty-one Thelephora species have been recorded in China (Table 4), in which 7 are edible and 4 are medicinal (T. aurantiotincta, T. ganbajun, T. terrestris, and T. vialis) with anticancer properties, treat leukemia, boost immunity, and are an anti-allergic agent (Table 5). Fleshy to coriaceous basidiocarps, a mild odor, and beef jerky flavor are characteristics of T. grandinioides. Several Thelephora species are known as edible or medicinal mushrooms, while our new species are potential edibles thus, secondary metabolite analyses of the two new species should be carried out in the future.

Table 5. Edible and medicinal species of Thelephora.

| Species              | Edible Value | Medicinal Value | Medicinal Efficacy | Reference       |
|----------------------|--------------|-----------------|--------------------|-----------------|
| Thelephora anthocephala | P            |                 | Anticancer         | [80]            |
| T. aurantiotincta     | Y            |                 | Anticancer         | [73,80–85]      |
| T. austrosinensis     | Y            |                 |                    | [5]             |
| T. caespitulans       | P            |                 | Anticancer         | [82]            |
| T. carophyllea        | P            |                 | Anticancer         | [82]            |
| T. fuscella           | Y            |                 |                    | [81]            |
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“Y” means have edible or medicinal value; “P” means have edible or medicinal potential.
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