Current Research in Environmental & Applied Mycology (Journal of Fungal Biology)
8(3): 360–371 (2018) ISSN 2229-2225

www.creamjournal.org **Article**

Doi 10.5943/cream/8/3/7
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Basidiome reduction in litter-inhabiting *Thelephorales* in boreal forest environments: morphological and molecular evidence

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Zmitrovich IV, Shchepin ON, Malysheva VF, Kalinovskaya NI, Volobuev SV, Myasnikov AG, Ezhov ON, Novozhilov YuK 2018 – Basidiome reduction in litter-inhabiting *Thelephorales* in boreal forest environments: morphological and molecular evidence. Current Research in Environmental & Applied Mycology (Journal of Fungal Biology) 8(3), 360–371, Doi 10.5943/cream/8/3/7

Abstract

Diversification of many taxa of thelephoroid fungi is associated with basidiome reduction via transition to life and sporulation within caverns of windfall-soil complexes as well as between fallen logs and moss cover in boreal forests. The present expertise observation regarding the xylotrophic fungi and its niches. The present report describes a number of boreal *Thelephorales* with reduced basidiomes with considerations on the evolution of basidiome within the group based on molecular phylogeny. Two new forms (*Hydnellum concrescens* f. *petaloides* and *Phellodon melaleucus* f. *suspensis*) were described, rare species *Hydnellum gracilipes* is characterized molecularly, and one replacing name (*Thelephora wakefieldii*) as well as two new combinations (*Th. ellisii* and *Th. umbrinella*) were made. The molecular characterization of *Phellodon secretus* holotype is given for the first time here.

Key words – basidiome reduction – boreal forests – molecular taxonomy – morphological rationalization – thelephoroid fungi

Introduction

Boreal forests are characterized by acidified and moistened litter, what increases the rate of mycogenous destruction of wood debris (Harvey et al. 1979, Renvall 1995, Zmitrovich 2011). As a result, rather a heterogeneous cover called “windfall-soil complexes” forms over the soil surface, where the wood is present at various stages of decomposition and is more or less immersed in moss cover (Smirnova 2004, Zmitrovich 2008). For lignotrophic ascomycetes and basidiomycetes (both white and brown rot producers), this structure offers a number of micro-niches where various fungal morphotypes can be realized (Zmitrovich et al. 2015b).

Thelephoroid fungi have a circumglobal distribution from polar deserts (Geml et al. 2011) to tropical forests (Corner 1968), but the maximum of their diversity is observed within the boreal

Submitted 9 April 2018, Accepted 28 May 2018, Published 27 June 2018
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zone of the planet (Kõljalg 1996). This group of fungi is involved into ectotrophic mycorrhizas (Erland & Taylor 1999, Zmitrovich et al. 2015b), but it is also capable of destroying wood debris as white rot producers (Zhishu et al. 1993). As mycorrhiza-formers, they play an important role in the pioneer microhabitats of boreal forests (Ezhov & Zmitrovich 2017). Diversification of many taxa is associated with basidiome reduction due to the transition to life and sporulation within caverns of windfall-soil complexes as well as between fallen logs and moss cover. The present report is devoted to the description of a number of interesting representatives of boreal *Thelephorales* with reduced basidiomes and investigation of their phylogenetic relationships.

Materials & Methods

Specimens of fungal basidiomes were collected and identified as described elsewhere (Ezhov et al. 2017) and materials from the mycological herbarium of the Komarov Botanical Institute (LE) were used. All specimens studied are listed in Table 1. Stereo microscope Carl Zeiss Stemi DV4 and light microscope Mikmed-6 were used for species determination. Detailed anatomical and morphological investigations was performed on a light microscope Carl Zeiss Axioskop-40 and stereo microscope Carl Zeiss Stereo Discovery V 12. Photographs of fruiting bodies and habitats of fungi were obtained with Nikon D80–AF Micro Nikkor 60 mm camera.

A total of four specimens from the mycological herbarium of the Komarov Botanical Institute (LE) were considered for molecular analysis: *Hydnellum gracilipes, H. concrescens, Phellodon melaleucus*, and a holotype specimen of *Phellodon secretus*. Additional 85 ITS sequences of other thelephoroid species were retrieved from GenBank (http://www.ncbi.nlm.nih.gov/Genbank/) and UNITE database (https://unite.ut.ee/). Environmental sequences of *Phellodon secretus* and *Phellodon melaleucus* originating from samples of deadwood from Nizhne-Svirsky Reserve, Russia, were also included in phylogenetic analysis (Shchepin et al. 2018). Information on sequences used for tree reconstruction is given in Table 1.

Table 1 Species of thelephoroid fungi involved into molecular phylogenetic analysis.

Species	GenBank accession or UNITE code	Origin (country, region)	Collection/herbarium number
Hydnellum aurantiacum	KP406543	Canada: British Columbia	UBC F28455
H. aurantiacum	EU622332	United Kingdom	E00139384
H. aurantiacum	EU622330	—	—
H. aurantiacum	AF347113	Finland: Inari	TAAM164119
H. concrescens	EU622360	—	—
H. concrescens	EU622357	—	—
H. concrescens	MH118168	Russia: Leningrad Region	LE303745
H. gracilipes	MH118169	Russia: Leningrad Region	LE303768
H. gracilipes	UDB000292	Finland: Inari	H (Renvall3728)
Phellodon melaleucus	MG597403	Russia: Leningrad Region	—
Ph. melaleucus	JN135197	USA: North Carolina	R.E. Baird 408
Ph. melaleucus f. *suspensis*	MH118171	Russia: Leningrad Region	LE287650
Ph. niger	JN135202	USA: North Carolina	R.E. Baird 46
Ph. niger	EU622373	United Kingdom	E00139386

Table 1 Continued.

Species	GenBank accession or UNITE code	Origin (country, region)	Collection/herbarium number
Ph. secretus	MG597404	Russia: Leningrad Region	—
Ph. secretus (type)	MH118170	Finland: North Karelia	H (Niemela7460)
Thelephora anthocephala	DQ974771	USA: California	src614
Th. anthocephala	KP454019	Canada: British Columbia	UBC F28410
Th. anthocephala	AF272927	Estonia	TAAM165304
Th. caryophyllea	EF655705	Austria: Ötz valley	IB20060087
Th. caryophyllea	AJ889980	Denmark: Jutland	TL-6566
Th. caryophyllea	KC152242	Mexico: Tlaxcala	R. Garibay Orijel-2010-163
Th. caryophyllea	KM085427	Poland	ID PAN 684
Th. penicillata	UDB025029	Estonia	TU(M)116217
Th. penicillata	UDB000214	Estonia	TAAM169453
Th. penicillata	UDB000775	Denmark	C (JV97-062)
Th. terrestris	MG786682	South Africa	—
Th. terrestris	KY693686	Spain	—
Tomentella badia	KM409442	Poland	—
T. badia	KM409415	Poland	—
T. badia	JQ711987	Canada: British Columbia	—
T. badia	EU726325	USA: California	—
T. bryophila	UDB025616	Estonia	TU(M)116842
T. bryophila	UDB000035	Denmark	C (MC01-548)
T. bryophila	UDB000254	Norway	TU(M)115212
T. cinerascens	UDB003309	Finland	TU(M)100735
T. cinerascens	UDB016193	Estonia	TU(M)108037
T. cinerascens	UDB016498	Italy: Sicily	TU(M)111378
T. cinerascens	UDB020332	Slovenia	TU(M)115637
T. coerulea	KT182919	Latvia	—
T. coerulea	KR019826	Latvia	—
T. coerulea	AF272934	Russia: Krasnodarsky Kray	TAAM149922
T. ellisii	DQ974775	USA: California	src846
T. ellisii	KT353046	Mexico: Mexico State	R. Garibay Orijel-2009-017
T. ellisii	DQ068971	Lithuania	—
T. ellisii	KP783473	Russia: Primorsky Krai	—
T. ferruginea	UDB028072	Estonia	TU(M)124081
T. ferruginea	EU819497	USA: Wisconsin	NAMA246
T. ferruginea	UDB016471	Estonia	TU(M)115605
Tomentella sp.	UDB028159	Estonia	TU(M)124166
T. fibrosa	AM412301	Seychelles: Vallée de Mai Nature Reserve	TAAM195065
T. fibrosa	KX426529	China: Inner Mongolia	—
T. fuscocinerea	JX145395	China: Inner Mongolia	—

Table 1 Continued.

Species	GenBank accession or UNITE code	Origin (country, region)	Collection/herbarium number
T. fuscocinerea	GU214812	Denmark	T. Læssøe 6662
T. lapida	UDB016653	Australia: Queensland	TU(M)100587
T. lapida	UDB000250	Norway	TU(M)115211
T. lapida	UDB016305	Estonia	TU(M)115440
T. lapida	UDB016346	Estonia	TU(M)115491
T. lateritia	UDB016705	Australia: Tasmania	TU(M)100385
T. stuposa	KY693712	Spain	—
T. stuposa	KM409444	Poland	—
T. stuposa	KP783475	Russia: Primorsky Krai	—
T. stuposa	KR019829	Latvia	—
T. sublilacina	KP814554	USA: California	—
T. sublilacina	KJ140725	USA: Wisconsin	CFMR:DLL2011-238
T. sublilacina	KY693713	Spain	—
T. sublilacina	KC952708	Germany	—
T. terrestris	KX426528	China: Inner Mongolia	—
T. terrestris	AF272911	Estonia	TAAM159557
T. terrestris	AF272901	Sweden	—

Note: Accession numbers refer to GenBank Nucleotide or UNITE database (numbers starting with UDB).

DNA was extracted using AxyPrep Multisource Genomic DNA Miniprep Kit (Axygen Biosciences, California, USA) following the manufacturer's recommendations. The ribosomal ITS1–5.8S–ITS2 region was amplified by PCR with the fungal specific primers ITS1F and ITS4B. The PCR products were purified using Fermentas Genomic DNA Purification Kit (Thermo Scientific). Sequencing was performed with ABI 3130 Genetic Analyzer (Applied Biosystems) using BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems) with the same primers. The raw data were processed using Sequencing Analysis 5.3.1 (Applied Biosystems).

Sequences were aligned using MAFFT (Katoh et al. 2017) with E-INS-i option. Ambiguously aligned portions of ITS-regions or multiple base gaps were excluded from the alignment for further analysis using GBlocks (Talavera & Castresana 2007). Phylogenetic reconstructions were performed with Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. ML was performed using IQ-TREE 1.5.5 (Nguyen et al. 2015) with 1000 ultrafast (UF) bootstrap replicates (Minh et al. 2013). TN+F+G4 was chosen by ModelFinder (Kalyaanamoorthy et al. 2017) as an optimal substitution model according to the Bayesian information criterion. BI was performed using MrBayes 3.1 (Ronquist & Huelsenbeck 2003) with two independent runs, each with 2,000,000 generations with GTR model and four chains with sampling every 100 generations.

Results

Distribution of reduced forms on thelephoroid tree

Telephoroid fungi with reduced basidiomes turn to be scattered over several clades of thelephoroid tree (Figs 1, 2), and some representatives having completely plagiotropic basidiomes (e.g., a number of resupinate *Thelephora* species considered currently within *Tomentella*) or with

pilei at least partially attached dorsally to lower part of fallen log and with strongly reduced peripheric stalk, turn out to belong to genera originally described on the basis of orthotropic basidiomes as *Hydnellum*, *Phellodon*, and *Thelephora*. These subpendent pilei with reduced stalk are characteristic for *Hydnellum gracilipes* described by Karsten (1879), and for recently described *Phellodon secterus* (Niemelä et al. 2003). In addition, we found that normally orthotropic thelephoroid species are capable of giving rise to lateral petaloid forms (*Hydnellum concrescens*), or give subpendent pilei along with normal ones (*Phellodon melaleucus*).

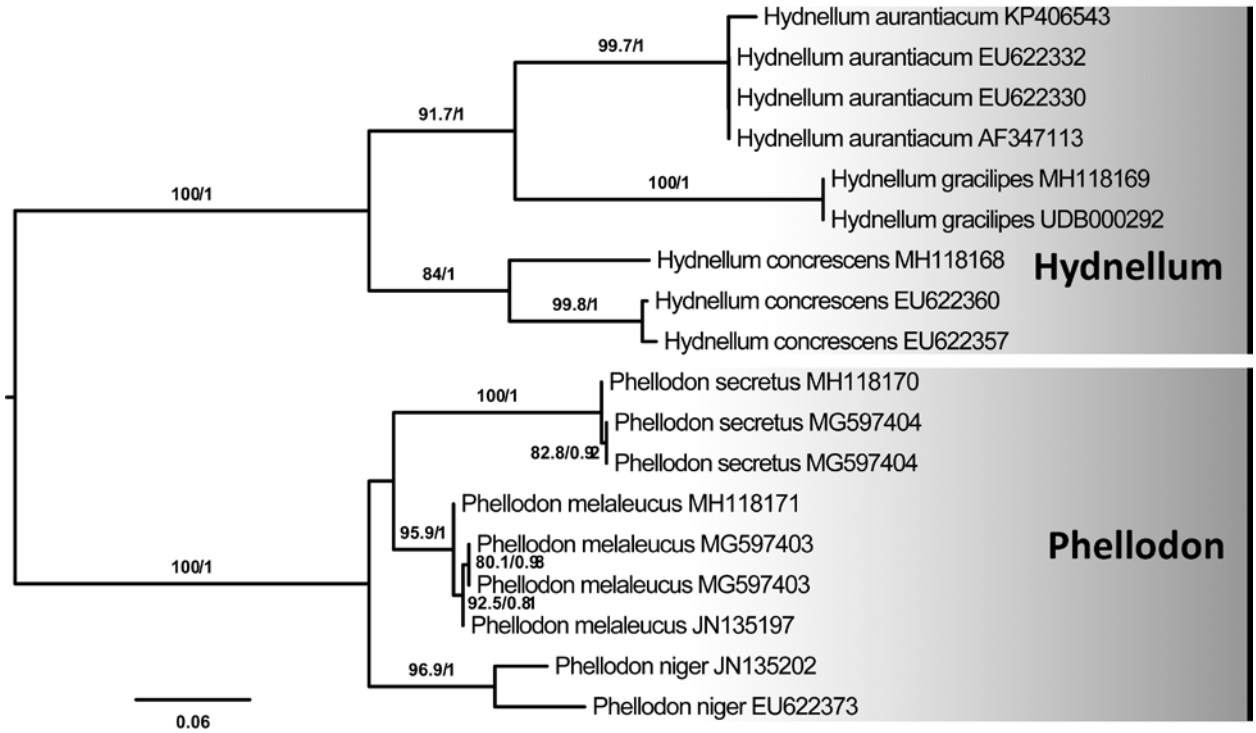

Fig. 1 – The best ML phylogenetic tree of the *Hydnellum* and *Phellodon* spp. obtained from the ML analysis of the ITS1–5.8S–ITS2 dataset. Ultrafast bootstrap values (%) from ML and posterior probabilities from BI analyses not less than 70 and 0.7 respectively are shown.

Taxa Description

Hydnellum concrescens f. ***petaloides*** Zmitr., Shchepin, Volobuev & Myasnikov, f. nov.

MycoBank number: MB824104

Description – Basidiomes minute, 3 × 3.5 × 0.1–0.5 cm, orthotropic, pleuropodal, petaloid, deeply lobate, with bulbil-like stem immersed into the ground. Upperside uneven, scrupose at the base, radially-ridged at periphery, subtomentose to matt, clay-vinaceous to cinnamon. Margin deeply lobate, naked, sterile. Hymenophore hydnoid, single spine layer ca. 1 mm thick, grayish-vinaceous-brown. Spines sharp, conical, dense, 0.2–1.2 mm long. Stem undergrown, 2.2 × 0.3–0.7 cm, wrinkled, inflated at the lower part, vinaceous-brown (Fig. 3a, b). Hyphal system monomitic with gloeoplerous hyphae. Generative hyphae 4.5–7 μm in diameter, simple-septate, thin-walled and hyaline or thick-walled and golden-brown, gloeoplerous hyphae 5–7 μm in diameter. Cystidia none. Basidia 18–35 × 6–7 μm, clavate, with 4 sterigmata 3–5 μm long, without a basal clamp. Basidiospores 4.1–5.2 × 5.8–7.2 μm, subglobose with oblique hilar appendage and tuberculate ornamentation, golden-brown in KOH, cyanophilous.

Holotype – LE 303745, Russia, Leningrad Region, Lodeynopolsky District, Nizhne-Svirsky Nature Reserve, Kut-Lakhta, Pinetum hylocomioso-vacciniosum, on soil within *Hylocomium* curtains, collected 12.09.2014 by NI Kalinovskaya, determined by VF Malysheva & IV Zmitrovich.

Etymology – *petaloides* – petal-shaped; a reference to pileus form and attachment.

The presented form demonstrates the morphogenetic tendency of transformation of the infundibuliform basidiome, characteristic for the modal morphotypes of this species, to the effuso-reflexed/pendent basidiome.

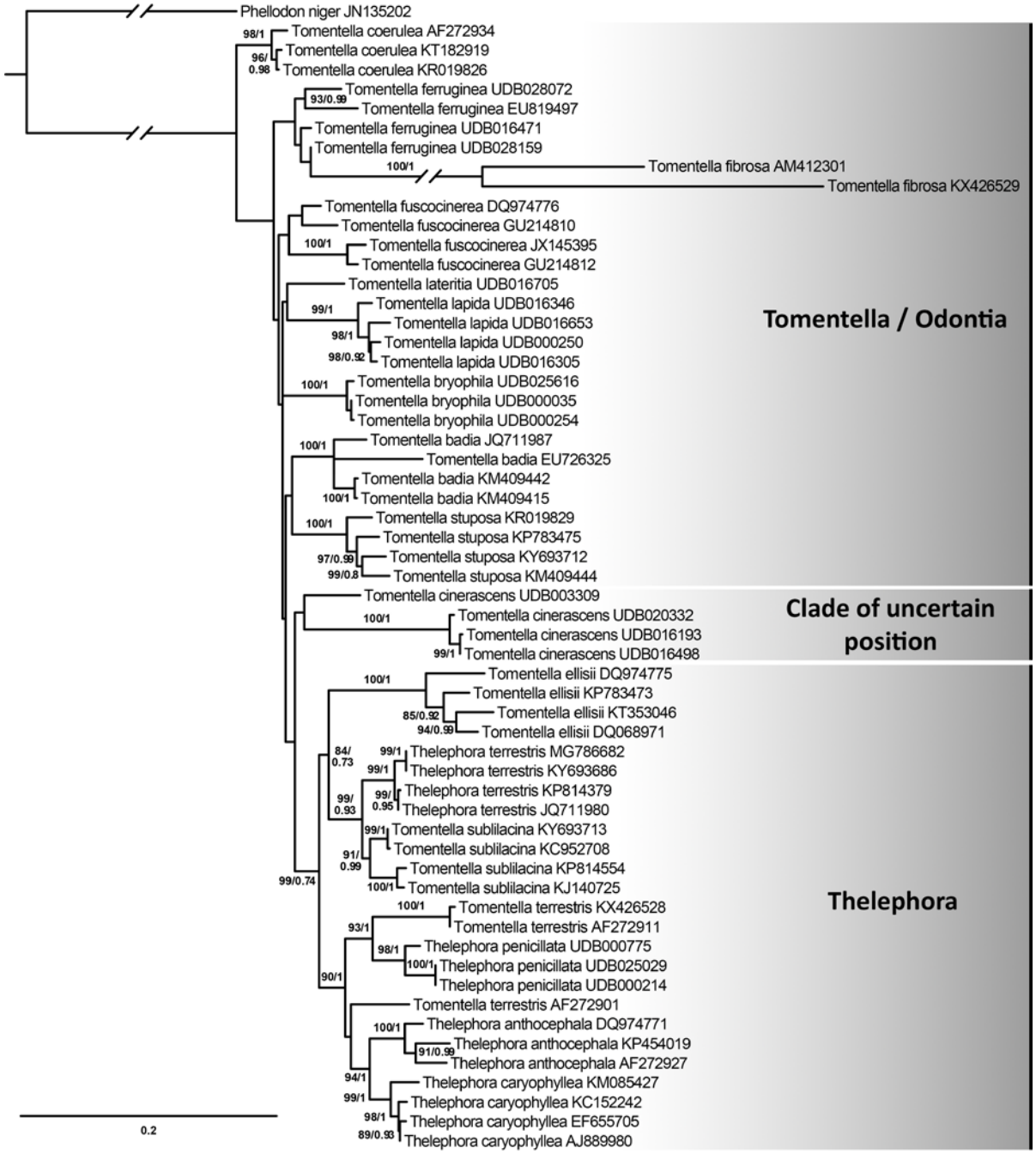

Fig. 2 – The best ML phylogenetic tree of the *Thelephora* spp. and related taxa obtained from the ML analysis of the ITS1–5.8S–ITS2 dataset. Ultrafast bootstrap values (%) from ML and posterior probabilities from BI analyses not less than 70 and 0.7 respectively are shown.

Hydnellum gracilipes (P. Karst.) P. Karst., 1879, Meddn Soc. Fauna Flora fenn. 5: 41.

Description – Basidiomes confluent or not, 1–5 × 0.5–3 × 1.5(2) mm, pendent, differentiated into prostrate pilei and eccentric rudimental stipes. Upperside azonate, chocolate brown with vinaceous tint. Margin prostrate, with yellowish-cream sterile zone in hymenophoral side. Hymenophore hydnoid, as a single spine layer up to 1.5 mm thick, purplish-brown when fresh, the red tint fade to more or less greyish brown during drying, concolorous with subiculum. Spines

more or less cylindrical, somewhat curved, tapering towards the sharp apex, 0.5–1.5 mm long (Fig. 3, *c*). Hyphal system monomitic, all hyphae simple-septate, 2–3.5 μm in diameter, hyaline to yellowish, thin-walled, gloeoplerous hyphae present, some hyphae with brownish, granular encrustation, hyphal cords absent in subiculum but present in stipes-rhizomorphs. Cystidia none. Basidia 20–24 × 4.5–6.5 μm, clavate, with 4 sterigmata 2–4 μm long, simple-septate at base. Basidiospores ellipsoid to subglobose, 3.0–4.0 × 2.8–3.8 μm, tuberculate, yellowish-brown in KOH, cyanophilous. Under fallen logs mostly in green-moss boreal communities. Mycorrhizal (Smith & Read 2008). According to Ainsworth et al. (2010), *H. gracilipes* belongs to phylogenetic radiation of *H. concrescens*. Kõljalg & Renvall (2000) have shown closer relationships of this species to *H. peckii*. According to our data, *H. gracilipes* is closer to *H. aurantiacum* than to *H. concrescens*.

Phellodon melaleucus f. ***suspensis*** Zmitr., Shchepin, Volobuev & Myasnikov, f. nov.

MycoBank number: MB824105

Description – Basidiomes confluent, minute, 1–3.5 × 0.8–2.8 × 0.1–0.2 cm, pendent, differentiated into prostrate pilei and eccentric rudimental stipes. The attachment of basidiome patches to the underside of fallen log and surrounding mosses is by means of marginal areas of the pilei. Upperside more or less even, matt, obscurely concentrically-zonate, olivaceous-brown at the centre, grayish-brown at the periphery. Margin sharp, moderately lobate, naked, sterile. Hymenophore hydnoid, as single spine layer ca. 0.5 mm thick, cream with grayish tints. Spines sharp, slender, dense, 0.1–0.5 mm long. Stipes 0.5–1.4 × 0.2–0.4 cm, rudimental, incurved, eccentric to lateral, matt, blackish-brown (Fig. 3d, e). Hyphal system monomitic, hyphae 3–6 μm in diameter, simple-septate, thin-walled and hyaline or thick-walled and grayish-brown. Cystidia none. Basidia 20–35 × 4.8–5.5 μm, clavate to stalked, with 4 sterigmata 3–5 μm long, without a basal clamp. Basidiospores 3.1–4.1 × 2.7–3.7 μm, subglobose with expressed hilar appendage and spinose ornamentation, hyaline, cyanophilous.

Holotype – LE 287650, Russia, Leningrad Region, Vsevolozhsk District, Chernaya Rechka vicinities, Pinetum polytrichosum, under *Pinus sylvestris* fallen log, collected 03.08.2016 by IV Zmitrovich & NI Kalinovskaya, molecularly identified by VF Malysheva.

Etymology – *suspensis* – suspended; refers to the feature of basidiome attachment.

This form resembles *Phellodon secretus*, another species with resupinate pilei and rudimental stipe (Niemelä et al. 2003). However, our data obtained from molecular comparison of two species support an isolated position of *Ph. secretus*. Other differences between two species are summarized in Table 2.

Table 2 Comparative characteristics of two *Phellodon* species.

Characters	***Phellodon melaleucus* f. *suspensis* (holotype)**	***Ph. secretus*, holotype (H!)**
Basidiospores	3.1–4.1 × 2.7–3.7 μm	2.9–3.3 × 2.7–3.1 μm
Spines length	0.1–0.5 mm	0.3–0.9(1.5) mm
Upperside	obscurely zonate, olivaceous-brown at the center, grayish-brown at the periphery	azonate, at first white with ash-gray tint, later darker gray or with hue of sepia

Thelephora ellisii (Sacc.) Zmitr., Shchepin, Volobuev & Myasnikov, comb. nov. (MB 824106).
Basionym: *Zygodesmus ellisii* Sacc., 1886, Syll. fung. 4: 808.
≡ *Tomentella ellisii* (Sacc.) Jülich & Stalpers, 1980, Verh. K. ned. Akad. Wet., tweede sect. 74: 236.

Description – Basidiomes resupinate, adhering to the substrate, continuous with clear margin, initially mucedinoid, then pellicular. Hymenophore even or finely verrucose, grayish-cinnamon, darker than subiculum, paler at the margin. Marginal zone rather expressed, byssoid to farinaceous,

yellowish-cream to wood-colored. Subiculum loose, in some cases with hyphal cords, ivory-white, yellowish-cream or wood-colored (Fig. 3f). Hyphal system is monomitic, all hyphae with clamps and more or less inflated segments, mean diameter 3–6 μm, hyaline or yellowish-brown in the subiculum, unchanged in KOH. Cystidia none. Basidia 38–70 × 7.5–10 μm, utriform, 4-spored, basally clamped, hyaline or greenish in KOH. Basidiospores obscurely triangular to ellipsoid, 7–13 μm in longest dimension, rather sparsely echinulate with spines 0.5 μm long, golden-brown in KOH. Colonizes all kinds of wood debris in boreal and temperate zones of the Northern Hemisphere. Mycorrhizal (Aučina et al. 2007).

Thelephora wakefieldiae Zmitr., Shchepin, Volobuev & Myasnikov, nom. nov. (MB 825554).

Replaced name: *Zygodesmus sublilacinus* Ellis & Holw., Bulletin of the Geological and Natural History Survey of Minnesota 3: 34, 1887. – Competing homonym: non *Thelephora sublilacina* Ellis & Everh., Bull. Lab. Nat. Hist. Iowa State Univ. 4: 67, 1896 (≡ *Septobasidium sublilacinum* (Ellis & Everh.) Burt).

Synonyms: *Hypochnus avellaneus* Burt, 1916, Annals of the Missouri Botanical Garden 3: 225, non *Thelephora avellana* Fr., Syst. Mycol. 1: 442, 1821 (q.e. *Hymenochaetopsis tabacina* (Sowerby) S.H. He & Jiao Yang). – *Tomentella porulosa* f. *albomarginata* Bourdot & Galzin, Hyménomyc. de France: 505, 1928, non *Thelephora albomarginata* Schwein., London J. Bot. 6: 324, 1847 (q.e. *Peniophora albobadia* (Schwein.) Boidin). – *Tomentella pseudopannosa* Wakef., 1969, Trans. Br. Mycol. Soc. 53(2): 189, 1969 (nom. inval., Art. 39.1).

Description – Basidiomes resupinate, adhering to the substrate, continuous with indeterminate margin, initially arachnoid, then pellicular. Hymenophore even or finely and unevenly papillose, vinaceous to lilaceous-gray, concolorous with subiculum or paler, without clear marginal zone. Subiculum loose, without hyphal cords, vinaceous-brown (Fig. 3g). Hyphal system is monomitic, all hyphae with clamps and more or less inflated segments, mean diameter 3–7 μm, hyaline to brown in the subiculum, more intensively colored in KOH. Cystidia none. Basidia 40–65 × 7.5–12 μm, utriform, 4-spored, basally clamped, hyaline in KOH. Basidiospores triangularly ellipsoid, more or less lobate, 7–10 μm in longest dimension, rather sparsely echinulate with spines 0.5 μm long, pale-brown in KOH. Colonizes all kinds of wood debris in boreal and temperate zones of the Northern Hemisphere. Mycorrhizal (Lilleskov & Bruns 2005).

Thelephora terrestris f. ***radiosa*** (P. Karst.) Zmitr., in Zmitr. et al., 2015, Macromycetes of Nizhnesvirsky Nature Reserve (St. Petersburg): 157.

= *Tomentella radiosa* (P. Karst.) Rick, 1934, Brotéria, N.S. 2(2): 79.

Description – Basidiomes resupinate, adhering to the substrate or not, continuous with clear (often ciliate or bearing a clavarioid processes) margin, initially pellicular, then crustose and cracking on drying. Hymenophore even or finely and unevenly papillose, fuscous, pale fawn, brown chocolate, paler at the margin. Marginal zone rather expressed, byssoid to farinaceous, yellowish-cream to wood-colored. Subiculum loose, with hyphal cords, yellowish-cinnamon (Fig. 3, *h*). Hyphal system is monomitic, all hyphae with clamps and more or less inflated segments, mean diameter 3–10 μm, hyaline to golden-brown in the subiculum, more intensively colored in KOH. Cystidia none. Basidia 35–55 × 8–12 μm, utriform, 4-spored, basally-clamped, hyaline in KOH. Basidiospores triangularly ellipsoid, more or less lobate, 7–10.5 μm in longest dimension, rather sparsely echinulate with spines 0.5 μm long, pale-brown in KOH, 1–several-guttate. Colonizes all kinds of wood debris in boreal and temperate zones of the Northern Hemisphere. Mycorrhizal (Tammi et al. 2001). An intraspecific nature of the fungus in question was revealed in 2001 (Tammi et al. 2001), whereas formal combination was made rather recently (Zmitrovich et al. 2015a). *Th. terrestris* f. *resupinata* (Bourdot & Galzin) Donk, which is more widely distributed in boreal forests (Zmitrovich 2000), is distinguished by true pendent basidiomes with traces of the upperside cilia at pileus margin.

Thelephora umbrinella (Bourdot & Galzin) Zmitr., Shchepin, Volobuev & Myasnikov, comb. nov. (MB 824109).
Basionym: *Tomentella spongiosa* subsp. *umbrinella* Bourdot & Galzin, 1924, Bull. trimest. Soc. mycol. Fr. 40(2): 154.
= *Zygodesmus terrestris* Berk. & Broome, 1881, Ann. Mag. nat. Hist., Ser. 5: 130, nec *Thelephora terrestris* Ehrh., 1787, Pl. Crypt. Linn. Exsicc.: no. 178.
Fig. 3i.

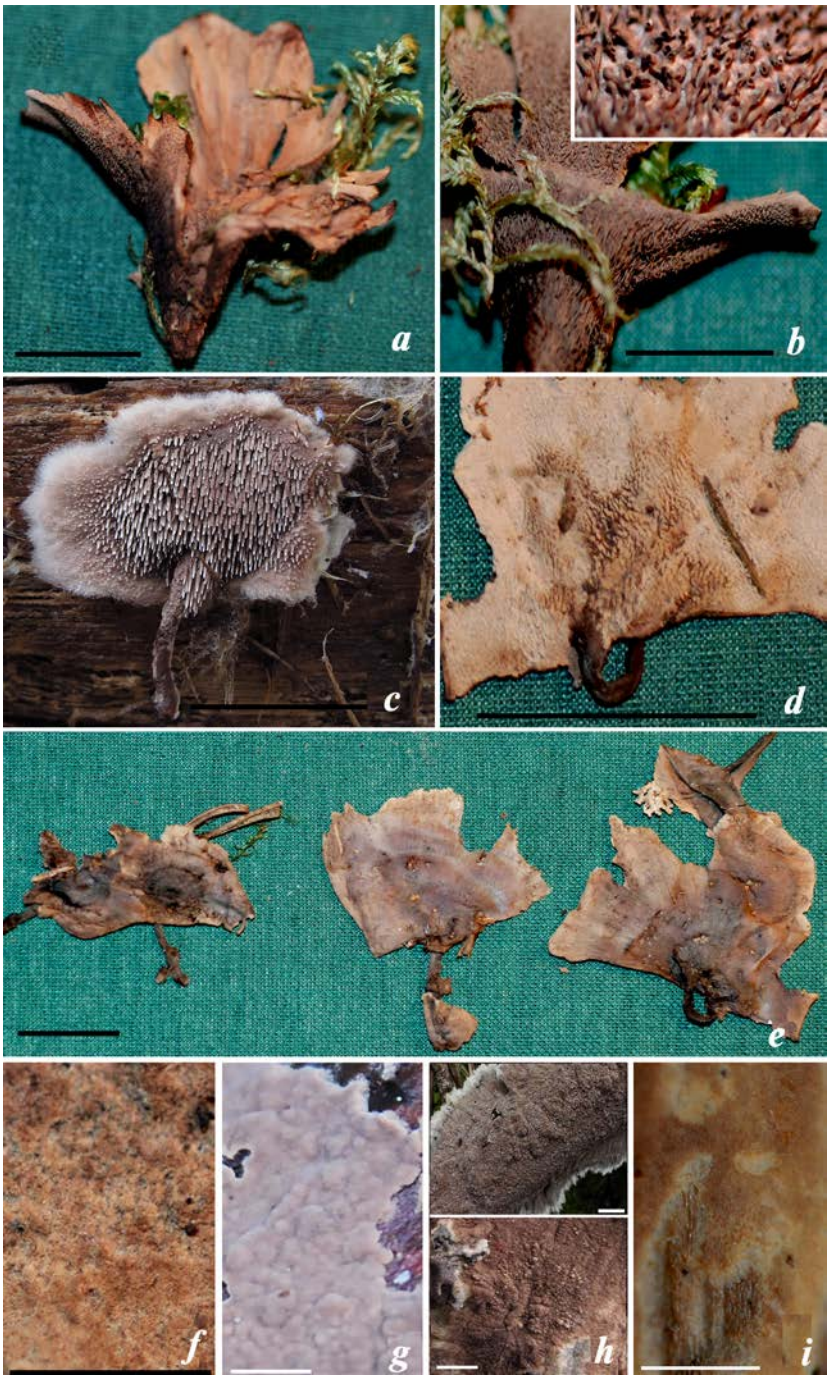

Fig. 3 – Representatives of thelephoroid fungi with reduced basidiome: a, b *Hydnellum concrescens* f. *petaloides*, type specimen (a – upperside, b – hymenophoral side). c *H. gracilipes* (LE 303768). d, e *Phellodon melaleucus* f. *suspensis*, type specimen (d – hymenophoral side, e – upperside). f *Thelephora ellisii* (AR 1179). g *Th. wakefieldiae* (AR 3118). h *Th. terrestris* f. *resupinata* (above, Kalinovskaya-181/13) and *Th. terrestris* f. *radiosa* (below, Myasnikov-789-9). i *Th. umbrinella* (LE 235635). Scale bars: a–f – 1 cm, g–i – 1 mm.

Description – Basidiomes resupinate, adhering to the substrate, continuous with indeterminate margin, initially pellicular, then crustose and cracking on drying. Hymenophore even, grayish-cinnamon, concolorous with subiculum, slightly paler at the margin. Subiculum loose, without hyphal cords, grayish-cinnamon. Hyphal system is monomitic, all hyphae with clamps and more or less inflated segments, mean diameter 3–6 μm, hyaline to golden-brown in the subiculum, more intensively colored in KOH. Cystidia none. Basidia 50–85 × 8–12(19) μm, utriform, 4-spored, basally-clamped, hyaline in KOH. Basidiospores triangularly ellipsoid, more or less lobate, 7–9.5 μm in longest dimension, rather sparsely echinulate with spines 0.5 μm long, pale-brown in KOH. Colonizes all kinds of wood debris in boreal and temperate zones of the Northern Hemisphere. Mycorrhizal (Walker et al. 2005).

Conclusion

Corner (1968) was the first who drew attention to a tendency towards a morphological rationalization of thelephoroid basidiomes and derivation of resupinate forms from pendent ones, postulating the loss of positive geotropic orientation of hymenophore in this process. Most of Corner's examples were limited to tropical forms of these fungi, but in boreal forests, as it appears, pendent or subpendent forms have a certain distribution too. The good example is *Hydnellum concrescens* which can give rise to effused-reflexed petaloid forms which in turn can become a morphogenetic source of a pendent form characteristic for *H. gracilipes*. The second one represents a certain reduced form related to centrally stipitate *Hydnellum* species. As the closely related taxa, such species as *H. peckii* (Kõljalg & Renvall 2000), *H. concrescens* (Ainsworth et al. 2010), and *H. aurantiacum* (the present study) were mentioned.

Concerning true resupinate forms, due to morphogenetic plasticity of the mycelium they can be derived from many (not only pendent) forms during transition to exploratory growth in litter cavities. It is possible that the heterogeneous assemblage still known as *Tomentella* originated this way. A number of species more related to the core of *Thelephora* we have endured from this conglomerate in the present work.

Results of the morphological investigations and molecular phylogenetic analyses presented herein suggest that basidiome reduction happened several times independently in evolution of thelephoroid fungi. Taxa with reduced basidiomes should be taken into account in the diagnoses of genera for which the initial descriptions do not cover a real spectrum of polymorphism and trends of morphological rationalization in connection with colonization of specific habitats.

Acknowledgements

The authors are very grateful to Prof. Cvetomir M. Denchev for valuable consultation in connection to *Zygodesmus sublilacinus* nomenclature, Dr. WA Spirin who kindly provided holotype of *Phellodon secretus* (H). The work by IV Zmitrovich, ON Shchepin, VF Malysheva, SV Volobuev, and YuK Novozhilov was carried out in frame of the State Task AAAA-A18-118031290108-6 of Komarov Botanical Institute of the Russian Academy of Sciences. The work by ON Ezhov was carried out in frame of the State Task 0409-2015-0141 of the Laverov Federal Center for Integrated Arctic Research. The molecular part of this work was supported by RFBR project (15-29-02622). All experimental work has been performed using the equipment of the Core Facility Center "Cell and Molecular Technologies in Plant Science" at the Komarov Botanical Institute of the Russian Academy of Sciences (Saint Petersburg).

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