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New Species of *Tomentella* (Thelephorales, Basidiomycota) from Temperate Continental Mountain Climate of China (Xinjiang Region)

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Abstract: Species in the genus *Tomentella* are distributed throughout the temperate and tropical regions worldwide, but few studies associated with the taxonomy and phylogeny of this genus had been reported from Northwest China. In this paper, molecular phylogenetic analyses of the nuclear ribosomal ITS (internal transcribed spacer: ITS1-5.8S-ITS2) and LSU (large subunit: 28S) sequences combined with morphological characteristics identified three new species from Xinjiang Autonomous Region in Northwest China, which were named *T. aurantispora*, *T. kanasensis*, and *T. schrenkiana*. Similar macromorphological and anatomical characteristics are shared by these new species: arachnoid basidiocarps; byssoid sterile margins; utriform basidia with a clamp connection at the base; the absence of rhizomorphs and cystidia; and slightly thick-walled, subglobose to globose basidiospores. Among these new species, the color of the hymenophoral surface, the size of the basidiospores, and some other features can be used for species delimitation. The new species and closely related species in the phylogenetic tree were discussed, and a key to the identified species of *Tomentella* from China was provided.

Keywords: ectomycorrhizal fungi; phylogeny; resupinate thelephoroid fungi; taxonomy; temperate mixed forest

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1. Introduction

Studies on the genus *Tomentella* Pers. have undergone a long and convoluted history in several regions worldwide. The name *Tomentella* was used first by Persoon in 1799 [1] and was published as a genus by Patouillard in 1887 [2]. The initial studies on taxonomy of this genus were mainly from North America and Eurasia [3,4], and some species were also reported from West India, Australia, and New Zealand [5–7]. In recent years, more species were subsequently reported from many regions worldwide, including Asia, Africa, South America, and so on [8–11].

Tomentella is closely related to *Odontia* Pers. and *Thelephora* Ehrh. ex Willd. They belong to Thelephoraceae Chevall., Thelephorales Corner ex Oberw. of Basidiomycota R.T. Moore [3–5]. *Odontia* is morphologically similar to *Tomentella* by the resupinate basidiocarps with gray to brown colors and the generative hyphae with simple septa or clamps [3,12]. The basidiocarps of *Odontia* and *Tomentella* are often found on fallen branches, leaves, twigs, and decayed wood debris in coniferous and deciduous forests [3,9,13]. The similar morphological features and habitats make it difficult to distinguish these two genera, and species of *Odontia* were originally recognized as *Tomentella*. Species of *Tomentella* had been found to form ectomycorrhizae with jack pine since the 1980s [14]. However, *Odontia* was declared a non-mycorrhizal genus, verified by stable isotope and phylogenetic analyses, and treated as a separate *Tomentella* [12,15]. *Thelephora* was categorized as an ectomycorrhizal genus slightly earlier than *Tomentella* [16,17], and species in this group often form paraphyletic clades in the phylogenetic trees [9,18]. *Thelephora* and *Tomentella* possess obviously different types of basidiocarps, which are epigeous and resupinate, respectively [3,19]. The tomentella-thelephora lineage has been found to be one of the most species-rich ectomycorrhizal (ECM) lineages in forest ecosystems [18,20,21].

ECM fungi have attracted much attention over the years, because they can play an essential role in nutrient cycling [22], seedling establishment [23], tree growth rate and survival [24,25], and biodiversity maintenance [26] in natural ecosystems. ECM fungi can produce conspicuous or inconspicuous basidiocarps, and about 70% of basidiomycete species with inconspicuous basidiocarps are comprised of resupinate tomentelloid fungi [27]. In China, a few studies on ECM fungal diversity and the community structure of Fagaceae, Pinaceae, and Salicaceae revealed that *Tomentella* was one of the most species-rich genera in some forests [28–31]. Studies on the ECM fungal communities of *Quercus fabri* Hance., *Q. liaotungensis* Koidz. in the family Fagaceae have identified 6 and 33 taxonomic units or species of *Tomentella*, respectively [29,32,33]. In addition, tomentella-thelephora lineages associated with Fagaceae species from 30 forest sites in China account for 26.4% of the total sequences in 92.8% of the samples [31]. Studies have also reported that the tomentella-thelephora lineage can account for 38.2% of the total ECM fungal reads from the mycorrhizal root tips of Betulaceae, Fagaceae, Pinaceae, and Tiliaceae [34]. These studies revealed that there are a large number of *Tomentella* species in China, but studies based on basidiocarps of *Tomentella* species are scarce in Xinjiang Autonomous Region of Northwest China. At present, 48 species distributed in Liaoning, Heilongjiang, and Jilin Provinces of northeastern China have been reported based on the collected specimens [10,11].

In this study, basidiocarps were collected from three regions in Xinjiang Autonomous Region, including the Kanas National Nature Reserve, Tianshan Tianchi National Park, and Tianshan Grand Canyon National Forest Park. The regions belong to the typical temperate continental mountain climate with the obvious temperature fluctuations between day and night. Their average annual temperatures are –0.2 °C, 2.6 °C, and 5 °C, respectively [35,36], with average annual precipitation of 1065, 610, and 600–800 mm [35–37]. Kanas National Nature Reserve is the only area characterized by European Siberian flora in China [35], with the domination of *Abies sibirica* Ledeb., *Betula pendula* Roth., *Larix sibirica* Ledeb., *Picea obovata* Ledeb., *Pinus sibirica* (Loud.) Mayr, and *Populus tremula* Linn [36]. Tianshan Tianchi National Park is dominated by the Schrenk spruce, *P. schrenkiana* Fisch. et Mey., mixed with *B. tianschanica* Ruprecht, *B. pendula*, and *L. sibirica* [38]. *P. schrenkiana* accounts for more than 91% of the trees in the Tianshan Grand Canyon National Forest Park, with a mixture of *Populus davidiana* Dode., *Betula* spp. and some other coniferous and deciduous species [37]. During this study, three undescribed species of *Tomentella* were detected using morphological and phylogenetic analyses of DNA sequences. The aim of this work is to update the species diversity of *Tomentella* in China and assess its taxonomic and phylogenetic status.

2. Materials and Methods

2.1. Morphological Studies

The specimens were collected from the Kanas National Nature Reserve (KNNR), Tianshan Tianchi National Park (TTNP), and Tianshan Grand Canyon National Forest Park (TGCNFP) in Xinjiang Autonomous Region of Northwest China and were deposited at the herbarium of the Institute of Applied Ecology, Chinese Academy of Sciences (IFP).

The macromorphological characteristics of the basidiocarps were observed using a stereomicroscope (Nikon SMZ 1000: Tokyo, Japan) at 4× magnification, and the special color terms followed Kornerup [39]. Observations of the microscopic characteristics followed Lu et al. [10], and these were examined on dried specimens rehydrated in 2.5% KOH and stained in cotton blue and Melzer's reagent. The following abbreviations were used in the text: IKI = Melzer's reagent; IKI- = neither amyloid nor dextrinoid; KOH = 2.5% potassium hydroxide; CB = cotton blue; CB+ = cyanophilous; CB- = acyanophilous; L = mean spore length (arithmetic average of all spores in lateral face excluding ornamentation); W = mean spore width (arithmetic average of all spores in lateral face excluding ornamentation); Q = variation in the L/W ratios; and n = number of spores measured from every specimen. Micromorphological characteristics were studied at magnifications up to 1000× using a Nikon Eclipse E600 microscope (Tokyo, Japan) with phase contrast illumination. Drawings were made with a drawing tube. The surface morphologies of the basidiospores were investigated by scanning electron microscopy (SEM) (Phenom ProX, Phenom-World, Eindhoven, The Netherlands) at 10 kV accelerating voltage and in a secondary electron detector (SED) imaging mode. A thin layer of gold was sputter coated on the samples to avoid electrostatic charging.

2.2. Molecular Procedures and Phylogenetic Analyses

DNA was extracted from dried basidiocarps using a Thermo Scientific Phire Plant Direct PCR Kit (Thermo Fisher Scientific, Waltham, MA, USA). ITS and LSU regions were amplified with SSU1318-Tom/LSU-Tom4 [40] and LROR/LR7 primer pairs [41], respectively. Protocols for the polymerase chain reaction (PCR) amplifications of ITS and LSU regions were as follows: initial denaturation at 95 °C for 5 min, followed by 39 cycles at 95 °C for 30 s, × °C for 30 s (the annealing temperatures for SSU1318-Tom/LSU-Tom4 and LROR/LR7 were 62 °C and 47.2 °C, respectively) [40,41], 72 °C for 20 s, and a final extension at 72 °C for 1 min. PCR reaction products were confirmed on 1% agarose electrophoresis gels stained with ethidium bromide [42] and sequenced at the Beijing Genomics Institute (BGI) with the same primers. The sequencing data were assembled and manually modified with the software DNAMAN 8.0 (Lynnon Biosoft, San Ramon, CA, USA). All newly generated sequences have been verified [43] and were deposited at GenBank (Table S1). Two hundred and thirteen sequences published in previous studies were downloaded from NCBI [44] and UNITE [45], and six newly generated sequences were used in this study. These sequences were aligned with MAFFT, which was available at http://mafft.cbrc.jp/alignment/server/large.html (accessed on 22 February 2021) [46] with manual adjustment. Output files in the FASTA format were directly loadable in the MAFFT online service and converted into NEXUS and PHYLIP files by ClustalX and EasyCodeMLv1.0, respectively [47]. Maximum likelihood (ML) analysis was conducted in RAxMLGUI1.5b2 with PHYLIP files under the GTRGAMMA model for 100 rapid bootstrap replicates under ML + rapid bootstrap mode [48]. Bayesian analysis was carried out in MrBayes 3.2.6 with NEXUS files [49] based on the Markov chain Monte Carlo (MCMC) technique, and the optimal models (K80 + G for ITS1 + 5.8S + ITS2 and GTR + I + G for LSU) for the ITS1, 5.8S, ITS2 and LSU regions were predicted using jModelTest 2.1.10 according to the corrected Akaike information criterion (AICc) [50]. As the model K80 + G was not available in MrBayes, and HKY + G as the most similar model was run instead of K80 + G. Four Markov chains were executed, starting from random trees and keeping one tree every 1000 generations until the average standard deviation of split frequencies was below 0.01. The initial 25% of trees were removed as burn-in.

3. Results

3.1. Phylogenetic Analysis

The combined dataset of the 217 sequences had an aligned length of 1675 sites with 669 bp ITS and 1006 bp LSU, which included 1077 constant characters, 87 parsimony-uninformative variable characters, and 511 parsimony-informative positions. A similar topology was obtained using ML and Bayesian analyses with two specimens of *Odontia ferruginea* as the outgroup [15], and only the ML tree is shown in Figure 1 with the ML bootstrap values and Bayesian posterior probabilities. The Bayesian analysis ran 10 million generations with an average standard deviation of split frequencies = 0.005051. Members of the genus *Tomentella* from regions in the world have been divided into 18 major clades with moderate support or high support (52 in ML/0.99 BPP for clade 1, 80 in ML/1.00 BPP for clade 2, 62 in ML/1.00 BPP for clade 3, 100 in ML/1.00 BPP for clade 4, 53 in ML for clade 5, 98 in ML/1.00 BPP for clade 6, 81 in ML/1.00 BPP for clade 7, 75 in ML/0.95 BPP for clade 8, 0.96 BPP for clade 9, 84 in ML/1.00 BPP for clade 10, 95 in ML/1.00 BPP for clade 11, 60 in ML/1.00 BPP for clade 12, 95 in ML/1.00 BPP for clade 13, 89 in ML/1.00 BPP for clade 14, 96 in ML/1.00 BPP for clade 15, 99 in ML/1.00 BPP for clade 16, 82 in ML/0.97 BPP for clade 17, and 60 in ML) based on the phylogenetic analyses of combined ITS and LSU sequence data.

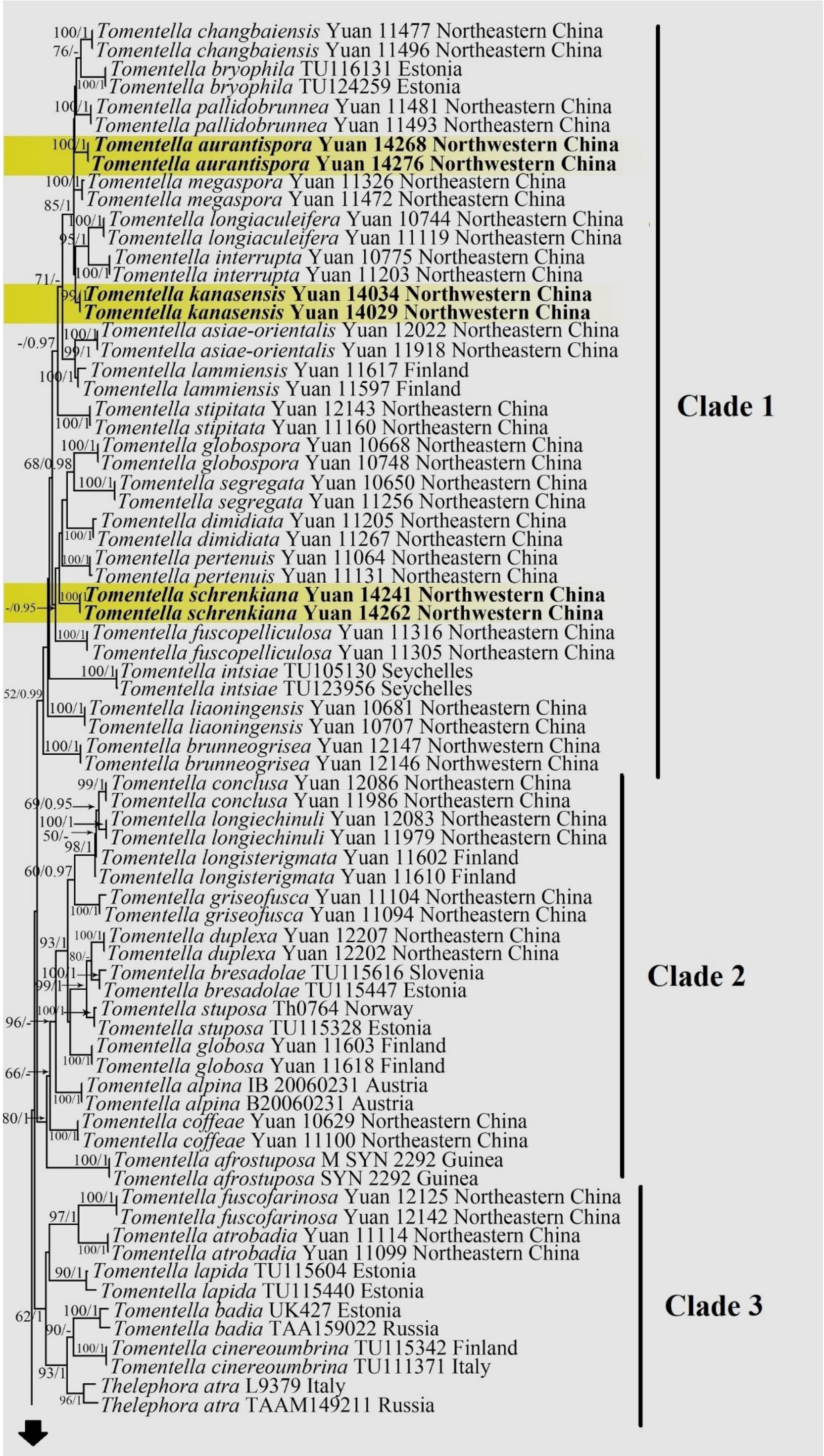

Figure 1. *Cont.*

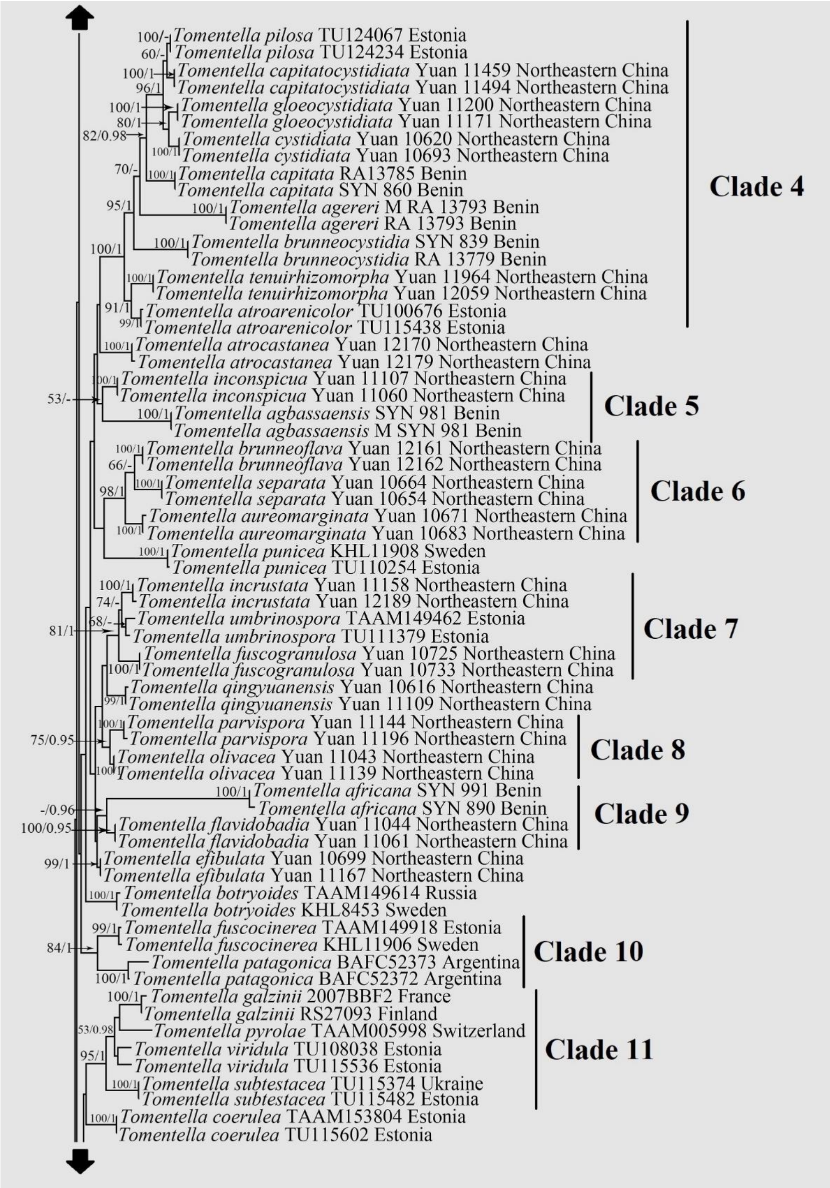

Figure 1. *Cont.*

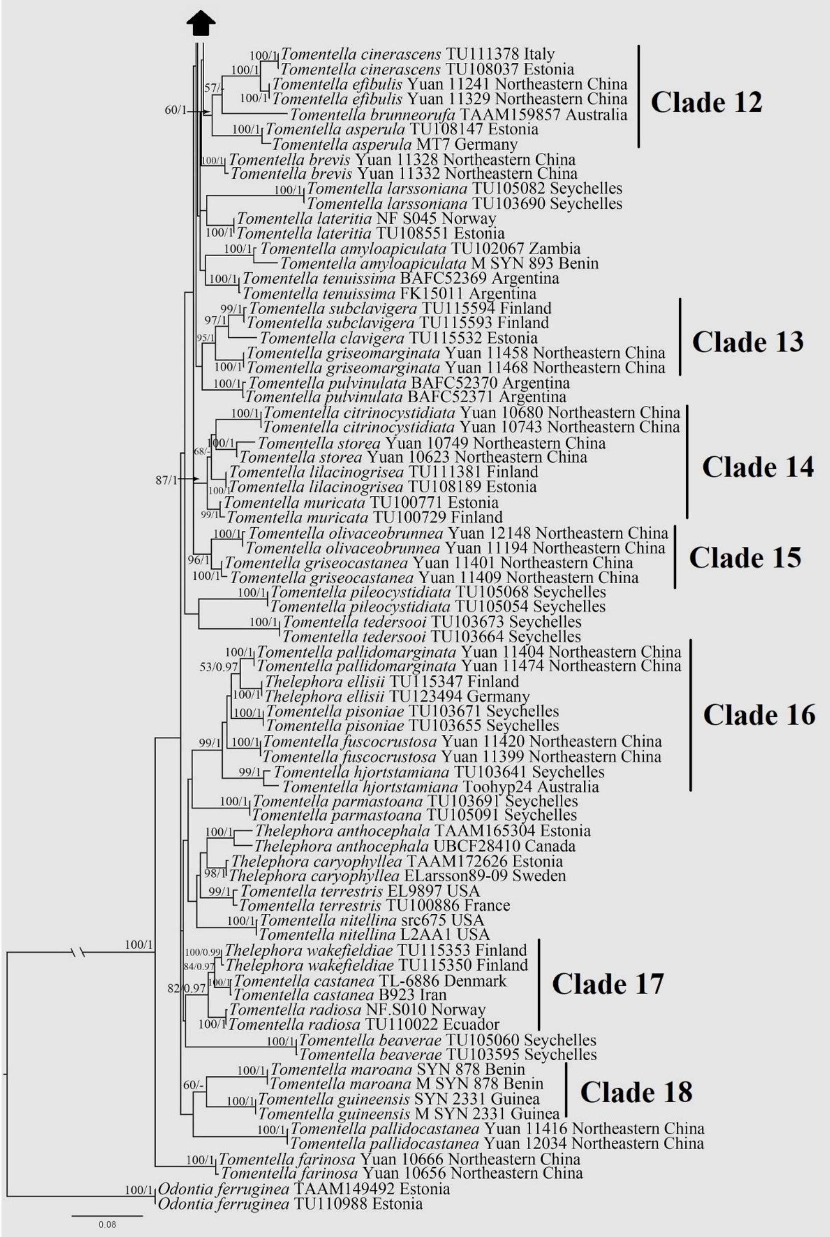

Figure 1. Maximum likelihood tree illustrating the phylogeny of *Tomentella aurantispora*, *T. kanasensis*, *T. schrenkiana*, and related taxa based on ITS + LSU nuclear rDNA sequences dataset. Branches are labeled with maximum likelihood bootstrap higher than 50% and Bayesian posterior probabilities higher than 0.95. The terminals indicate the regions where they were distributed. New species are in bold (black).

The six sampled specimens formed three strongly supported lineages (*T. aurantispora*, *T. kanasensis*, and *T. schrenkiana*: 100 in ML/1.00 BPP for *T. aurantispora* and *T. schrenkiana* and 99 in ML/1.00 BPP for *T. kanasensis*), which clustered together with other species from Northeast China, Estonia, Finland, and Seychelles in clade 1 with moderate support (52 in ML/0.99 BPP). The confirmed distribution range of a new species, *T. kanasensis*, spans Xinjiang and Jilin Provinces located in the northwest and northeast of China, respectively.

3.2. *Taxonomy*

Tomentella aurantispora X. Lu & H.S. Yuan, sp. nov.
MycoBank no. MB 834867
(Figures 2a, 3a,b and 4)

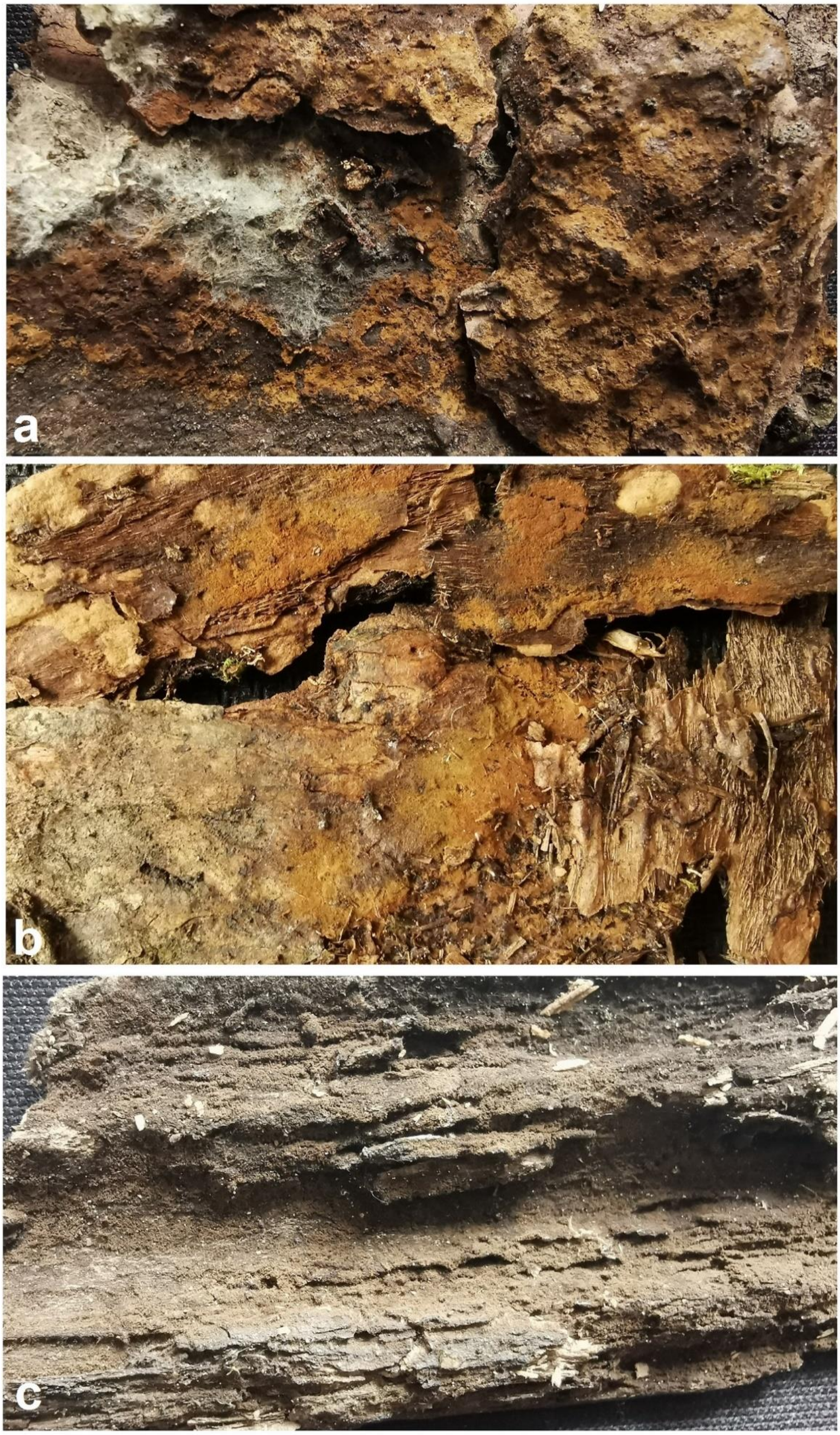

Figure 2. Basidiocarps of *Tomentella* species. (**a**) *T. aurantispora* (holotype Yuan 14268); (**b**) *T. kanasensis* (holotype Yuan 14034); (**c**) *T. schrenkiana* (holotype Yuan 14262).

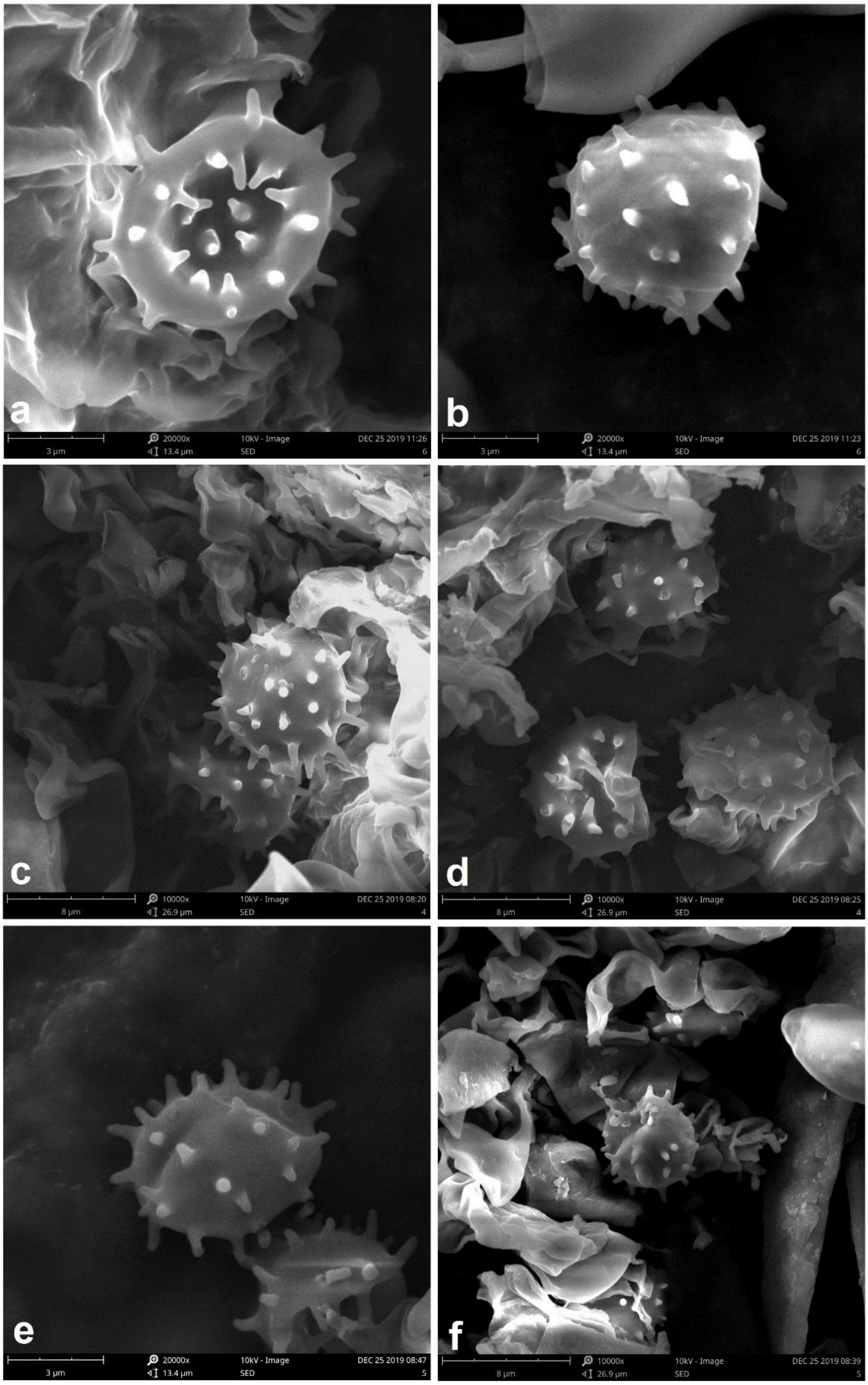

Figure 3. SEM of basidiospores of *Tomentella* species. (**a**,**b**) *T. aurantispora* (holotype Yuan 14268); (**c**,**d**) *T. kanasensis* (holotype Yuan 14034); (**e**,**f**) *T. schrenkiana* (holotype Yuan 14262).

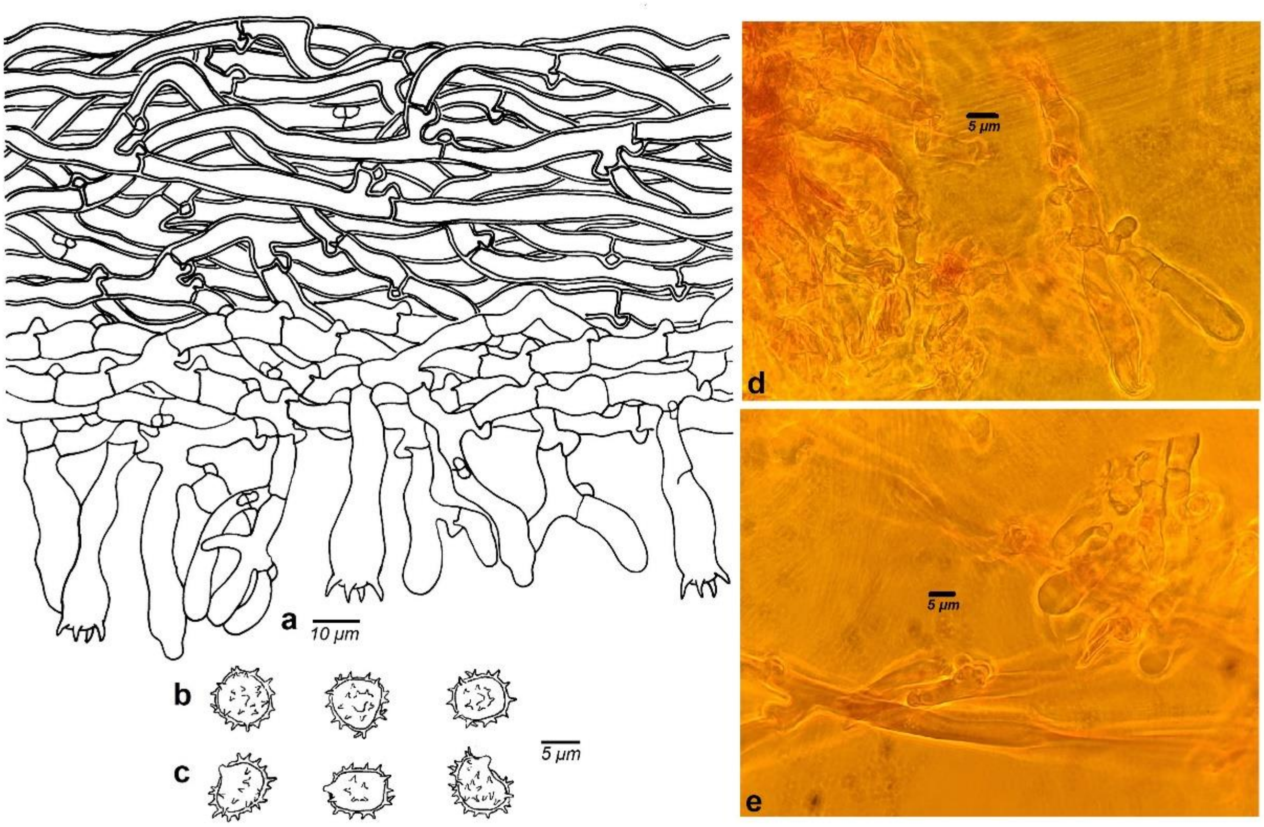

Figure 4. Microscopic structures of *Tomentella aurantispora* (drawn from holotype Yuan 14268). (**a**) A section through basidiocarp. (**b**) Basidiospores in frontal view. (**c**) Basidiospores in lateral view. (**d**) Optical microscope images of subhymenial hyphae. (**e**) Optical microscope images of subicular hyphae and basidia.

Diagnosis. Basidiocarps: arachnoid. Hymenophoral surface: yellowish brown to brown. Sterile margin: byssoid and brown. Generative hyphae: clamped. Basidia: utriform. Basidiospores: subglobose to globose, slightly thick-walled, echinulate; echinuli up to 1 µm long.

Type: CHINA, Xinjiang Autonomous Region, Urumqi, Tianshan Grand Canyon National Forest Park, 43°49′17″ N, 87°43′59″ E, 1968 m, on fallen branch of *Picea schrenkiana*, 17.VIII.2019, Yuan 14268 (holotype: IFP 019365, GenBank ITS: MT152155; LSU: MT154238).

Etymology. *Aurantispora* (Lat.), referring to the orange-yellow basidiospores in distilled water.

Basidiocarps: annual, resupinate, adherent to the substrate, arachnoid, without odor or taste when fresh, 0.2–0.5 mm thick, continuous. Hymenophoral surface: smooth, yellowish brown to brown (5D8–6F8) and turning paler than subiculum. Sterile margin: often determinate, byssoid, darker than hymenophore, brown (6F8).

Rhizomorphs absent.

Subicular hyphae: monomitic; generative hyphae: clamped, thick-walled, 4–6.5 µm diam, without encrustation, grayish yellow in KOH and distilled water, CB+, IKI-. Subhymenial hyphae: clamped, thin-walled, 3–7 µm diam, without encrustation; hyphal cells: short and inflated, grayish yellow in KOH and in distilled water, CB-, IKI-.

Cystidia absent.

Basidia: 20–45 µm long and 4–9 µm diam at apex, 3–5 µm at base, with a clamp connection at base, utriform, not stalked, sinuous, without transverse septa, pale brown in KOH and distilled water, 4-sterigmata; sterigmata: 3–5 µm long and 1–1.5 µm diam at base.

Basidiospores: thick-walled, (6.5–)7–9(–9.5) × (5.5–)6–8(–8.5) µm, L = 7.82 µm, W = 6.95 µm, Q = 1.08–1.15 (n = 60/2), subglobose to globose in frontal and later face, echinulate to aculeate, brown in KOH, orange-yellow in distilled water, CB+, IKI-; echinuli usually grouped in two or more, up to 1 µm long.

Additional specimens (paratype) examined: CHINA, Xinjiang Autonomous Region, Urumqi, Tianshan Grand Canyon National Forest Park, 43°49′17″ N, 87°43′59″ E, 2028 m, on fallen branch of *Picea schrenkiana*, 17.VIII.2019, Yuan 14276 (paratype: IFP 019366, GenBank ITS: MT152156; LSU: MT154239).

Tomentella kanasensis X. Lu & H.S. Yuan, sp. nov.

MycoBank no. MB 834868

(Figures 2b, 3c,d and 5)

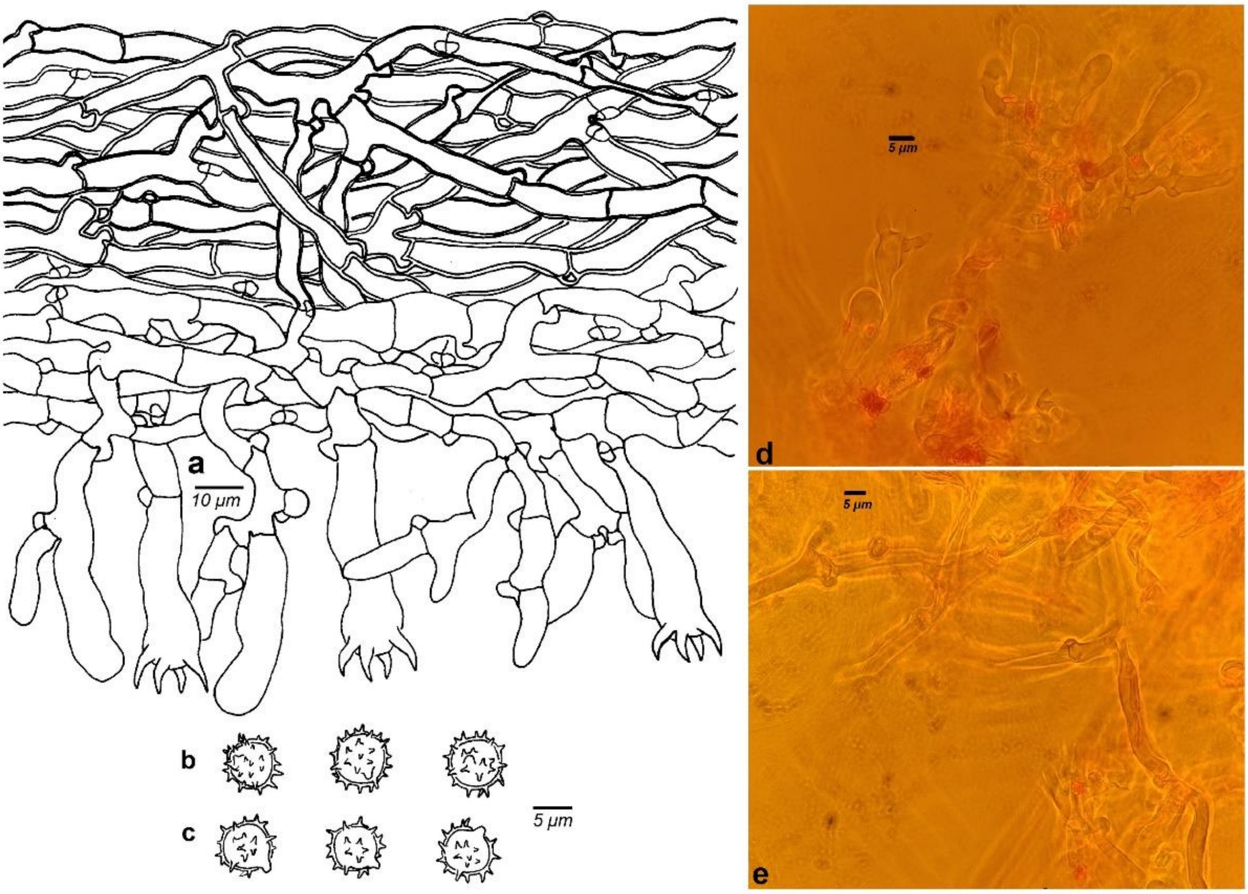

Figure 5. Microscopic structures of *Tomentella kanasensis* (drawn from holotype Yuan 14034). (**a**) A section through basidiocarp. (**b**) Basidiospores in frontal view. (**c**) Basidiospores in lateral view. (**d**) Optical microscope images of subhymenial hyphae and basidia. (**e**) Optical microscope images of subicular hyphae.

Diagnosis. Basidiocarps: arachnoid. Hymenophoral surface: light brown to dark brown. Sterile margin: byssoid and dark brown. Generative hyphae: clamped and rarely simple-septate. Basidia: utriform. Basidiospores: subglobose to globose, slightly thick-walled, echinulate; echinuli up to 1.5 µm long.

Type: CHINA, Xinjiang Autonomous Region, Buerjin County, Kanas National Nature Reserve, 48°37′23″ N, 87°02′55″ E, 1342 m, on fallen branch of *Picea obovata*, 6.VIII.2019, Yuan 14034 (holotype: IFP 019362, GenBank ITS: MT152151; LSU: MT154234).

Etymology. *Kanasensis* (Lat.), referring to the specimens collected from Kanas National Nature Reserve.

Basidiocarps: annual, resupinate, adherent to the substrate, arachnoid, without odor or taste when fresh, 0.3–0.5 mm thick, continuous. Hymenophoral surface: smooth, light brown to dark brown (6D4–6E8) and turning darker than subiculum. Sterile margin: often determinate, byssoid, darker than hymenophore, dark brown (6E8).

Rhizomorphs absent.

Subicular hyphae: monomitic; generative hyphae: clamped and rarely simple-septate, slightly thick- to thick-walled, occasionally collapsed, 4–6 µm diam, without encrustation, light brown in KOH and distilled water, CB+, IKI-. Subhymenial hyphae: clamped and rarely simple-septate, thin-walled, 4–7 µm diam, without encrustation; hyphal cells: short and occasionally inflate up to 10 µm, yellow in KOH and in distilled water, acyanophilous, IKI-.

Cystidia absent.

Basidia: 15–62 µm long and 8–11 µm diam at apex, 4.5–6 µm at base, with a clamp connection at base, utriform, not stalked, sinuous, without transverse septa, yellow in KOH and distilled water, 4-sterigmata; sterigmata: 6–8.5 µm long and 2–3 µm diam at base.

Basidiospores: thick-walled, (7–)7.5–9(–9.5) × (6–)6.5–8(–8.5) µm, L = 8.44 µm, W = 6.98 µm, Q = 1.18–1.24 (n = 60/2), subglobose to globose in frontal and later face, echinulate, light brown in KOH and distilled water, CB+, IKI-; echinuli usually isolated, up to 1.5 µm long.

Additional specimens (paratypes) examined: CHINA, Xinjiang Autonomous Region, Buerjin County, Kanas National Nature Reserve, Wolong Bay, 48°36′58″ N, 87°01′55″ E, 1328 m, on fallen branch of *Picea obovata*, 6.VIII.2019, Yuan 14029 (IFP 019361, GenBank ITS: MT152152; LSU: MT154235); Jilin Province, Jiaohe City, Qianjin Village, 43°57′52″ N–43°58′02″ N, 127°44′11″ E–127°44′66″ E, 459–517 m, on fallen angiosperm branch, 3.IX.2017, Yuan 12556, 12557, 12565, 12571 & 12579 (paratypes: IFP 019367–IFP 019371, GenBank ITS: MT152157–MT152161; LSU: MT154240–MT154244).

Tomentella schrenkiana X. Lu & H.S. Yuan, sp. nov.

MycoBank no. MB 834869

(Figures 2c, 3e,f and 6)

Diagnosis. Basidiocarps: arachnoid. Hymenophoral surface: grayish brown to dark brown. Sterile margin: byssoid and grayish brown. Generative hyphae: clamped. Basidia: utriform. Basidiospores: subglobose to globose, slightly thick-walled, echinulate; echinuli up to 1 µm long.

Type: CHINA, Xinjiang Autonomous Region, Fukang City, Tianshan Tianchi National Park, 43°53′51″ N, 88°06′42″ E, 1899 m, on fallen trunk of *Picea schrenkiana*, 16.VIII.2019, Yuan 14262 (holotype: IFP 019364, GenBank ITS: MT152153; LSU: MT154236).

Etymology. *Schrenkiana* (Lat.), referring to the substrate of this species.

Basidiocarps: annual, resupinate, adherent to the substrate, arachnoid, without odor or taste when fresh, 0.2–0.5 mm thick, continuous. Hymenophoral surface: smooth, grayish brown to dark brown (7F3–7F6) and concolorous with the subiculum. Sterile margin: often indeterminate, byssoid, concolorous with hymenophore.

Rhizomorphs absent.

Subicular hyphae: monomitic; generative hyphae: clamped, thick-walled, occasionally collapsed, 2.5–5 µm diam, without encrustation, brown in KOH and distilled water, CB+, IKI-. Subhymenial hyphae: clamped, thin- to slightly thick-walled, 2.5–5.5 µm diam, without encrustation; hyphal cells: short and not inflated, grayish brown in KOH and in distilled water, CB+, IKI-.

Cystidia absent.

Basidia: 20–35 µm long and 4–8 µm diam at apex, 3–5 µm at base, with a clamp connection at base, utriform, not stalked, sinuous, without transverse septa, grayish brown in KOH and distilled water, 4-sterigmata; sterigmata: 3–6 µm long and 1.5–2 µm diam at base.

Basidiospores: slightly thick-walled, (5–)5.5–6.5(–7) × (4.5–)5–5.5(–6) µm, L = 6.04 µm, W = 5.2 µm, Q = 1.15–1.18 (n = 60/2), subglobose to globose in frontal and later face, echinulate, brown in KOH and distilled water, CB+, IKI-; echinuli usually grouped in two or more, up to 1 µm long.

Additional specimens (paratype) examined: CHINA, Xinjiang Autonomous Region, Fukang City, Tianshan Tianchi National Park, 43°53′23″ N, 88°06′38″ E, 1854 m, on fallen branch of *Picea schrenkiana*, 16.VIII.2019, Yuan 14241 (paratype: IFP 019363, GenBank ITS: MT152154; LSU: MT154237).

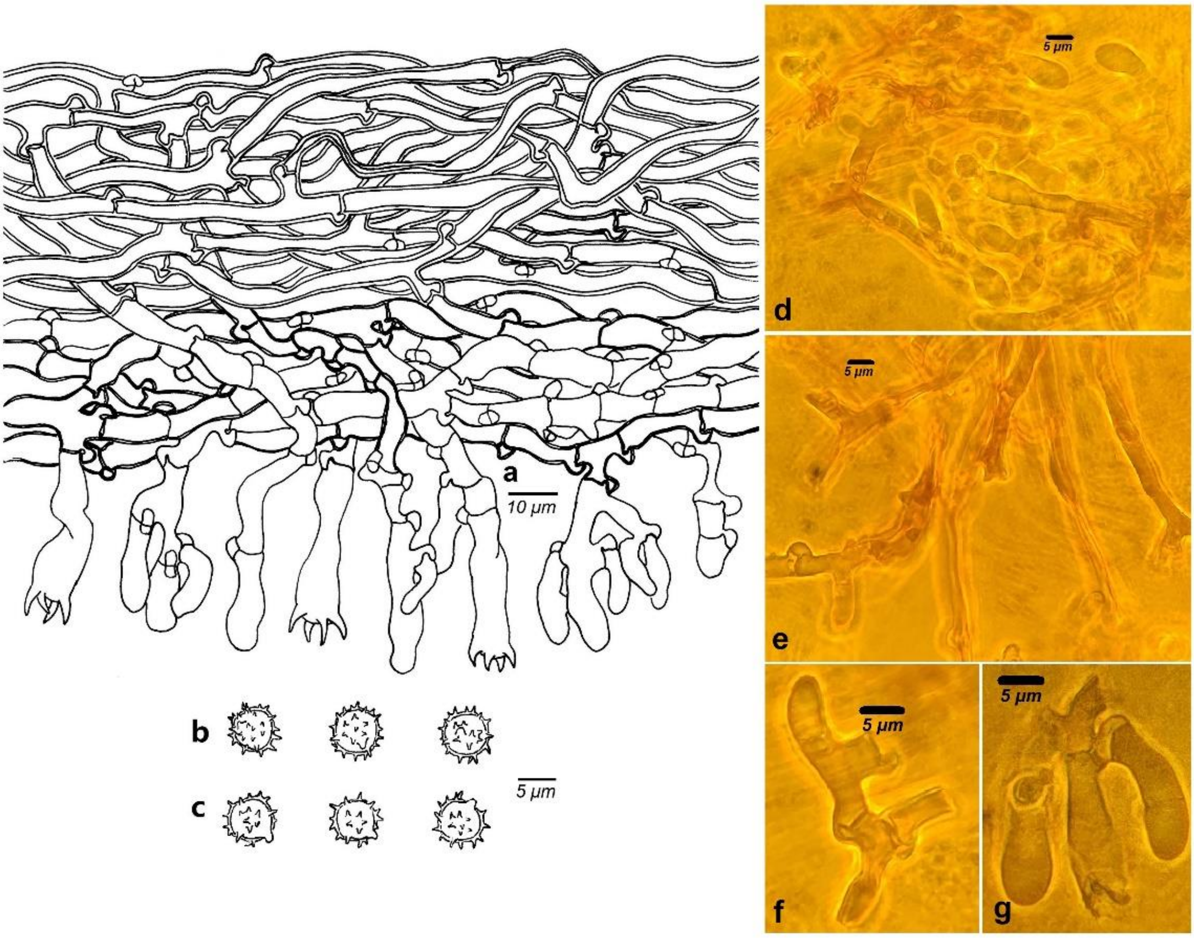

Figure 6. Microscopic structures of *Tomentella schrenkiana* (drawn from Yuan 14262). (**a**) A section through basidiocarp. (**b**) Basidiospores in frontal view. (**c**) Basidiospores in lateral view. (**d**) Optical microscope images of subhymenial hyphae and basidia. (**e**) Optical microscope images of subicular hyphae. (**f**,**g**) Optical microscope images of basidia.

4. Discussion

Three new *Tomentella* species distributed in Xinjiang of northwest China were identified by phylogenetic analysis based on a combined ITS and LSU sequence dataset and morphological characteristics. Phylogenetic analyses and morphological features were able to distinguish the three new species from other *Tomentella* species. The deeper nodes of the tree are weakly supported, which is consistent with previous studies [9]. In the phylogenetic tree, most species from global regions have scattered in the 18 main clades. Species in the clade with moderate support or high support present unique features. Species in clade 1 have basidiocarps with similar color; species in clade 7 and clade 8 have rhizomorphs; species in clade 10 have a simple-septate hyphal system and basidiospores with the same size; species in clade 14 have separable basidiocarps with similar color; species in clade 15 have similar anatomical structure; species in clade 16 have cystidia. In addition, *T. brunneocystidiata* Yorou & Agerer, *T. capitata* Yorou & Agerer, *T. capitatocystidiata* Yuan et al., *T. cystidiata* Yuan et al., *T. gloeocystidiata* Yuan et al., and *T. pilosa* (Burt) Bourdot & Galzin in clade 4 also share common features: the capitate cystidia. *T. aureomarginata* Yuan et al., *T. brunneoflava* Yuan et al., and *T. separata* Yuan et al. in clade 6 also have common features: light brown to brown basidiocarps and the presence of rhizomorphs.

In the phylogenetic tree, *T. aurantispora* and *T. kanasensis* are closely related to *T. bryophila* (Pers.) M.J. Larsen, *T. changbaiensis* Yuan et al., *T. interrupta* Yuan et al., *T. longiaculeifera* Yuan et al., *T. megaspora* Yuan et al., and *T. pallidobrunnea* Yuan et al. with strong support (85 in ML and 1.00 BPP), and they formed a highly supported (0.97 BPP) relationship with *T. asiae-orientalis* Yuan et al., *T. lammiensis* Lu et al., and *T. stipitata* Yuan et al. These species share some similar characteristics: clamped hyphal system, globose to subglobose basidiospores, and the absence of rhizomorphs and cystidia [3,11] except for the ellipsoid, triangular, or lobed basidiospores of *T. lammiensis* and *T. stipitata* [11,51]. *T. aurantispora* also presents some other similar morphological characteristics with *T. changbaiensis* and *T. megaspora*: byssoid sterile margin, short and inflated subhymenial hyphal cell, and utriform basidia. But *T. changbaiensis* differs from *T. aurantispora* by the separable basidiocarps and larger basidiospores with longer echinuli (L = 8.45 µm, W = 7.83 µm, echinuli up to 1.5 µm) [11]. *T. megaspora* can be distinguished from *T. aurantispora* based on the larger basidiospores with longer echinuli (L = 9.88 µm, W = 9.08 µm, echinuli up to 2.5 µm) [11]. Morphologically, *T. aurantispora* and *T. asiae-orientalis* also share some other common characteristics: arachnoid basidiocarps adherent to the substrate and byssoid sterile margin. Moreover, *T. asiae-orientalis* can be delimited from *T. aurantispora* by the more or less uniform subhymenial hyphal cells, clavate basidia, and basidiospores with longer echinuli (echinuli up to 2.5 µm) [11].

Macroscopically, *T. kanasensis* and *T. aurantispora* possess the same arachnoid basidiocarps with similar color (yellowish brown to brown and light brown to dark brown) and byssoid sterile margin. But *T. aurantispora* differs by the length of sterigmata (3–5 µm long) and the hyphal system without simple septa in comparison with *T. kanasensis*. Some features of *T. changbaiensis* can be also observed in *T. kanasensis*, such as the byssoid sterile margin and the equally sized basidiospores. However, *T. changbaiensis* differs markedly from *T. kanasensis* by the duplex basidiocarps, pale brown sterile margin, and hyphal system without simple septa [11]. *T. bryophila* also forms short and inflated subhymenial hyphal cells and utriform basidia similar to those of *T. kanasensis*. However, the encrusted hyphae of *T. bryophila* are different from *T. kanasensis* [3].

The phylogenetic tree shows that *T. schrenkiana* clusters phylogenetically together with *T. dimidiata* Yuan et al., *T. fuscopelliculosa* Yuan et al., *T. globospora* Yuan et al., *T. pertenuis*, and *T. segregata* Yuan et al. with a strong support (0.95 BPP), and they possess the globose to subglobose basidiospores, with the exception of *T. dimidiata* with lobed basidiospores [3,11,52]. *T. schrenkiana* and *T. fuscopelliculosa* also have some other common anatomical structures, such as short subhymenial hyphal cells, utriform basidia, and the absence of rhizomorphs and cystidia. However, *T. fuscopelliculosa* differs by its pelliculose basidiocarps, inflated subhymenial hyphal cells, and distinctly larger basidiospores with longer echinuli (L = 8.75 µm, W = 8.23 µm, echinuli up to 2 µm) in comparison with *T. schrenkiana* [11]. *T. schrenkiana* also shows similar anatomical features to *T. globospora*, *T. pertenuis*, and *T. segregata*, including basidiocarps adherent to the substrate and the absence of rhizomorphs and cystidia. However, the mucedinoid basidiocarps, farinaceous sterile margin, utriform basidia, and slightly larger basidiospores with longer echinuli (L = 7.05 µm, W = 6.35 µm, echinuli up to 1.5 µm) [51] of *T. globospora* are very different from *T. schrenkiana.* In comparison with *T. schrenkiana*, *T. segregata* can be distinguished in producing discontinuous basidiocarps, a farinaceous sterile margin, and larger basidiospores with isolated and longer echinuli. The continuous basidiocarps and clamped generative hyphae of *T. pertenuis* also resemble *T. schrenkiana*, but the farinaceous sterile margin and larger basidiospores (L = 7.99 µm, W = 7.41 µm) [11] of *T. pertenuis* are good delimitation characteristics.

As *Picea* spp. constituted the dominant tree distributed in the investigated regions of Xinjiang Autonomous Region, we speculate that *T. aurantispora* and *T. schrenkiana* may form ectomycorrhizae with *P. schrenkiana.* Specimens of *T. kanasensis* have also been observed in Jilin Province, and the climate of this region is apparently different from Xinjiang. *Picea*-dominated forests in Xinjiang have quite different tree species in comparison to the mixed broadleaf– conifer forests in Jilin Province dominated by *Pinus koraiensis* Siebold & Zucc., *Acer pictum* subsp. *mono* (Maxim.) Ohashi, *A. mandshuricum* Maxim., *Tilia amurensis* Rupr., and *Carpinus cordata* Blume mixed with shrub species [53]. The host tree species of *T. kanasensis* from Xinjiang and Jilin Provinces may be *P. obovata* and *P. koraiensis*, respectively. At present, 51 species of *Tomentella* have been identified based on morphological and molecular characteristics of the *Tomentella* collections from Northeast China (Liaoning, Heilongjiang, and Jilin Provinces) and Northwest China (Xinjiang Autonomous Region) [10,11]. While several *Tomentella* spp. of ECM associated with plant roots in Pinaceae and Fagaceae were also reported in previous studies from China, they were not available for identification [29,30,34], and the cryptic or atypical basidiocarps of *Tomentella* may be easily overlooked in diverse studies. Therefore, we speculate that an increasing number of species in this genus will be found at more sites in China.

5. The Types of Rhizomorphs Used in the Key

Agerer recognized six categories of rhizomorph structure (types A–F) [54], and the dimitic hypal system of rhizomorphs named type G was reported in 2020 [11].

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12111531/s1, Table S1: GenBank/UNITE accession numbers, voucher numbers, substrates, localities and references for the specimens included in this study. The newly generated sequences are in bold.

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Data Availability Statement: The datasets presented in this study are openly available. All resulting alignments were deposited in TreeBASE (http://www.treebase.org (accessed on 21 September 2021; accession number 28802)). All newly generated sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/ (accessed on 6 March 2020; Table S1)). All new taxa were deposited in Mycobank.

Conflicts of Interest: The authors declare that there is no conflict of interest regarding the design of the study, the writing of the manuscript, the decision to publish the results, and the collection, analyses, or interpretation of data.

Key to Species of *Tomentella* from China

1. Basidiospores globose to subglobose in frontal view	2
1. Basidiospores lobed in frontal view	20
2. Rhizomorphs absent	3
2. Rhizomorphs absent	4
3. Length of subhymenial hyphal cell $\geq$ 15 µm	*T. tenuirhizomorpha*
3. Length of subhymenial hyphal cell < 15 µm	*T. brunneogrisea*
4. Basidiocarps separable from the substrate	5
4. Basidiocarps adherent to the substrate	7
5. Sterile margin byssoid	*T. changbaiensis*
5. Sterile margin farinaceous	6
6. Subicular hyphae without encrustation	*T. atrocastanea*

6. Subicular hyphae with encrustation	*T. longiaculeifera*
7. Basidiocarps arachnoid	8
7. Basidiocarps mucedinoid, crustose, and pelliculose	11
8. Basidia clavate	*T. asiae-orientalis*
8. Basidia utriform	9
9. Basidiospores $L < 7$ μm and $W < 6$ μm	*T. schrenkiana*
9. Basidiospores $L \geq 7$ μm and $W \geq 6$ μm	10
10. Echinuli of basidiospores ≤ 1 μm, sterigmata of basidia ≤ 5 μm	*T. aurantispora*
10. Echinuli of basidiospores > 1 μm, sterigmata of basidia > 5 μm	*T. kanasensis*
11. Basidia clavate	12
11. Basidia utriform	14
12. Subicular hyphae without encrustation	*T. globospora*
12. Subicular hyphae with encrustation	13
13. Basidiocarps pelliculose	*T. duplexa*
13. Basidiocarps mucedinoid	*T. griseomarginata*
14. Sterigmata of basidia ≥ 10 μm	*T. conclusa*
14. Sterigmata of basidia < 10 μm	15
15. Length of subhymenial hyphal cell ≥ 15 μm, not inflated	*T. pertenuis*
15. Length of subhymenial hyphal cell < 15 μm, inflated	16
16. Basidiocarps crustose or pelliculose	17
16. Basidiocarps mucedinoid	19
17. Basidiocarps crustose	*T. griseofusca*
17. Basidiocarps pelliculose	18
18. Sterigmata of basidia ≤ 5 μm, echinuli of basidiospores > 2 μm	*T. megaspora*
18. Sterigmata of basidia > 5 μm, echinuli of basidiospores ≤ 2 μm	*T. fuscopelliculosa*
19. Echinuli usually isolated, sterile margin farinaceous	*T. segregata*
19. Echinuli usually grouped in 2 or more, sterile margin byssoid	*T. pallidobrunnea*
20. Rhizomorphs present	21
20. Rhizomorphs absent	43
21. Cystidia present	22
21. Cystidia absent	25
22. Basidiocarps pelliculose	*T. citrinocystidiata*
22. Basidiocarps arachnoid	23
23. Basidiocarps brown or dark brown	24
23. Basidiocarps olive yellow to olive	*T. gloeocystidiata*
24. Echinuli of basidiospores ≤ 1.5 μm	*T. cystidiata*
24. Echinuli of basidiospores > 1.5 μm	*T. capitatocystidiata*
25. Rhizomorphs of type G	26
25. Rhizomorphs of other types	29
26. Basidiocarps pelliculose and separable from the substrate	*T. incrustata*
26. Basidiocarps arachnoid and adherent to the substrate	27
27. Subicular hyphae without encrustation	*T. dimidiata*
27. Subicular hyphae with encrustation	28
28. Rhizomorphs of type C	29
28. Rhizomorphs of other types	30
29. Basidiocarps mucedinoid and discontinuous	*T. brevis*
29. Basidiocarps arachnoid and continuous	*T. qingyuanensis*
30. Rhizomorphs of type A	31
30. Rhizomorphs of type B	32
31. Sterile margin of basidiocarps pale yellow	*T. pallidomarginata*
31. Sterile margin of basidiocarps brown	*T. fuscocrustosa*
32. Subicular hyphae with encrustation	*T. fuscogranulosa*
32. Subicular hyphae without encrustation	33
33. Basidiocarps discontinuous	*T. interrupta*
33. Basidiocarps continuous	34
34. Hymenophoral surface granulose	35
34. Hymenophoral surface smooth	39
35. Basidiocarps separable from the substrate	36

35. Basidiocarps adherent to the substrate	37
36. Basidiocarps dark brown, subicular hyphae simple-septate	*T. efibulata*
36. Basidiocarps olive brown, subicular hyphae clamped	*T. olivacea*
37. Hyphae of rhizomorphs simple-septate	*T. efibulis*
37. Hyphae of rhizomorphs clamped	38
38. Basidiocarps pelliculose	*T. inconspicua*
38. Basidiocarps mucedinoid	*T. parvispora*
39. Basidiocarps separable from the substrate	40
39. Basidiocarps adherent to the substrate	41
40. Basidiocarps mucedinoid, subicular hyphae clamped	*T. flavidobadia*
40. Basidiocarps pelliculose, subicular hyphae clamped and simple-septate	*T. separata*
41. Basidia utriform	*T. aureomarginata*
41. Basidia clavate	*T. brunneoflava*
42. Basidia clavate	43
42. Basidia utriform	48
43. Subicular hyphae with encrustation	44
43. Subicular hyphae without encrustation	45
44. Basidiocarps mat-like	*T. storea*
44. Basidiocarps arachnoid	*T. farinosa*
45. Sterile margin byssoid	*T. pallidocastanea*
45. Sterile margin farinaceous	46
46. Basidiocarps brownish grey to olive brown	*T. olivaceobrunnea*
46. Basidiocarps grayish brown to dark blond or brown	47
47. Length of subhymenial hyphal cell > 15 µm, not inflated	*T. liaoningensis*
47. Length of subhymenial hyphal cell ≤ 15 µm, inflated	*T. griseocastanea*
48. Sterile margin byssoid	*T. atrobadia*
48. Sterile margin farinaceous	49
49. Basidiocarps arachnoid or pelliculose	50
49. Basidiocarps mucedinoid	51
50. Basidiocarps arachnoid, echinuli of basidiospores ≤ 1.5 µm	*T. fuscofarinosa*
50. Basidiocarps pelliculose, echinuli of basidiospores > 1.5 µm	*T. longiechinuli*
51. Basidiocarps clavate, sterigmata of basidia ≤ 5 µm	*T. coffeae*
51. Basidia utriform, sterigmata of basidia > 5 µm	*T. stipitata*

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