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# Morphological and molecular identification of three new species of *Tomentella* from Finland

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3 Xu Lu

4 *CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology,*

5 *Chinese Academy of Sciences, Shenyang 110164, P. R. China; University of the Chinese*

6 *Academy of Sciences, Beijing 100049, China*

7 Kari Steffen

8 *Department of Environmental Sciences, Section of Environmental Ecology, Niemenkatu 73,*

9 *15100 Lahti, Finland*

10 Hai-Sheng Yuan

11 *Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese*

12 *Academy of Sciences, Shenyang 110164, P. R. China*

13 **ABSTRACT**

14 Three new species of *Tomentella* (Thelephorales) from Finland, *T. globosa*, *T. lammiensis* and

15 *T. longisterigmata*, are described and illustrated with morphological characteristics and nuc

16 rDNA ITS1-5.8S-ITS2 sequences (ITS). *T. globosa* is characterized by mucedinoid, pale to

17 dark brown basidiocarps adherent to the substrate, generative hyphae with clamps and rarely

18 with simple septa and echinulate globose basidiospores (echinuli up to 1.5 µm long). *T.*

19 *lammiensis* is characterized by mucedinoid, oxide yellow to golden brown basidiocarps

20 separable from the substrate, generative hyphae with clamps and echinulate ellipsoid,

21 triangular or lobbed basidiospores (echinuli up to 2 µm long). *T. longisterigmata* is

22 characterized by mucedinoid, dark brown to chestnut basidiocarps separable from the

1 substrate, generative hyphae clamped and rarely with simple septa, the long basidial  
2 sterigmata (7–11 µm long) and echinulate globose basidiospores (echinuli up to 2 µm long).  
3 An absence of rhizomorphs and cystidia is their common morphological feature. Molecular  
4 analyses by maximum likelihood, maximum parsimony and Bayesian analysis confirm the  
5 phylogenetic position of these three new species. The discriminating characters of these new  
6 species and their closely related species are discussed in this study. A key to the species from  
7 Finland is provided in order to facilitate future studies of the genus.

8 **KEY WORDS:** ITS, phylogeny, taxonomy, Tomentelloid fungi

## 9 **INTRODUCTION**

10 The genus *Tomentella* Pers. ex Pat. belongs to Thelephoraceae, Thelephorales, Basidiomycota.  
11 Species of this genus usually grow on fallen wood, leaf litter, soil and other substrates and  
12 form a cottony or spider web-like reproductive structure on them (Larsen 1974; Kõljalg 1996;  
13 Erland and Taylor 1999; Tedersoo et al. 2003). Current evidence suggests that the genus  
14 *Tomentella* is composed by exclusively mycorrhizal species (Erland and Taylor 1999; Jakucs  
15 et al. 2005; Kõljalg et al. 2000; Geml et al. 2012). Species of *Tomentella* can form  
16 ectomycorrhiza with different plant hosts and receive energy from their host plants and  
17 transport nutrients to their hosts (Danielson et al. 1984; Erland and Taylor 1999; Tedersoo et  
18 al. 2003; Jakucs and Erős-Honti 2008) and they are of great ecological importance as  
19 ectomycorrhiza formers in temperate and tropical forests (Gardes and Bruns 1996; Erland and  
20 Taylor 1999; Haug et al. 2005; Jakucs et al. 2015; Kuhar et al. 2016).

21 The genus *Tomentella* is characterized by an annual habitat, resupinate and arachnoid,  
22 mucedinoid, crutose or pelliculose basidiocarps, which are separable from or adherent to the  
23 substrate; white, reddish brown, yellow or green hymenophore; smooth, granulose, colliculose  
24 or hydroid hymenophoral surface; the monomitic or dimitic hyphal system with clamped or

1 simple septate generative hyphae; the monomitic or dimitic hyphal cords present in subiculum  
2 and margins or absent; cystidia absent or arising from subhymenial hyphae or subicular  
3 hyphae; thick- or thin-walled, triangular, lobed, ellipsoid, subglobose to globose basidiospores  
4 with echinulate or bifurcate ornamentation (Larsen 1966; 1968; 1974; Kõljalg 1996).

5 *Tomentella* was reported to be widely distributed in the world in places such as  
6 Eurasia (Larsen 1998), North America (Alvarez-Manjarrez et al. 2015), South America (Haug  
7 et al. 2005; Kuhar et al. 2016), India (Thind and Rattan 1971), Korea (Jung 1994), West  
8 Africa (Yorou and Agerer 2008; Yorou et al. 2012), Australia (Agerer et al. 2001) and so on.  
9 The descriptions of the genus were based mainly on morphological characteristics before  
10 2000, and mycologists may not distinguish closely related species that have limited  
11 characteristic differences. In the recent decades most species of the genus were described on  
12 the basis of rDNA sequence analyses combining with morphological characteristics  
13 descriptions. Morphological and phylogenetic analyses have provided more accurate  
14 identification for distinguishing the closely related species.

15 There are many studies on species diversity and taxonomy of *Tomentella* reported in  
16 Europe, while systematic collection, genetic diversity researches and classification of this  
17 species is still scarce in Finland at present, and approximately 23 species were recorded  
18 (Kotiranta et al. 2009; Kunttu et al. 2012; Kunttu et al. 2015; Kuhar et al. 2016). However,  
19 three species, *T. crinalis* (Fr.) M.J. Larsen, *T. ferruginea* (Pers.) Pat. and *T. fibrosa* (Berk. &  
20 M.A. Curtis) Kõljalg, were translocated to *Odontia* Pers. according to the recent phylogenetic  
21 and the stable isotopes study (Tedersoo et al. 2014). Thus, 20 species of *Tomentella* were  
22 recorded. In 2016, several investigations of wood-inhabiting fungi in Finland were carried out,  
23 and dozens of *Tomentella* specimens were collected from the forests surrounding Lammi  
24 Biological Station of Helsinki University. The forests are mainly dominated by coniferous  
25 trees such as *Larix* spp., *Picea* spp., *Pinus* spp., and a small number of broad-leaved trees are

1 scattered in the forests. During the study of these specimens, three undescribed species were  
2 found using morphological characters and phylogenetic analyses of internal transcribed spacer  
3 (ITS) sequences. Here we described them as new species.

#### 4 **MATERIALS AND METHODS**

5 *Morphological studies.*—The studied specimens were deposited at the herbarium of Institute  
6 of Applied Ecology, Chinese Academy of Sciences (IFP). The microscopic procedures  
7 followed He and Dai (2012). Microscopic drawings were made with the aid of a drawing tube.  
8 Microscopic measurements were made from slide preparations stained with cotton blue and  
9 Melzer's reagent. Cotton blue: 0.1 mg aniline blue dissolved in 60 g pure lactic acid; Melzer's  
10 reagent: 1.5 g KI (potassium iodide), 0.5 g I (crystalline iodine), 22 g chloral hydrate, distilled  
11 water 20 mL. The following abbreviations were used in the text: KOH = 5% potassium  
12 hydroxide, IKI = Melzer's reagent, IKI– = neither amyloid nor dextrinoid, CB = cotton blue,  
13 CB+ = cyanophilous, CB– = acyanophilous, L = mean spore length (arithmetic average of all  
14 spores), W = mean spore width (arithmetic average of all spores), Q = variation in the ratios  
15 of L/W between specimens studied, n = number of spores measured from a given number of  
16 specimens. Special color terms follow Kornerup (Kornerup and Wanscher 1981). Sections  
17 were studied at magnifications up to  $\times 1000$  using a Nikon Eclipse E600 microscope with  
18 phase contrast illumination, and dimensions were estimated subjectively with an accuracy of  
19 0.1  $\mu\text{m}$ . Special color terms are cited from Rayner (1970).

20 *Molecular procedures and phylogenetic analyses.*—DNA was extracted from dried herbarium  
21 specimens with a Thermo Scientific Phire Plant Direct PCR Kit (for USA Thermo Fisher  
22 Scientific) according to the manufacturer's instructions. PCR reactions were performed in 30  
23  $\mu\text{L}$  reaction mixtures containing 15  $\mu\text{L}$  of 2 $\times$ Phire® Plant PCR buffer, 0.6  $\mu\text{L}$  Phire® Hot  
24 Start II DNA Polymerase, 1.5  $\mu\text{L}$  of each PCR primer (10  $\mu\text{M}$ ), 10.5  $\mu\text{L}$  doubly deionized

1 H<sub>2</sub>O, and 0.9 μL template DNA. The nuc rDNA ITS1-5.8S-ITS2 regions (ITS) was amplified  
2 with the primers ITS5 (5' GGAAGTAAAAGTCGTAACAAGG 3') and ITS4 (5'  
3 TCCTCCGCTTATTGATATGC 3') (Lang et al. 2011; Tedersoo et al. 2014), SSU1318-Tom  
4 (5' CGATAACGAACGAGACCTTAT 3') and LSU-Tom4 (5'  
5 GCCCTGTTCCAAGAGACTTA 3') (Taylor and McCormick 2008). The partial 28S regions  
6 was amplified with the primers LROR (5' ACCCGCTGAACTTAAGC 3') and LR3 (5'  
7 CCGTGTTTCAAGACGGG 3') (Jumpponen et al. 2015).

8 The PCR thermal cycling program condition was set as follows: initial denaturation at  
9 98 C for 5 min, followed by 39 cycles at 98 C for 30 s, × C for 30 s, 72 C for 30 s, and a final  
10 extension at 72 C for 1 min. The PCR products were sequenced at Beijing Genomics Institute  
11 (BGI), with primer ITS5 and ITS4, SSU1318-Tom and LSU-Tom4. Six ITS rDNA sequences  
12 of these three new species were deposited in GenBank NCBI. Additional ITS rDNA  
13 sequences in the dataset used to establish phylogenetic relationships were downloaded from  
14 GenBank (<http://www.ncbi.nlm.nih.gov/genbank>) and UNITE (<https://unite.ut.ee/index.php>)  
15 (TABLE 1).

16 The ITS sequences were used to determine the phylogenetic position of the new  
17 species. DNA sequences were aligned with MUSCLE in MEGA 7 (Kumar et al. 2016).  
18 Alignments were manually adjusted to allow maximum alignment and minimize gaps, and  
19 deposited in TreeBASE (study no. 21889). Maximum parsimony (MP), maximum likelihood  
20 (ML) and Bayesian analysis were applied to the ITS dataset. All characters were weighted,  
21 and gaps were treated as missing data. MP analyses were conducted with PAUP\* version  
22 4.0b10 (Swofford 2002). Trees were inferred by the heuristic search option with TBR branch  
23 swapping and 1,000 random sequence additions. Max-trees were set to 5000 and no-increase,  
24 branches of zero length were collapsed and all parsimonious trees were saved. Clade stability  
25 was assessed with bootstrap (BT) analyses with 1,000 replicates (Gaget et al. 2017).

1 Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI),  
2 rescaled consistency index (RC), and homoplasy index (HI) were calculated for all trees  
3 generated under different optimality criteria. Bayesian analysis with MrBayes 3.2.4  
4 (Cannatella 2015) implementing the Markov chain Monte Carlo (MCMC) technique and  
5 parameters predetermined with MRMODELTEST 2.3 (Posada and Crandall 1998; Nylander  
6 2004) were performed, and the parameters in MrBayes were set as follows: lset nst=6, rates=  
7 invgamma. Four simultaneous Markov chains were run starting from random trees, and  
8 keeping one tree every 100th generation until the average standard deviation of split  
9 frequencies was below 0.01. The value of burn-in was set to discard 25% of trees when  
10 calculating the posterior probabilities. Bayesian posterior probabilities were obtained from the  
11 50% majority rule consensus of the trees kept. An ML tree with bootstrap support values was  
12 reconstructed with RAxML (implemented in raxmlGUI1.5b1), RAxML is currently among  
13 the fastest and most accurate programs for phylogenetic tree inference under the maximum  
14 likelihood (ML) criterion (Silvestro and Michalak 2012; Hundsdoerfer and Kitching 2017).

## 15 **RESULTS**

16 The dataset includes six ITS sequences of the newly described species and 108 sequences of  
17 59 other species. *Odontia fibrosa* was used as the outgroup. In the alignment of the 114  
18 samples, the data matrix comprised 630 bp with 266 constant characters, 55 parsimony-  
19 uninformative variable characters and 309 parsimony informative positions. MP and ML  
20 analyses produced a similar topology (TL = 1842, CI = 0.318, RI = 0.697, RC = 0.221, HI =  
21 0.682). The ML tree is shown in FIG. 1. Only bootstrap values superior to 50% are displayed  
22 on the tree figures. The same dataset and alignment was analyzed with MrBayes 3.2.4.  
23 Bayesian analysis ran 7 million generation and resulted in an average standard deviation of  
24 split frequencies = 0.007198. The Bayesian analysis yielded a topology similar to that  
25 generated by MP. In the phylogenetic tree, six sampled specimens formed three single clades

1 with full support (100 % in ML, 100 % in MP and 1.00 BPP), and clustered in the clade that  
2 comprised most species of *Tomentella*. It confirmed the affinity of these new species in  
3 *Tomentella*. *T. globosa* and *T. longisterigmata* clustered together with strong support (100 %  
4 in ML, 98 % in MP and 1.00 BPP) and formed a clade with *T. bresadolae* with moderate  
5 support (93 % in ML, 87 % in MP and 0.99 BPP); *T. lammiensis* clustered with *T. bryophila*  
6 with strong support (86 % in ML, 94 % in MP and 0.99 BPP).

## 7 TAXONOMY

8 *Tomentella globosa* X. Lu, K. Steffen & H.S. Yuan, sp. nov. FIGS. 2–4

9 MycoBank MB824716

10 *Typification*: Finland. Lammi Biological Station, on rotten angiosperm wood debris, 14 Sep  
11 2016, *Yuan 11603* (**holotype** IFP 19180). UNITE Accession No.

12 *Etymology*: *Globosa*: from the latin globosus, in reference to the globose basidiospores.

13 *Diagnosis*: Differs from *Tomentella bresadolae* in having mucedinoid basidiocarps adherent  
14 to the substrate, farinaceous sterile margin, shorter basidia and smaller basidiospores with  
15 shorter echinuli.

16 Basidiocarps annual, resupinate, adherent to the substrate, mucedinoid, without odor or taste  
17 when fresh, 0.5–0.8 mm thick, continuous. Hymenophoral surface granulose or smooth, pale  
18 to dark brown (6F4-6F7) and turning darker than the subiculum when dry. Sterile margin  
19 often indeterminate, farinaceous, lighter than hymenophore, pale brown.

20 Rhizomorphs absent.

21 Subicular hyphae monomitic, generative hyphae clamped and rarely with simple septa, thick-  
22 walled, 3–6 µm diam., without encrustation, pale to dark brown in 2.5% KOH and in distilled



1 water, cyanophilous, inamyloid. Subhymenial hyphae clamped and rarely with simple septa,  
2 thin-walled, 4–7 µm diam., without encrustation, hyphal cells short and inflated, pale or dark  
3 brown in 2.5% KOH and in distilled water, slightly cyanophilous, inamyloid.

4 Cystidia and cystidioles absent.

5 Basidia 20–55 µm long and 5–12 µm diam. at apex, 3–7 µm at base, with a clamp connection  
6 at base, utriform, not stalked, sinuous, without transverse septa, pale brown in 2.5% KOH and  
7 in distilled water, 4 sterigmata; sterigmata 4–8 µm long and 2–3 µm diam. at base.

8 Basidiospores slightly thick-walled, (6–)6.5–7.5(–8) × (5.5–)6–7(–7.5) µm, L = 7.05 µm, W =  
9 6.35 µm, Q = 1.11–1.15 (n = 60/2), subglobose to globose frontal and lateral face, echinulate,  
10 yellow brown in 2.5% KOH and in distilled water, cyanophilous, inamyloid; echinuli usually  
11 isolated, up to 1.5 µm long.

12 *Additional specimen examined:* Finland. Lammi Biological Station, on rotten angiosperm  
13 wood debris, 14 Sep 2016, *Yuan 11618* (**paratype** IFP 19180).

14 ***Tomentella lammiensis*** X. Lu, K. Steffen & H.S. Yuan, sp. nov.

FIGS. 5–7

15 MycoBank MB824717

16 *Typification:* Finland. Lammi Biological Station, on rotten angiosperm wood debris, 14 Sep  
17 2016, *Yuan 11617* (**holotype** IFP 19182). UNITE Accession No.

18 *Etymology:* *Lammiensis*: in reference to the Lammi Biological Station, where the specimens  
19 were found.

20 *Diagnosis:* Differs from *Tomentella galzinii* in having continuous basidiocarps separable from  
21 the substrate, oxide yellow to golden brown hymenophore, thick-walled subicular hyphae and  
22 an absence of cystidia.

- 1 Basidiocarps annual, resupinate, separable from the substrate, mucedinoid, without odor or  
2 taste when fresh, 0.6–1 mm thick, continuous. Hymenophoral surface granulose or smooth,  
3 oxide yellow to golden brown (5C7-5D7) and concolorous with the subiculum when dry.  
4 Sterile margin often indeterminate, byssoid, often paler than hymenophore, pale yellowish.  
5 Rhizomorphs absent.
- 6 Subicular hyphae monomitic, generative hyphae clamped, thick-walled, 4–7  $\mu\text{m}$  diam.,  
7 without encrustation, pale brown in 2.5% KOH and in distilled water, cyanophilous,  
8 inamyloid. Subhymenial hyphae clamped, thin-walled, 5–8  $\mu\text{m}$  diam., hyphal cells short and  
9 inflated, yellowish in 2.5% KOH and in distilled water, cyanophilous, inamyloid.
- 10 Cystidia and cystidioles absent.
- 11 Basidia 20–60  $\mu\text{m}$  long and 5–9  $\mu\text{m}$  diam. at apex, 3–6  $\mu\text{m}$  at base, with a clamp connection  
12 at base, utriform, not stalked, sinuous, without transverse septa, yellowish in 3% KOH and in  
13 distilled water, 4 sterigmata; sterigmata 3–6  $\mu\text{m}$  long and 2–4  $\mu\text{m}$  diam. at base.
- 14 Basidiospores thick-walled, (8–)8.5–9.5(–10)  $\times$  (7–)7.5–8.5(–9)  $\mu\text{m}$ , L = 8.12  $\mu\text{m}$ , W = 7.27  
15  $\mu\text{m}$ , Q = 1.08–1.12 (n = 60/2), ellipsoid, triangular or lobed frontal and ellipsoid lateral face,  
16 echinulate, golden yellow in 2.5% KOH and in distilled water, cyanophilous, inamyloid;  
17 echinuli usually isolated, sometimes grouped in 2 or more, up to 2  $\mu\text{m}$  long.
- 18 *Additional specimen examined:* Finland. Lammi Biological Station, on rotten angiosperm  
19 wood debris and broad leaf litter, 14 Sep 2016, *Yuan 11597* (**paratype** IFP 19178).
- 20 *Tomentella longisterigmata* X. Lu, K. Steffen & H.S. Yuan, sp. nov. FIGS. 8–10
- 21 MycoBank MB824718

1 *Typification*: Finland. Lammi Biological Station, on rotten angiosperm wood debris, 14 Sep  
2 2016, *Yuan 11610* (**holotype** IFP 19181). UNITE Accession No.

3 *Etymology*: *longisterigmata*: in reference to the long sterigmata of the basidia.

4 *Diagnosis*: Differs from *Tomentella lapida* in having basidiocarps separable from the  
5 substrate, dark brown to chestnut smooth hymenophore and an absence of Rhizomorpha.

6 Basidiocarps annual, resupinate, separable from the substrate, mucedinoid, without odor or  
7 taste when fresh, 0.6–1.0 mm thick, continuous. Hymenophoral surface smooth, dark brown  
8 to chestnut (6E7-6F7) and turning darker than the subiculum when dry. Sterile margin often  
9 indeterminate, byssoid, paler than hymenophore.

10 Rhizomorpha absent.

11 Subicular hyphae monomitic, generative hyphae clamped and rarely with simple septa, thick-  
12 walled, 4–7  $\mu\text{m}$  diam., without encrustation, light brown in 2.5% KOH and in distilled water,  
13 cyanophilous, inamyloid. Subhymenial hyphae clamped and rarely with simple septa, thin- to  
14 slightly thick-walled, 5–8  $\mu\text{m}$  diam.; hyphal cells not short and not inflated, hyaline to light  
15 brown in 2.5% KOH and in distilled water, cyanophilous, inamyloid.

16 Cystidia and cystidioles absent.

17 Basidia 20–55  $\mu\text{m}$  long and 6–9  $\mu\text{m}$  diam. at apex, 5–7  $\mu\text{m}$  at base, with a clamp connection  
18 at base, utriform, not stalked, sinuous, hyaline in 2.5% KOH and in distilled water, 4  
19 sterigmata; sterigmata 7–11  $\mu\text{m}$  long and 2–3  $\mu\text{m}$  diam. at base.

20 Basidiospores thick-walled, (7–)7.5–8.5(–9)  $\times$  (6–)7–8(–8.5)  $\mu\text{m}$  in lateral and frontal face, L  
21 =8.03  $\mu\text{m}$ , W =7.39  $\mu\text{m}$ , Q = 1.05–1.09 (n = 60/2), subglobose to globose frontal and lateral

1 face, echinulate, light brown in 2.5% KOH and in distilled water, cyanophilous, inamyloid;  
2 echinuli usually isolated, up to 2  $\mu\text{m}$  long.

3 *Additional specimen examined*: Finland. Lammi Biological Station, on rotten angiosperm  
4 wood debris, 14 Sep 2016, *Yuan 11602* (**paratype** IFP 19179).

## 5 **DISCUSSION**

6 As the tree topologies of the previous studies for *Tomentella* had shown, molecular  
7 phylogenetic analyses of the ITS dataset by ML, MP and MrBayes in this study showed a low  
8 rate of support in the deeper nodes of the topology, but high support at the species level (De  
9 Smet et al. 2015; Jakucs et al. 2015; Kuhar et al. 2016). In our phylogenetic tree, *T.*  
10 *albomarginata* and *T. sublilacina* formed a clade with weak support. *T. albomarginata* was  
11 treated as the synonym of *T. sublilacina* in previous studies (Kõljalg 1996; Jakucs et al.  
12 2005), and share the similar characteristics: mucedinoid basidiocarps, smooth hymenophore  
13 and an absence of cystidia. However, *T. albomarginata* differs from *T. sublilacina* by having  
14 the dark brown to umber hymenophore and monomitic rhizomorphs (Kõljalg 1996; Larsen  
15 1970), and we suggest that *T. albomarginata* and *T. sublilacina* should be kept as two  
16 independent species. *T. bresadolae* was reported to be a synonym of *T. stuposa* (Kõljalg 1996;  
17 Daemmrich 2006; Peintner and Dänmrich 2012), but the previous study has shown that they  
18 may represent the different species (Kuhar et al. 2016), and our molecular phylogenetic  
19 analyses showed *T. bresadolae* were distantly from *T. stuposa* again. Here we suggested to  
20 keep them as different species.

21 *Tomentella globosa* and *T. bresadolae* reveal a close phylogenetic relationship in the  
22 phylogenetic tree. They have globose basidiospores and some similar morphological  
23 characteristics, such as pale to dark brown, smooth hymenophore and an absence of  
24 rhizomorphs and cystidia. (Larsen 1969; Peintner and Dänmrich 2012). However, *T.*

1 *bresadolae* can be distinguished by having arachnoid basidiocarps separable from substrate,  
2 comparatively long-celled subicular hyphae, thin-walled subhymenial hyphae, longer basidia  
3 (55–70  $\mu\text{m}$ ) and thin-walled larger basidiospores (8.5–11  $\mu\text{m}$ ) (Larsen 1969; Daemmrich 2006;  
4 Peintner and D ämmrich 2012). Besides these, *T. globosa* also resembles *T. cinereoumbrina*  
5 and *T. fuscocinerea* mentioned in the previous paragraph from Finland, including  
6 basidiocarps adherent to the substrate, pale brown basidiospores and absence of rhizomorphs  
7 and cystidia. However, *T. cinereoumbrina* differs from *T. globosa* in having crustose  
8 basidiocarps, grey to light brown hymenophore, colorless to brown subicular hyphae,  
9 colourless to light brown subhymenial hyphae and pale brown basidiospores with triangular  
10 frontal and ellipsoid lateral face, also with short echinuli (0.4-1  $\mu\text{m}$ ) (K õljalg 1996;  
11 Daemmrich 2006). The main difference between *T. fuscocinerea* and *T. globosa* is that the  
12 former has thin-walled subicular hyphae (K õljalg 1996; Daemmrich 2006).

13         The main feature of *Tomentella lammi* is the oxide yellow to golden brown  
14 hymenophore that is somewhat similar to *T. galzinii* with pale brown to yellowish  
15 hymenophores. In addition, pale brown subicular hyphae and subhymenial hyphae, the  
16 absence of rhizomorphs and basidiospores with triangular or lobed frontal and ellipsoid lateral  
17 face of *T. galzinii* are quite similar to *T. lammi*, and *T. galzinii* differs from *T. lammi* by  
18 discontinuous basidiocarps, granulose or smooth hymenophore, thin-walled basidiospores and  
19 a presence of cystidia (K õljalg 1996; Daemmrich 2006). Another special characteristic of *T.*  
20 *lammi* is that its echinuli of basidiospores sometimes grouped in 2 or more; this trait can also  
21 be observed in *T. radiosa* and *T. agbassaensis*, but *T. radiosa* exhibits slightly bi- or trifurcate  
22 echinuli of basidiospores with short echinuli (< 1 $\mu\text{m}$ ) and *T. agbassaensis* presents isolated  
23 echinuli with very short echinuli (0.2–0.5  $\mu\text{m}$ ) (K õljalg 1996; Yorou et al. 2012).

24         *Tomentella longisterigmata* presents unique characteristics: basidia with long  
25 sterigmata and subglobose to globose homogeneous dense basidiospores with long echinuli

1 coincide with those of *T. lapida* and *T. africana* Yorou & Agerer (Melo et al. 2006; Yorou  
2 and Agerer 2008). *T. longisterigmata* and *T. lapida* also have common characteristics  
3 including mucedinoid basidiocarps, dark grayish brown smooth hymenophore, pale brown  
4 subicular hyphae, thin-walled subhymenial hyphae, the size of basidiospores and an absence  
5 of rhizomorphs and cystidia. However, *T. lapida* is differentiated from *T. longisterigmata* by  
6 having discontinuous basidiocarps adherent to the substrate, bluish green subhymenial hyphae  
7 and monomitic rhizomorphs (50-70  $\mu\text{m}$ ) (Melo et al. 2006). *T. longisterigmata* also closely  
8 related to *T. africana* in having dark brown to chestnut smooth hymenophore, thick-walled  
9 basidiospores and an absence of cystidia. Although they have some morphological deviations,  
10 *T. africana* differs from *T. longisterigmata* by having light yellow to yellow subicular hyphae,  
11 yellowish subhymenial hyphae, monomitic rhizomorphs, colorless to light yellow basidia and  
12 light yellow to pale brown, subglobose or triangular to lobed basidiospores with shorter  
13 echinuli (up to 1.5  $\mu\text{m}$ ) (Yorou and Agerer 2008).

14 *Toментella longisterigmata* and *T. globosa* are closely related in the phylogenetic tree  
15 and share similar morphological and anatomical characteristics: dark brown or rust brown  
16 hymenophore, globose basidiospores with isolated echinuli and an absence of rhizomorphs  
17 and cystidia. However, *T. globosa* can be differentiated from *T. longisterigmata* by its  
18 basidiocarps adherent to the substrate, granulose or smooth hymenophore, shorter sterigmata  
19 of basidia and smaller basidiospores with shorter and sparsely distributed echinuli.

20 The species of *Toментella* can form ectomycorrhizas with different host tree species  
21 of Pinaceae and Fagaceae, such as *Pinus banksiana*, *Picea glauca*, *Populus alba*, *Quercus*  
22 *cerris*, *Quercus robur* (Danielson et al. 1984; Danielson and Pruden 1989; Křijal 1996;  
23 Erland and Taylor 1999; Jakucs and Erős-Honti 2008). The specimens involved in this study  
24 were collected from the forests dominated by coniferous trees such as *Larix* spp., *Picea* spp.,  
25 *Pinus* spp., and also scattered a small number of broad-leaved trees (*Alnus* spp., *Acer* spp.,

1 *Betula* spp., *Quercus* spp. and *Populus* spp.). Although the specimens were found on the  
 2 substrates of rotten angiosperm wood debris, their hosts maybe the coniferous trees.

### 3 **KEY TO SPECIES OF TOMENTELLA FROM FINLAND**

- 4 1. Cystidia present .....2
- 5 1. Cystidia absent .....5
- 6 2. Cystidia acuminate or rarely hyphoid .....3
- 7 2. Cystidia clavate or capitate .....4
- 8 3. Basidiocarps mostly discontinuous; hymenophore greenish .....*T. galzinii*
- 9 3. Basidiocarps mostly continuous; hymenophore brownish .....*T. subtestacea*
- 10 4. Cystidia clavate, without encrustation .....*T. subclavigera*
- 11 4. Cystidia capitate, often encrusted .....*T. viridula*
- 12 5. Rhizomorphs present; sterile margin determinate .....6
- 13 5. Rhizomorphs absent; sterile margin indeterminate .....12
- 14 6. Subicular hyphae and subhymenial hyphae simple-septate .....*T. fuscocinerea*
- 15 6. Subicular hyphae and subhymenial hyphae clamped .....7
- 16 7. Subhymenial hyphae cells often or sometimes short and inflated .....8
- 17 7. Subhymenial hyphae cells more or less uniform .....10
- 18 8. Subicular hyphae thin-walled and sometimes inflated .....*T. ellisii*
- 19 8. Subicular hyphae thin- to thick-walled or thick-walled and without inflated .....9

- 1 9. Basidiocarps crustose .....*T. radiosa*
- 2 9. Basidiocarps mucedinoid or arachnoid .....*T. albomarginata*
- 3 10. Basidiospores with ellipsoid or subglobose frontal face .....*T. cinerascens*
- 4 10. Basidiospores with triangular or lobed frontal face .....11
- 5 11. Basidiocarps adhere to the substrate; sterile margin farinaceous or rarely byssoid ...
- 6 .....*T. coerulea*
- 7 11. Basidiocarps separable from the substrate; sterile margin byssoid to fimbriate .....
- 8 .....*T. punicea*
- 9 12. Basidiocarps crustose .....13
- 10 12. Basidiocarps mucedinoid or arachnoid .....15
- 11 13. Subicular hyphae and subhymenial hyphae simple-septate; basidia simple-septate at base
- 12 .....*T. cinereoumbrina*
- 13 13. Subicular hyphae and subhymenial hyphae clamped; basidia clamped at base .....
- 14 .....14
- 15 14. Subicular hyphae thin- to thick-walled; basidia often with transverse septa .....
- 16 .....*T. terrestris*
- 17 14. Subicular hyphae thick-walled; basidia rarely with transverse septa ·*T. atramentaria*
- 18 15. Basidiospores with triangular or lobed frontal and ellipsoid lateral face .....16
- 19 15. Basidiospores with subglobose to globose frontal and lateral face .....19





- 1 22. Hymenophore ferruginous brown to orange when dry; basidia rarely with transverse  
 2     septa .....*T. bryophila*
- 3 22. Hymenophore pale to dark brown when dry; basidia often with transverse septa .....  
 4     .....*T. stuposa*

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 11 Academy of Sciences (Project No. ZSBR-015).

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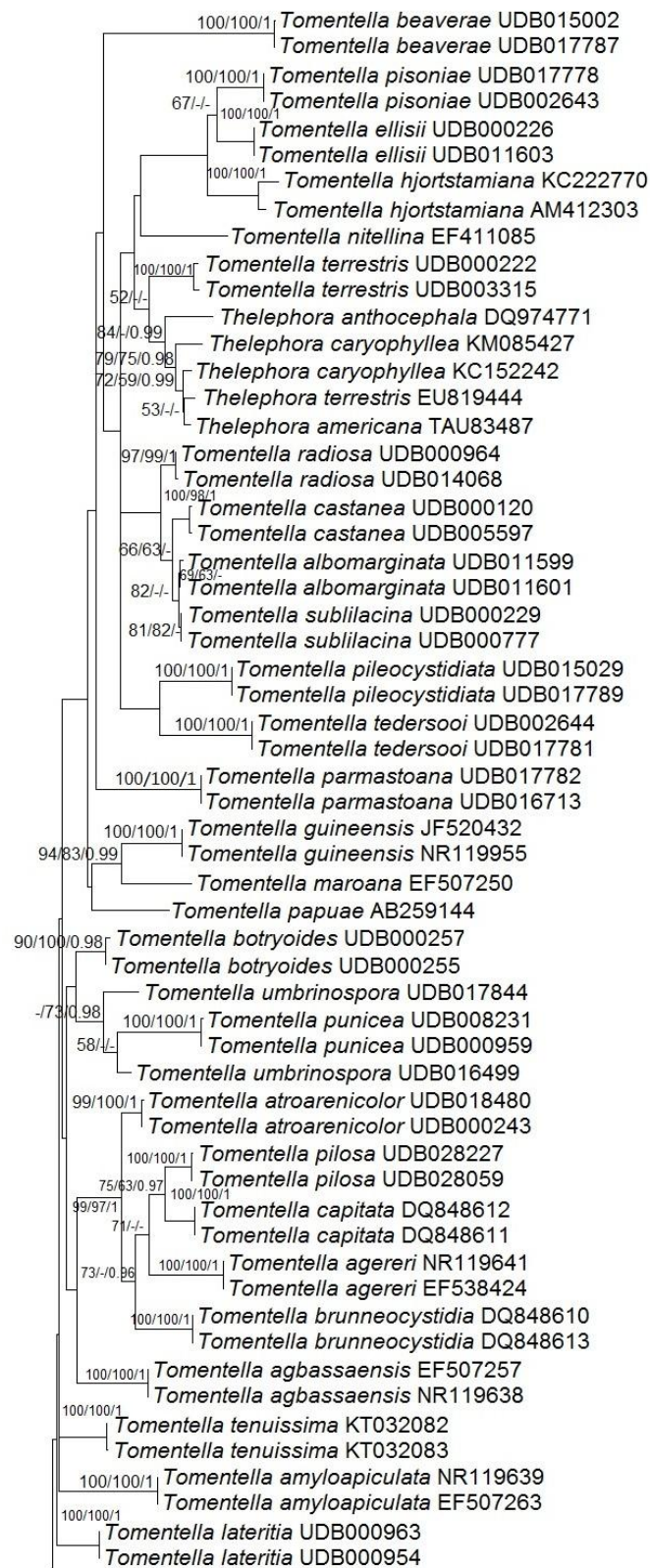
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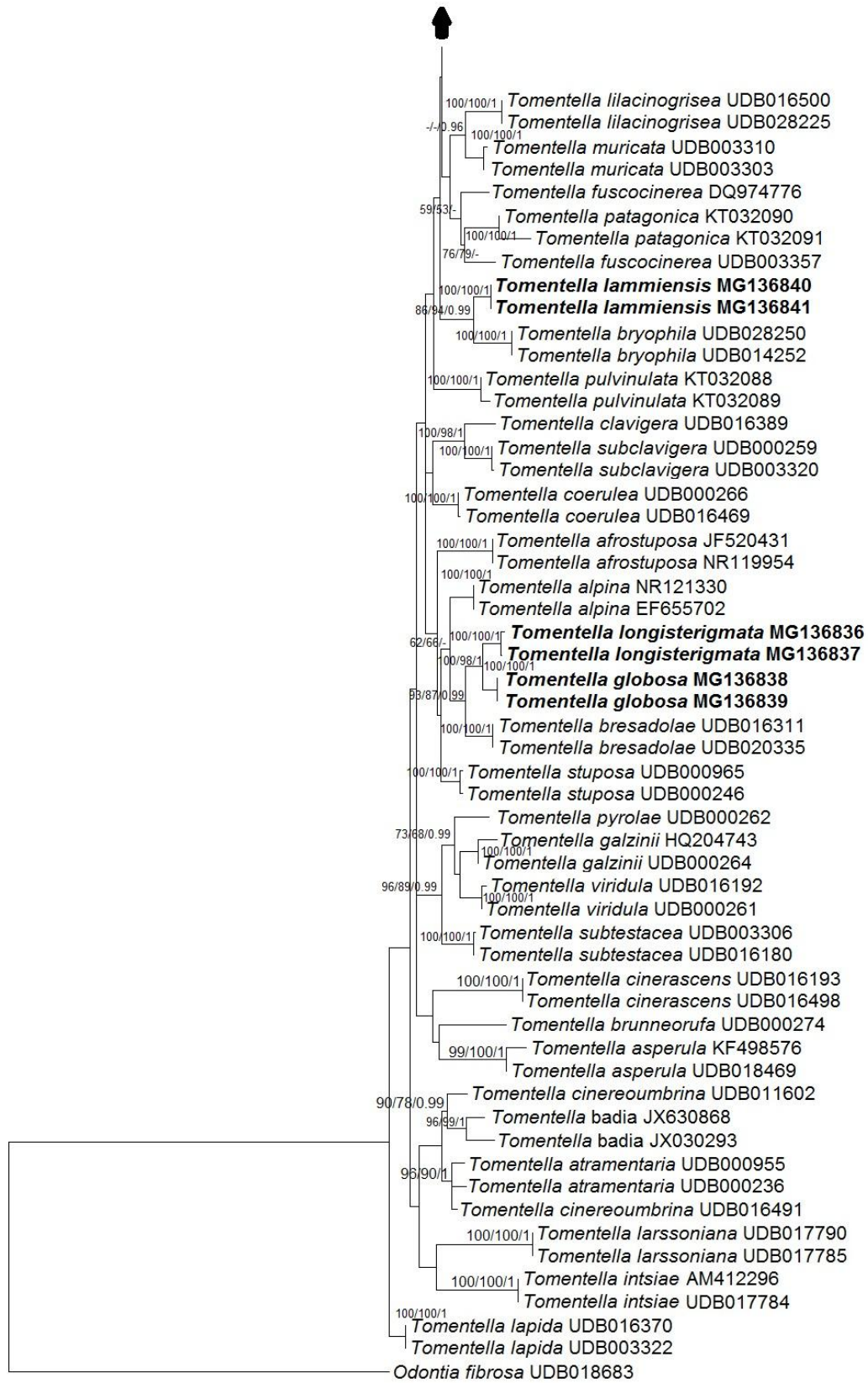
#### 4 LEGENDS

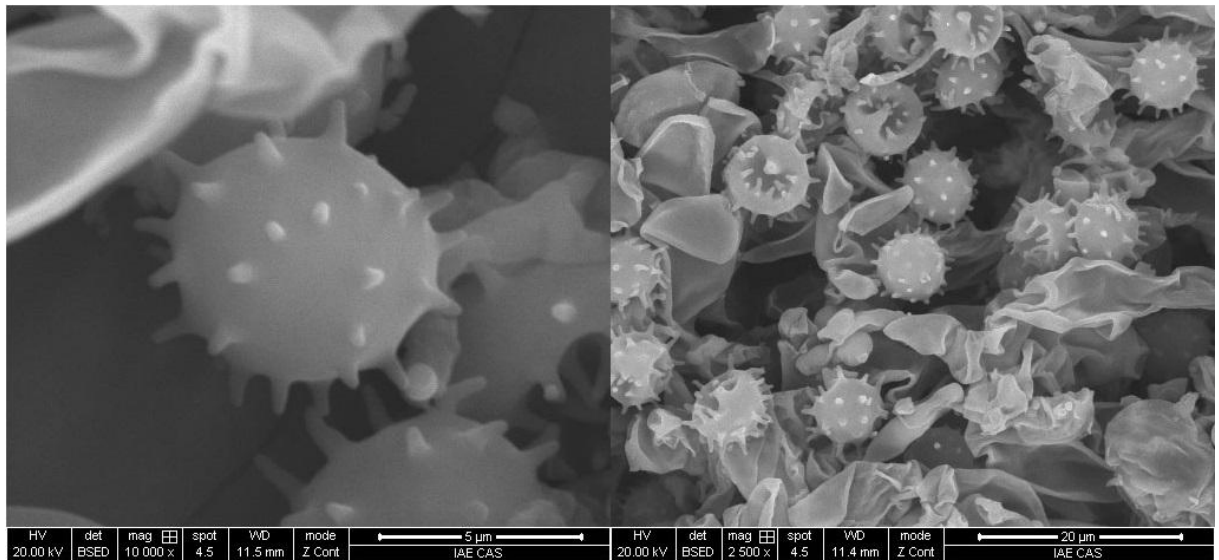
- 5 **Figure 1.** Maximum likelihood tree illustrating the phylogeny of *Tomentella globosa*, *T.*  
6 *lammiensis*, *T. longisterigmata* and related taxa, based on ITS sequence dataset. Branches are  
7 labeled with maximum likelihood bootstrap higher than 50%, parsimony bootstrap  
8 proportions higher than 50% and Bayesian posterior probabilities more than 0.95.
- 9 **Figure 2.** A basidiocarp of *Tomentella globosa* (holotype *Yuan 11603*).
- 10 **Figure 3.** SEM of basidiospores of *Tomentella globosa* (holotype *Yuan 11603*).
- 11 **Figure 4.** Microscopic structures of *Tomentella globosa* (drawn from *Yuan 11603*). a: Section  
12 through a basidiocarp; b: Basidiospores in lateral face; c: Basidiospores in frontal face.
- 13 **Figure 5.** Basidiocarps of *Tomentella lammiensis* (holotype *Yuan 11617*).
- 14 **Figure 6.** SEM of basidiospores of *Tomentella lammiensis* (holotype *Yuan 11617*).
- 15 **Figure 7.** Microscopic structures of *Tomentella lammiensis* (drawn from *Yuan 11617*). a:  
16 Section through a basidiocarp; b: Basidiospores in lateral face; c: Basidiospores in frontal face.
- 17 **Figure 8.** A basidiocarp of *Tomentella longisterigmata* (holotype *Yuan 11610*).
- 18 **Figure 9.** SEM of basidiospores of *Tomentella longisterigmata* (holotype *Yuan 11610*).
- 19 **Figure 10.** Microscopic structures of *Tomentella longisterigmata* (drawn from *Yuan 11610*). a:  
20 Section through a: basidiocarp; b: Basidiospores in lateral face; c: Basidiospores in frontal  
21 face.

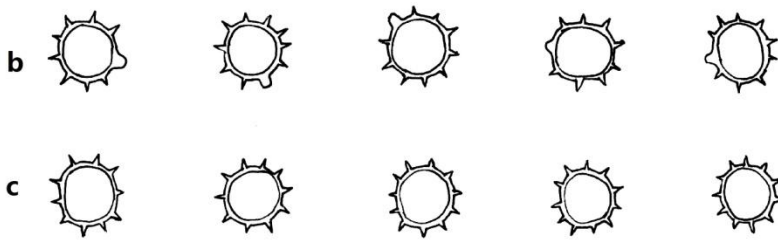
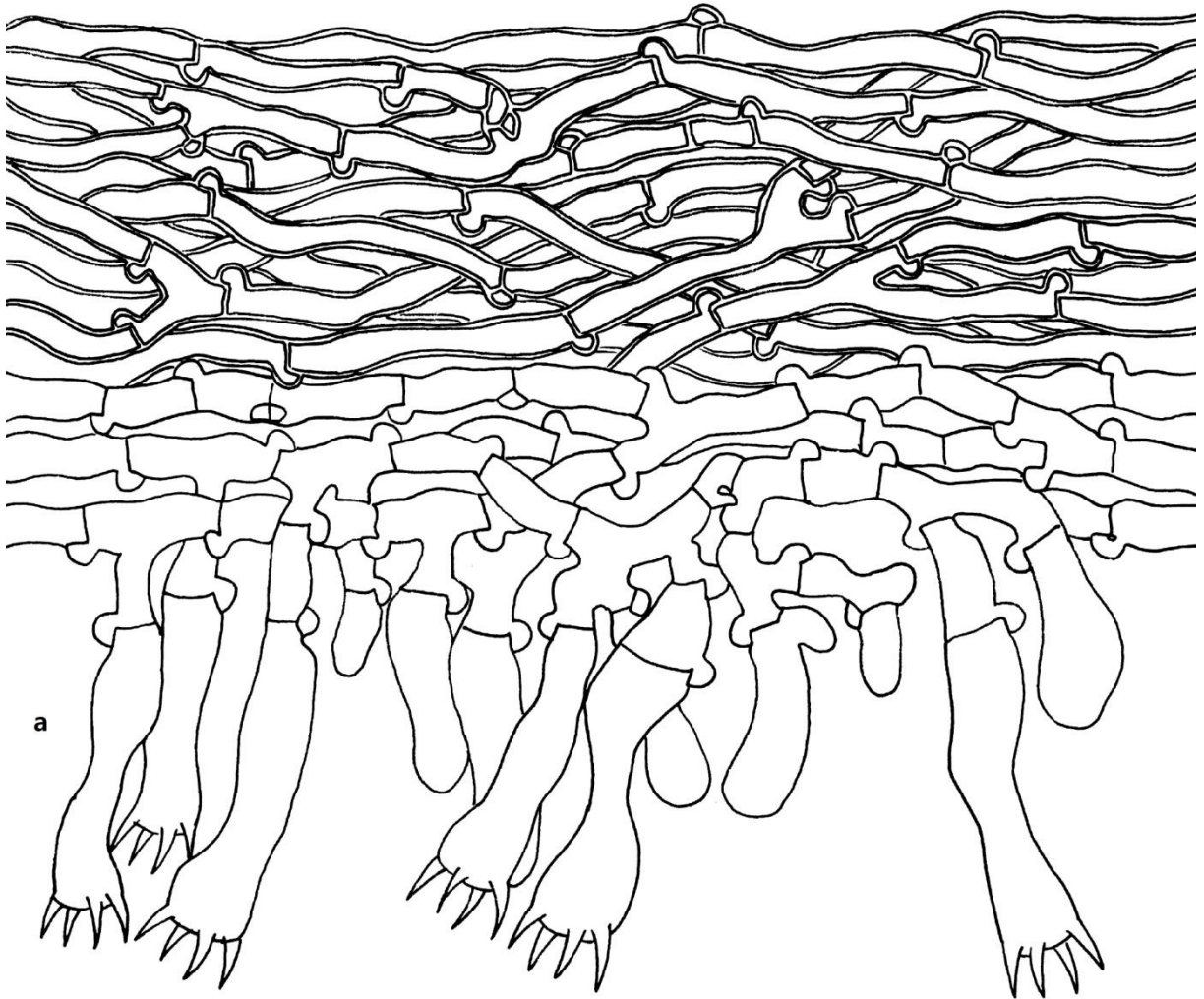
**1 FOOTNOTES**

2 Corresponding author: E-mail: [hsyuan@iae.ac.cn](mailto:hsyuan@iae.ac.cn); tel. & fax number: +86 -24- 83970347



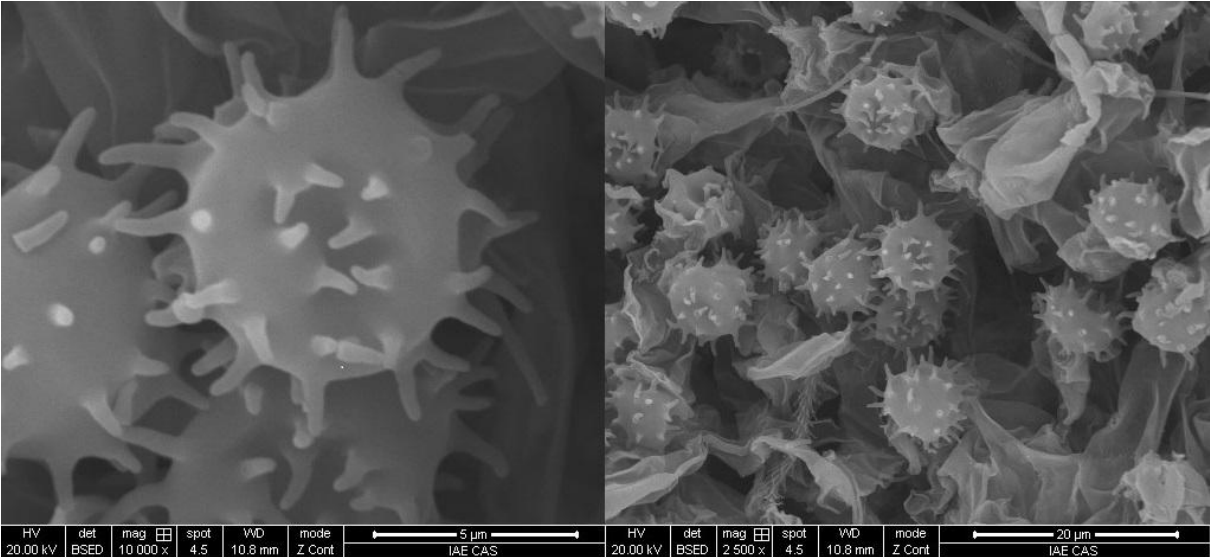




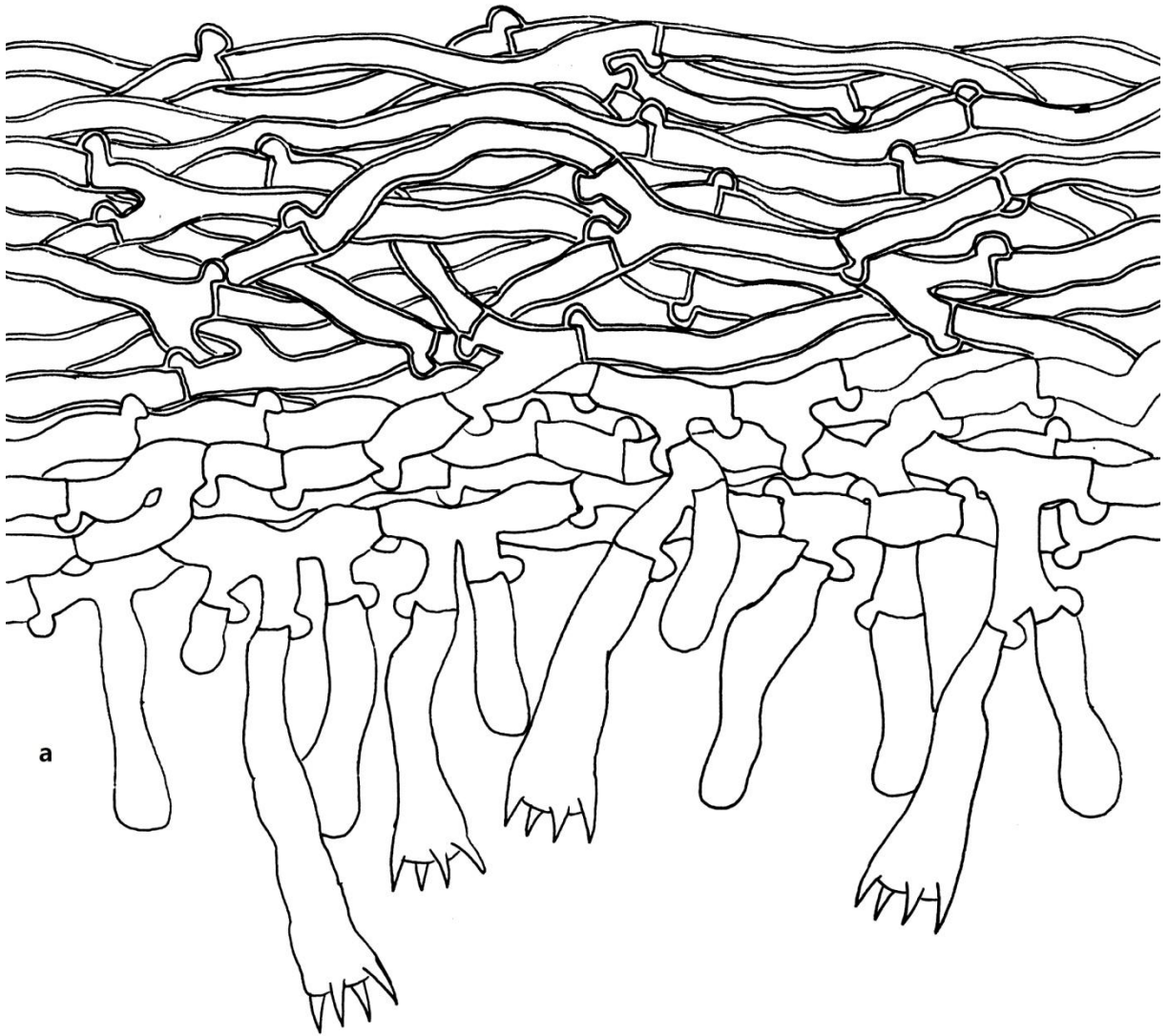




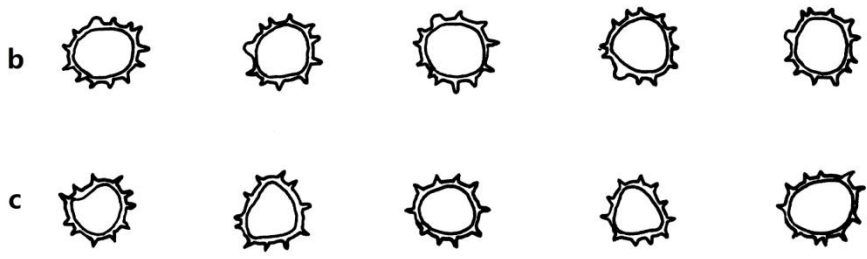
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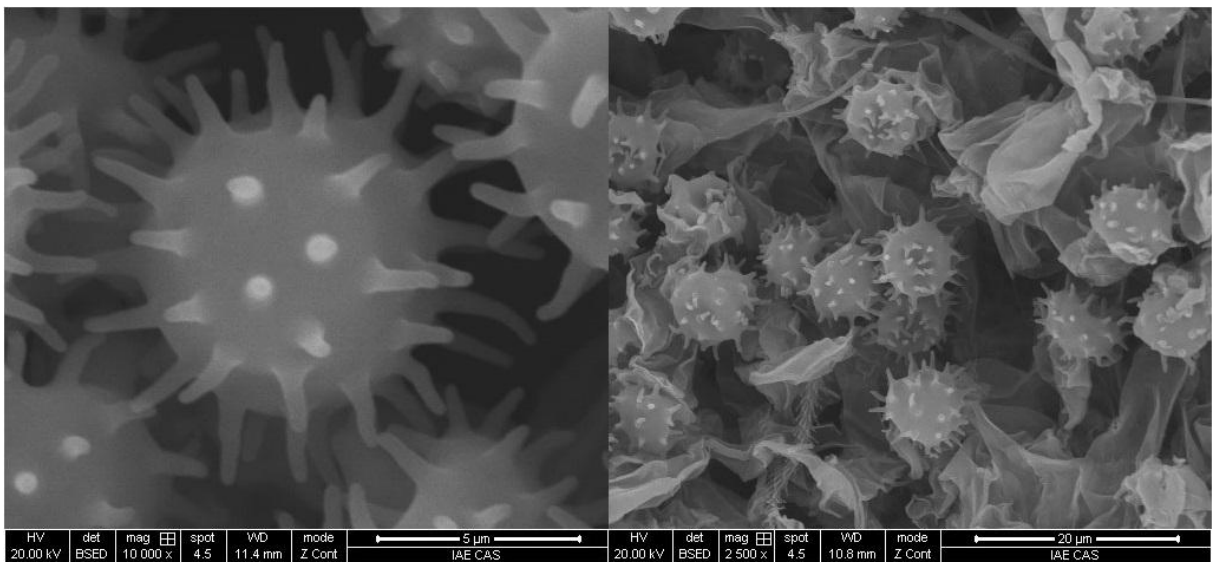
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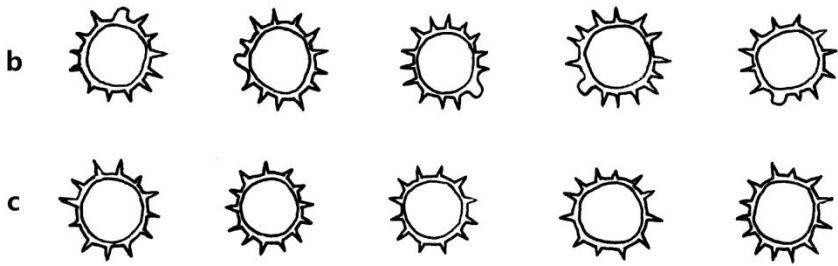
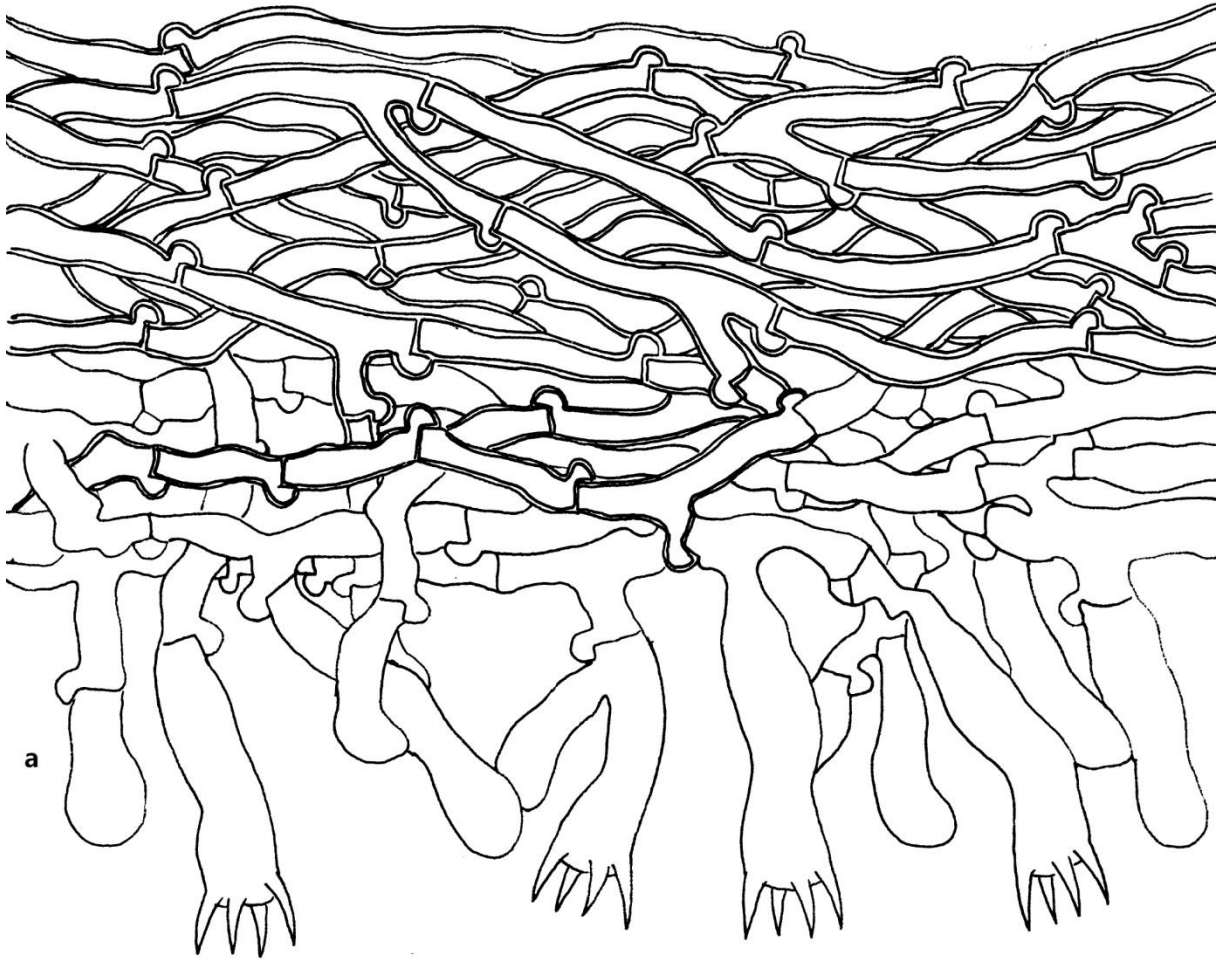


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1 TABLE 1. Specimens, strains, and sequences used in this study.

Species	GenBank Accession No./UNITE Database	Specimen ID/culture voucher	Location
<i>Odontia fibrosa</i>	UDB018683	TU115714	India
<i>Thelephora americana</i>	TAU83487	JMT17465	USA
<i>T. anthocephala</i>	DQ974771	src614	USA
<i>T. caryophyllea</i>	KM085427	ID PAN 684	Poland
<i>T. caryophyllea</i>	KC152242	GO-2010-163	Mexico
<i>T. terrestris</i>	EU819444	JMP0086	USA
<i>Tomentella afrostoposa</i>	JF520431	SYN 2292(M)	Guinea
<i>T. afrostoposa</i>	NR119954	M:SYN 2292	Guinea
<i>T. agbassaensis</i>	EF507257	SYN 981 (M)	Benin
<i>T. agbassaensis</i>	NR119638	M:SYN 981	Benin
<i>T. agereri</i>	EF538424	RA 13793 (M)	Benin
<i>T. agereri</i>	NR119641	M:RA 13793	Benin
<i>T. albomarginata</i>	UDB011601	TU115353	Finland
<i>T. albomarginata</i>	UDB011599	TU115350	Finland
<i>T. alpina</i>	EF655702	IB20060231	Austria
<i>T. alpina</i>	NR121330	IB:20060231	Austria

<i>T. amyloapiculata</i>	EF507263	SYN 893 (M)	Benin
<i>T. amyloapiculata</i>	NR119639	M:SYN 893	Benin
<i>T. asperula</i>	UDB018469	TU108147	Estonia
<i>T. asperula</i>	KF498576	—	Germany
<i>T. atramentaria</i>	UDB000236	TU123491	Germany
<i>T. atramentaria</i>	UDB000955	TU108866	Estonia
<i>T. atroarenicolor</i>	UDB000243	TAAM149946	Russia
<i>T. atroarenicolor</i>	UDB018480	TU100676	Estonia
<i>T. badia</i>	JX630868	—	Canada
<i>T. badia</i>	Jx030293	—	USA
<i>T. beaverae</i>	UDB015002	TU105060	Seychelles
<i>T. beaverae</i>	UDB017787	TU103595	Seychelles
<i>T. botryoides</i>	UDB000255	KHL8453	Sweden
<i>T. botryoides</i>	UDB000257	TAAM149614	Russia
<i>T. bresadolae</i>	UDB020335	TU115616	Slovenia
<i>T. bresadolae</i>	UDB016311	TU115447	Estonia
<i>T. brunneocystidia</i>	DQ848613	SYN 839 (M)	Benin
<i>T. brunneocystidia</i>	DQ848610	RA 13779	Benin
<i>T. brunneorufa</i>	UDB000274	TAAM159857	Australia

<i>T. bryophila</i>	UDB014252	TU116131	Estonia
<i>T. bryophila</i>	UDB028250	TU124259	Estonia
<i>T. capitata</i>	DQ848611	RA13785	Benin
<i>T. capitata</i>	DQ848612	SYN 860 (M)	Benin
<i>T. castanea</i>	UDB005597	—	Iran
<i>T. castanea</i>	UDB000120	TL-6886	Denmark
<i>T. cinerascens</i>	UDB016193	TU108037	Estonia
<i>T. cinerascens</i>	UDB016498	019AS	Italy
<i>T. cinereoumbrina</i>	UDB011602	—	Finland
<i>T. cinereoumbrina</i>	UDB016491	012AS	Italy
<i>T. clavigera</i>	UDB016389	UDB016389	Estonia
<i>T. coerulea</i>	UDB016469	TU115602	Estonia
<i>T. coerulea</i>	UDB000266	TAAM153804	Estonia
<i>T. ellisii</i>	UDB011603	—	Finland
<i>T. ellisii</i>	UDB000226	5b-A.Heller	Germany
<i>T. fuscocinerea</i>	DQ974776	src813	USA
<i>T. fuscocinerea</i>	UDB003357	LISU 178262	Portugal
<i>T. galzinii</i>	UDB000264	RS27093	Finland
<i>T. galzinii</i>	HQ204743	—	France

<i>T. globosa</i>	MG136838 <sup>a</sup>	Yuan11618	Finland
<i>T. globosa</i>	MG136839 <sup>a</sup>	Yuan11603	Finland
<i>T. guineensis</i>	JF520432	SYN 2331(M)	Guinea
<i>T. guineensis</i>	NR119955	M:SYN 2331	Guinea
<i>T. hjortstamiana</i>	AM412303	TU103641	Seychelles
<i>T. hjortstamiana</i>	KC222770	—	Australia
<i>T. intsiae</i>	AM412296	—	Seychelles
<i>T. intsiae</i>	UDB017784	TU105130	Seychelles
<i>T. lammi</i>	MG136840 <sup>a</sup>	Yuan11617	Finland
<i>T. lammi</i>	MG136841 <sup>a</sup>	Yuan11597	Finland
<i>T. lapida</i>	UDB016370	—	Estonia
<i>T. lapida</i>	UDB003322	TU100884	France
<i>T. larssoniana</i>	UDB017785	TU103690	Seychelles
<i>T. larssoniana</i>	UDB017790	TU105082	Seychelles
<i>T. lateritia</i>	UDB000963	NF.S045	Norway
<i>T. lateritia</i>	UDB000954	TU108551	Estonia
<i>T. lilacinogrisea</i>	UDB028225	TU124232	Estonia
<i>T. lilacinogrisea</i>	UDB016500	023 AS	Italy
<i>T. longisterigmata</i>	MG136836 <sup>a</sup>	Yuan11610	Finland

<i>T. longisterigmata</i>	MG136837 <sup>a</sup>	Yuan11602	Finland
<i>T. maroana</i>	EF507250	SYN 878 (M)	Benin
<i>T. muricata</i>	UDB003303	—	Estonia
<i>T. muricata</i>	UDB003310	TU100729	Finland
<i>T. nitellina</i>	EF411085	—	USA
<i>T. papuae</i>	AB259144	—	Japan
<i>T. parmastoana</i>	UDB016713	—	Seychelles
<i>T. parmastoana</i>	UDB017782	TU103691	Seychelles
<i>T. patagonica</i>	KT032091	BAFC52373	Argentina
<i>T. patagonica</i>	KT032090	BAFC52372	Argentina
<i>T. pileocystidiata</i>	UDB015029	TU105068	Seychelles
<i>T. pileocystidiata</i>	UDB017789	TU105054	Seychelles
<i>T. pilosa</i>	UDB028059	TU124067	Estonia
<i>T. pilosa</i>	UDB028227	TU124234	Estonia
<i>T. pisoniae</i>	UDB002643	TU103671	Seychelles
<i>T. pisoniae</i>	UDB017778	TU103655	Seychelles
<i>T. pulvinulata</i>	KT032089	BAFC52371	Argentina
<i>T. pulvinulata</i>	KT032088	BAFC52370	Argentina
<i>T. punicea</i>	UDB008231	TU110254	Estonia



<i>T. punicea</i>	UDB000959	KHL11908	Sweden
<i>T. pyrolae</i>	UDB000262	TAAM005998	Switzerland
<i>T. radiosa</i>	UDB014068	TU110022	Ecuador
<i>T. radiosa</i>	UDB000964	NF.S010	Norway
<i>T. stuposa</i>	UDB000246	TAAM159816	Finland
<i>T. stuposa</i>	UDB000965	NF.S051	Norway
<i>T. subclavigera</i>	UDB000259	TU115207	Norway
<i>T. subclavigera</i>	UDB003320	TU100877	France
<i>T. sublilacina</i>	UDB000229	TU115204	Norway
<i>T. sublilacina</i>	UDB000777	RK03-04	Denmark
<i>T. subtestacea</i>	UDB016180	TU115374	Ukraine
<i>T. subtestacea</i>	UDB003306	TU100715	Estonia
<i>T. tedersooi</i>	UDB017781	TU103673	Seychelles
<i>T. tedersooi</i>	UDB002644	TU103664	Seychelles
<i>T. tenuissima</i>	KT032083	CIEFAP FK15011	Argentina
<i>T. tenuissima</i>	KT032082	BAFC52369	Argentina
<i>T. terrestris</i>	UDB000222	EL9897	USA
<i>T. terrestris</i>	UDB003315	TU100886	France
<i>T. umbrinospora</i>	UDB017844	TU111410	Italy

<i>T. umbrinospora</i>	UDB016499	TU111379	Italy
<i>T. viridula</i>	UDB016192	TU108038	Estonia
<i>T. viridula</i>	UDB000261	TU108165	Sweden

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1 <sup>a</sup> Sequences newly generated in this study.