



# Taxonomy and multigene phylogeny of *Pseudohydnum* (*Auriculariales*, *Basidiomycota*)

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## Abstract

Taxonomy of *Pseudohydnum gelatinosum* and its sister taxa is revised via morphological data and a four-gene dataset (ITS, nr LSU rDNA, *TEF1*, *RPB1*). Identity of *P. gelatinosum* and *Tremellodon pusillus* is re-established based on newly collected and sequenced material from their type localities. *Pseudohydnum alienum* from Europe; *P. umbrosum* from temperate East Asia; *P. cystidiatum*, *P. meridianum*, and *P. placibile* from Vietnam; and *P. omnipavum* from North America are described as new to science; *P. translucens* and *P. brunneiceps* from East Asia are redescribed. Most *Pseudohydnum* collections from North America belong to *P. gelatinosum* ssp. *pusillum*. A significant divergence of *TEF1* sequences in *P. gelatinosum* is discussed.

**Keywords** Heterobasidiomycetes · Phylogeny · 6 new species · 4 new typifications

## Introduction

*Pseudohydnum gelatinosum* (Scop.) P. Karst. is a jelly fungus recognizable because of its substantial, pale-coloured, stipitate basidiocarps with a spiny hymenophore. The species was considered as having a worldwide distribution, with records from Europe, North America, and South America, as well as Asia, Australia, and New Zealand (Wojewoda 1981). A highly peculiar habit of the basidiocarps and rather uniform anatomical structure of specimens collected in different continents maintained this viewpoint although Bourdot and Galzin (1927) pointed at morphologically deviating collections of *P. gelatinosum* from Europe. Holtermann (1898), Hennings (in Warburg 1899), Martin (1944), Lowy (1959,

1971), and Courtecuisse and Lowy (1990) described aberrant specimens of *P. gelatinosum* from the tropics. Recently, Chen et al. (2020) introduced a new species from the south-eastern part of China, *P. brunneiceps* Y.L. Chen, M.S. Su & L.P. Zhang, albeit identity of *P. gelatinosum* elsewhere remained unquestioned. Thereafter, Zhou et al. (2022, 2023) introduced eight more *Pseudohydnum* species from China, Australia, and New Zealand. A high divergence of *P. gelatinosum* DNA sequences in public repositories induced us to study the identity of this species and related taxa more closely. Because of the lack of recent material from Slovenia where *P. gelatinosum* was originally described from, we conducted extensive collecting there in 2019–2020 and supplemented it with sampling in Asia (Siberia, Russian Far East, and Vietnam), other parts of Europe, and North America. Here, we present results of this study.

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## Material and methods

### Morphological study

Specimens from herbaria BPI, GB, H, LE, LJF, PC, TAAM, and UPS were studied. Herbarium acronyms are given according to Thiers (2022). Microscopic routine and terminology follow Spirin et al. (2020). For microscopic study, small cross-sections of dried basidiocarps were rehydrated for 30–40 min and then mounted in lactic acid-based Cotton

Blue for a few hours. All measurements were made with the use of phase contrast and oil immersion lens (Leitz Diaplan microscope,  $\times 1250$  magnification). At least 20 basidia, 20 hyphae from the context, 20 subhymenial hyphae, and 30 basidiospores were measured per each specimen studied. The following abbreviations are used in taxonomic section: L — mean basidiospore length, W — mean basidiospore width, Q' — L/W ratio, Q — mean L/W ratio, and n — number of measurements per specimens measured.

A matrix with 1440 values was constructed, where each species was represented by at least 30 measurements of the basidiospore length and width. Statistical analysis and scatter plot of these data was performed using the programming language R 3.5.1 (R Core Team 2018) in the software environment RStudio 2022.07.2 (RStudio Team 2022).

### DNA study

In total, 54 specimens of *Pseudohydnum* spp. were selected for molecular sampling (Table 1). The procedure of DNA extraction completely corresponded to the manufacturer's protocol of the Phytosorb Kit (ZAO Syntol, Russia). The following primers were used for both amplification and sequencing: the primers ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990) for the ITS1-5.8S-ITS2 region, primers EF1-983F and EF1-1567R (Rehner & Buckley 2005) for a part of the *TEF1* region, primers RPB1-Af and RPB1-C2f (Matheny et al. 2002) for RNA polymerase II subunit 1 (*RPB1*), and primers JS1 (Landvik 1996) and LR5 (Vilgalys & Hester 1990) for D1-D3 domains of nc LSU rDNA region. PCR products were purified applying the GeneJET Gel Extraction and DNA Cleanup Micro Kit (Thermo Scientific, USA). Sequencing was performed with an ABI model 3500 Genetic Analyser (Applied Biosystems, USA). Raw data were edited and assembled in MEGA X (Kumar et al. 2018). Molecular studies were carried out at the centre for collective use of scientific equipment "Cellular and molecular technology of studying plants and fungi" (BIN RAS) and Finnish Museum of Natural History, University of Helsinki (Finland).

### Phylogenetic analyses

For this study, 53 ITS, 42 nc LSU rDNA, 19 *RPB1*, and 26 *TEF1* sequences were generated (Table 1). Additionally, 72 ITS and 35 nc LSU rDNA sequences, including the outgroup for the order-level phylogeny, were retrieved from GenBank and UNITE ([www.ncbi.nlm.nih.gov/genbank/](http://www.ncbi.nlm.nih.gov/genbank/); <https://unite.ut.ee/>). The sequences were aligned with webPRANK (Löytynoja & Goldman 2010). Highly divergent sites with questionable homology were removed; the final alignments were adjusted manually.

We compiled six datasets for phylogenetic analyses:

- (1) ITS + nc LSU rDNA dataset for main lineages in the *Auriculariales*. The final alignment contained 966 characters of which 211 bp were parsimony informative. Substitution models: SYM + I + G (ITS) and GTR + I + G (LSU),
- (2) ITS + nc LSU rDNA dataset for *Pseudohydnum* spp. The final alignment contained 1254 characters of which 138 bp were parsimony informative. Substitution models: SYM + I + G (ITS) and GTR + I (LSU),
- (3) ITS + nc LSU rDNA + *RPB1* dataset for *Pseudohydnum* spp. The final alignment contained 1600 characters of which 111 were parsimony informative. Substitution models: SYM + G (ITS), GTR + I (LSU), and HKY + I (*RPB1*).
- (4) ITS dataset for *P. translucens* complex. The final alignment contained 514 characters of which 29 were parsimony informative. Substitution model: SYM + I.
- (5) ITS dataset for *P. gelatinosum* complex. The final alignment contained 522 characters of which 23 were parsimony informative. Substitution model: K80 + I.
- (6) *TEF1* dataset for *Pseudohydnum* spp. The final alignment contained 656 characters of which 238 were parsimony informative. Substitution model: GTR + G.

The outgroup choice for the order-level phylogeny (*Sebacina incrustans* (Pers.) Tul. & C. Tul., *Sebacinales*) was guided by the current JGI Basidiomycota tree ([https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;\\_FJDXL?organism=basidiomycota](https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;_FJDXL?organism=basidiomycota)) where *Sebacinales* were recovered as a sister group of the *Auriculariales*. Five other trees were midpoint-rooted.

Phylogenetic reconstructions were performed with maximum likelihood (ML) and Bayesian inference (BI) analyses. Before the analyses, a best-fit substitution model for each marker in each of the alignments was estimated based on the Akaike information criterion (AIC) using ModelTest-NG v0.2.0. A partition homogeneity test (PHT) between different datasets was performed with PAUP 4.0b10\* (Swofford 2002). The PHT resulted in a *p* value of 0.01 for combined ITS + *TEF1* dataset, indicating that gene sequences are incongruent and these datasets should be analysed separately.

Maximum likelihood analysis was run on RAxML-NG 1.1.0 (Kozlov et al. 2019) with one thousand bootstrap replicates. Bayesian analyses were performed with the MrBayes 3.2.6 software (Ronquist et al. 2012) by implementing three independent runs each with eight chains and 4 million generations (except 8 million for *TEF1* dataset) sampling every 2000 generations, temp = 0.1. In all cases, average standard deviation of split distances reached < 0.01, indicating convergence of the runs. All phylogenetic analyses were conducted in CSC-IT Center for Science (Espoo, Finland) multi-core computing environment.

**Table 1** DNA sequences obtained for the present study

Species	Specimen/herbarium	Country (ISO code)	Host	GenBank accession numbers			
				nrITS	nrLSU	<i>TEF1</i>	<i>RPB1</i>
<i>Pseudohydnum alienum</i>	Kotiranta 22407 (H)	FI	<i>Thuja</i> sp.	OM451494	OM451435	OM796098	
<i>P. alienum</i>	LE 253853	RU-KC	<i>Picea orientalis</i>	OM451493	OM451430	OM796097	OM974204
<i>P. brunneiceps</i>	Härkönen K884 (H)	CN	fallen log	ON117827			
<i>P. cystidiatum</i>	LE 313656	VN	decayed wood	OM451503	OM451463	OM796102	OM974207
<i>P. cystidiatum</i>	LE 313657	VN	decayed wood	OM451502	OM451464		OM974208
<i>P. gelatinosum</i>	LE 38784	BY	<i>Picea abies</i>		OM451451	OM796084	
<i>P. gelatinosum</i>	Heikurainen 1999 (H)	FI	<i>P. abies</i>	OM451474	OM451437		OM974195
<i>P. gelatinosum</i>	Härkönen 32 (H)	FI	<i>P. abies</i>	OM451477	OM451440		
<i>P. gelatinosum</i>	Niemelä 9164 (H)	FI	<i>P. abies</i>	OM451473	OM451436	OM796088	OM974194
<i>P. gelatinosum</i>	Miettinen 19872.2 (H)	FI	<i>P. abies</i>	ON117828	ON117842		
<i>P. gelatinosum</i>	Miettinen 21866 (H)	FI	<i>P. abies</i>	ON117838	OM451461	ON191499	ON217543
<i>P. gelatinosum</i>	Pekampalo 2011 (H)	FI	<i>P. abies</i>	OM451475	OM451438		OM974196
<i>P. gelatinosum</i>	Schigel 6434 (H)	PL	<i>P. abies</i>	OM451478	OM451442		OM974198
<i>P. gelatinosum</i>	LE 265229	RU-AL	conifer	OM451471	OM451432	OM796086	
<i>P. gelatinosum</i>	LE 38780	RU-BA	<i>Larix sibirica</i>	OM451485	OM451449	OM796095	
<i>P. gelatinosum</i>	LE 38791	RU-IRK	<i>L. sibirica</i>	OM451483	OM451447	OM796085	
<i>P. gelatinosum</i>	Kotiranta 23028 (H)	RU-KK	<i>Picea obovata</i>	ON117829	ON117841		
<i>P. gelatinosum</i>	Kotiranta 26434 (H)	RU-KRA	<i>P. obovata</i>	ON117830	ON117840	ON191495	
<i>P. gelatinosum</i>	LE 313583	RU-KRA	<i>Picea</i> sp.	OM451492	OM451458		
<i>P. gelatinosum</i>	LE 313584	RU-KRA	<i>Picea</i> sp.	OM451490	OM451457		
<i>P. gelatinosum</i>	LE 313587	RU-KRA	<i>Abies sibirica</i>	OM451489	OM451454		
<i>P. gelatinosum</i>	Spirin 10388 (H)	RU-LEN	<i>P. abies</i>	OM451476	OM451439	OM796093	OM974197
<i>P. gelatinosum</i>	Spirin 12948 (H)	RU-LEN	<i>P. abies</i>	OM451479	OM451443	OM796091	OM974199
<i>P. gelatinosum</i>	LE 313779	RU-LEN	<i>P. abies</i>	OM451470	OM451431		
<i>P. gelatinosum</i>	LE 208530	RU-LEN	<i>P. abies</i>	OM451484	OM451448	OM796083	
<i>P. gelatinosum</i>	LE 315333	RU-MOS	<i>Pinus sylvestris</i>	OM451486	OM451450		OM974202
<i>P. gelatinosum</i>	LE 313661	RU-PRI	decayed wood	OM451469	OM451466		OM974192
<i>P. gelatinosum</i>	LE 313662	RU-PRI	decayed wood	OM451468	OM451467		OM974191
<i>P. gelatinosum</i>	LE 222719	RU-PSK	<i>P. sylvestris</i>	OM451487			
<i>P. gelatinosum</i>	LE 313565	RU-SAK	conifer	OM451491		OM796094	
<i>P. gelatinosum</i>	LE 313567	RU-SAK	conifer	OM451488		OM796087	
<i>P. gelatinosum</i>	Spirin 13196 (H)	SI	<i>P. abies</i>	OM451481	OM451445	OM796089	OM974200
<i>P. gelatinosum</i>	Spirin 13211 (H)	SI	<i>P. abies</i>	OM451480	OM451444	OM796092	
<i>P. gelatinosum</i>	Spirin 13369 (H)	SI	<i>P. abies</i>	OM451472	OM451434	OM796096	OM974193
<i>P. gelatinosum</i>	Spirin 13446 (H)	SI	<i>P. abies</i>	OM451482	OM451446	OM796090	OM974201
<i>P. gelatinosum</i>	Spirin 14001 (H)	SI	<i>Abies alba</i>	ON117831		ON191496	
- ssp. <i>pusillum</i>	Miettinen 16894 (H)	US-NY	<i>Tsuga / Picea</i> sp.	ON117832			
- ssp. <i>pusillum</i>	Miettinen 18987.2 (H)	US-WA	<i>Tsuga heterophylla</i>	ON117833			
- ssp. <i>pusillum</i>	Miettinen 19625.1 (H)	US-NC	conifer	ON117834	ON117839		
- ssp. <i>pusillum</i>	Miettinen 19671 (H)	US-TN	<i>Tsuga canadensis</i>	ON117835		ON191497	
<i>P. meridianum</i>	LE 313568	VN	decayed wood	OM451501	OM451452	OM796103	
<i>P. meridianum</i>	LE F-347479	VN	decayed wood	OQ450479		OQ689698	
<i>P. meridianum</i>	LE F-347480	VN	decayed wood	OQ450480			
<i>P. meridianum</i>	LE F-347478	VN	decayed wood	OQ450478			

**Table 1** (continued)

Species	Specimen/herbarium	Country (ISO code)	Host	GenBank accession numbers			
				nrITS	nrLSU	<i>TEF1</i>	<i>RPB1</i>
<i>P. meridianum</i>	LE F-347477	VN	decayed wood	OQ450477			
<i>P. omnipavum</i>	Spirin 8667 (H)	US-ID	<i>Pseudotsuga menziesii</i>	OM451499	OM451441	OM796100	OM974203
<i>P. omnipavum</i>	Miettinen 18877 (H)	US-ID	<i>T. heterophylla</i>	ON117836	OM451460		
<i>P. placibile</i>	LE 313658	VN	decayed wood	OM451505	OM451465		OM974206
<i>P. placibile</i>	LE 313659	VN	decayed wood	OM451504	OM451462	OM796101	OM974205
<i>P. sibiricum</i>	LE 313582	RU-KRA	<i>A. sibirica</i>	OM451498	OM451459		
<i>P. sibiricum</i>	LE 313585	RU-KRA	<i>A. sibirica</i>	OM451497	OM451456		
<i>P. sibiricum</i>	LE 313586	RU-KRA	<i>A. sibirica</i>	OM451496	OM451455		
<i>P. sibiricum</i>	LE 262798	RU-PRI	conifer	OM451495	OM451433	OM796099	
<i>P. umbrosum</i>	LE 312767	RU-KRA	conifer	OM451500	OM451453		

## Results

In ITS–nc LSU rDNA-based phylogeny of the *Auriculariales*, eight described *Pseudohydnum* spp. and a number of undescribed species recover in the well-supported clade (pp = 1, bs = 83%) (Fig. 1). In ITS–nc LSU rDNA-based phylogeny of *Pseudohydnum*, the species included in the analysis are divided into seven lineages and sixteen species (Fig. 2). The ITS–nc LSU rDNA–*RPB1* phylogeny corroborates this division as far as the two overlap, while providing more information on how these lineages are related (Fig. 3). The lineages (subclades) are as follows (see Fig. 2):

(1) *P. totarae* (Lloyd) J.A. Cooper known only from New Zealand (Zhou et al. 2022).

(2) *P. orbiculare* J.A. Cooper and *P. tasmanicum* Y.C. Dai & G.M. Gates from Tasmania and New Zealand (Zhou et al. 2022).

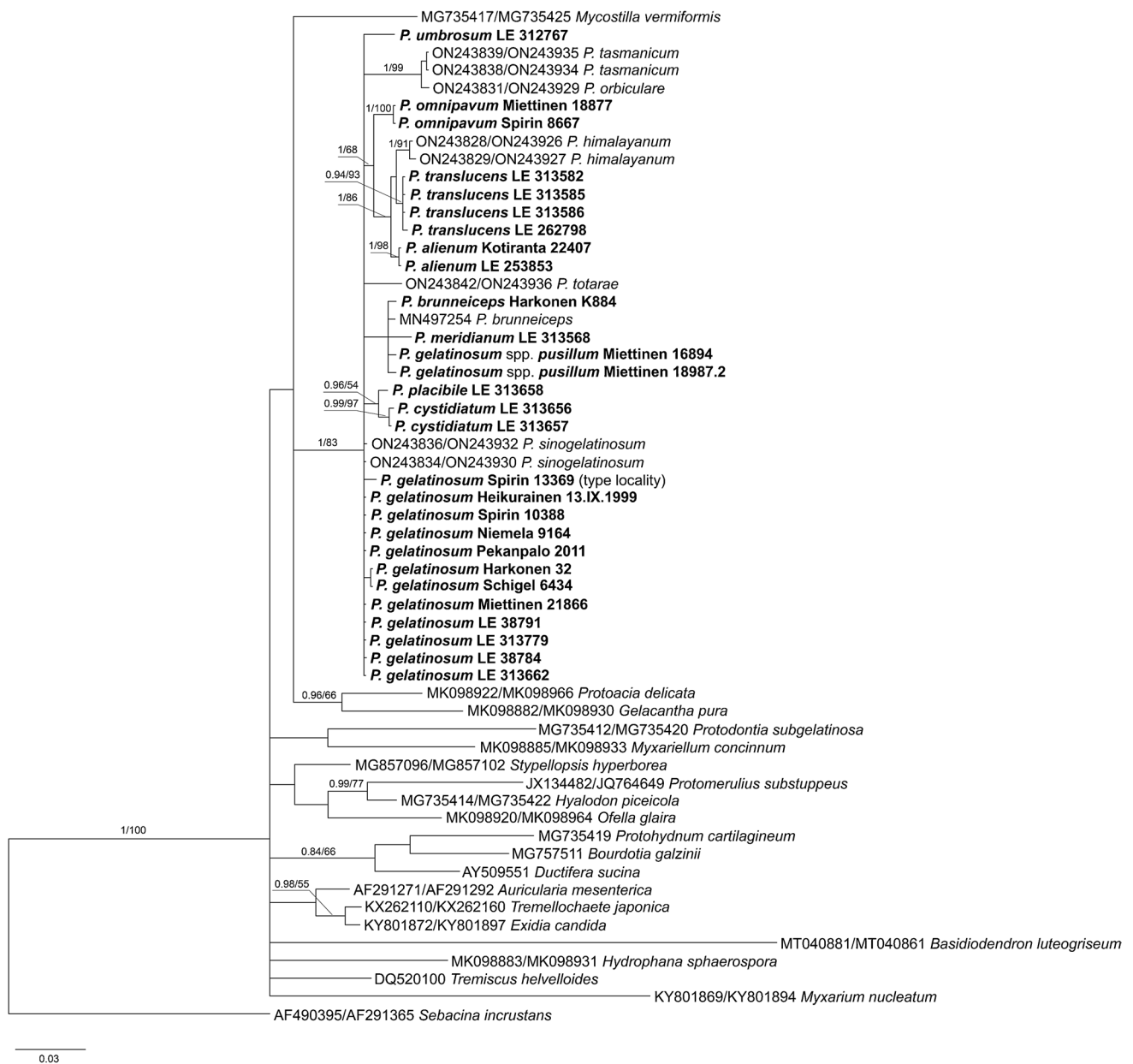
(3) The third subclade consists of a large cluster of sequences belonging to *P. gelatinosum* s.l. from the temperate–boreal forests of the northern hemisphere, plus *P. abietinum* H.M. Zhou & Jung Si and *P. sinogelatinosum* Y.C. Dai, F. Wu & H.M. Zhou from China. This lineage receives good support in the ITS–LSU–*RPB1* dataset (pp = 1, bs = 98%) (Fig. 3), but in the wider ITS–LSU dataset, it is weakly supported in the Bayesian analysis only (pp = 0.92) (Fig. 2). Taxonomic interpretation of this group is difficult. ITS sequences of *P. gelatinosum* from Eurasia are different in seven positions from the North American ones and up to sixteen positions versus *P. abietinum* and *P. sinogelatinosum*. These differences exceed those ones between *P. alienum* and *P. translucens*, two sister species from the fifth subclade (see below). As opposed to these two species,

European and North American specimens of *P. gelatinosum* show no differences in the LSU region, and morphology does not allow to separate them either. In the ITS phylogeny of *P. gelatinosum* complex, European and North American sequences of *P. gelatinosum* recover in one clade (pp = 1, bs = 85%) (Fig. 4).

(4) Two Vietnamese newly introduced species, *P. cystidiatum* and *P. placibile*, comprise this subclade. Both have rather small basidiocarps with a papillate (not hairy) upper surface.

(5) The fifth subclade is represented by the East Asian *P. translucens* Lloyd (= *P. candidissimum* H.M. Zhou, T. Bau & Jing Si), the recently introduced *P. himalayana* Y.C. Dai, F. Wu & H.M. Zhou and *P. sinobisporum* T. Bau, H.M. Zhou & Jing Si, and two newly described species from temperate–boreal coniferous forests of the northern hemisphere, i.e., *P. alienum* from Europe and *P. omnipavum* from the northwestern part of North America. The latter two species and *P. translucens* possess pale-coloured basidiocarps, narrow hyphae (if compared with the macroscopically similar *P. gelatinosum*), and slender hyphidia.

Both ITS–LSU and ITS–LSU–*RPB1* phylogenies (Figs. 2 and 6) support separation of closely related *P. alienum* and *P. translucens*, but this is not the case with the ITS, as shown by the phylogeny constructed for the *P. translucens* subclade (data not shown). Reason behind this is that ITS differs only a little between *P. alienum* and *P. translucens* (pairwise distance < 1%, 3 bp), while the differences are more robust in LSU (pairwise distance 0.7–1%, 5 bp), *RPB1* (pairwise distance < 1%, 5 bp), and *TEF1* (pairwise distance 4.8–5%, 21 bp). Morphological traits separating the two



**Fig. 1** Combined phylogenetic ITS–nc LSU rDNA topology from Bayesian analysis showing main lineages within the *Auriculariales*. All sequences generated for this study are indicated in bold. Gen-

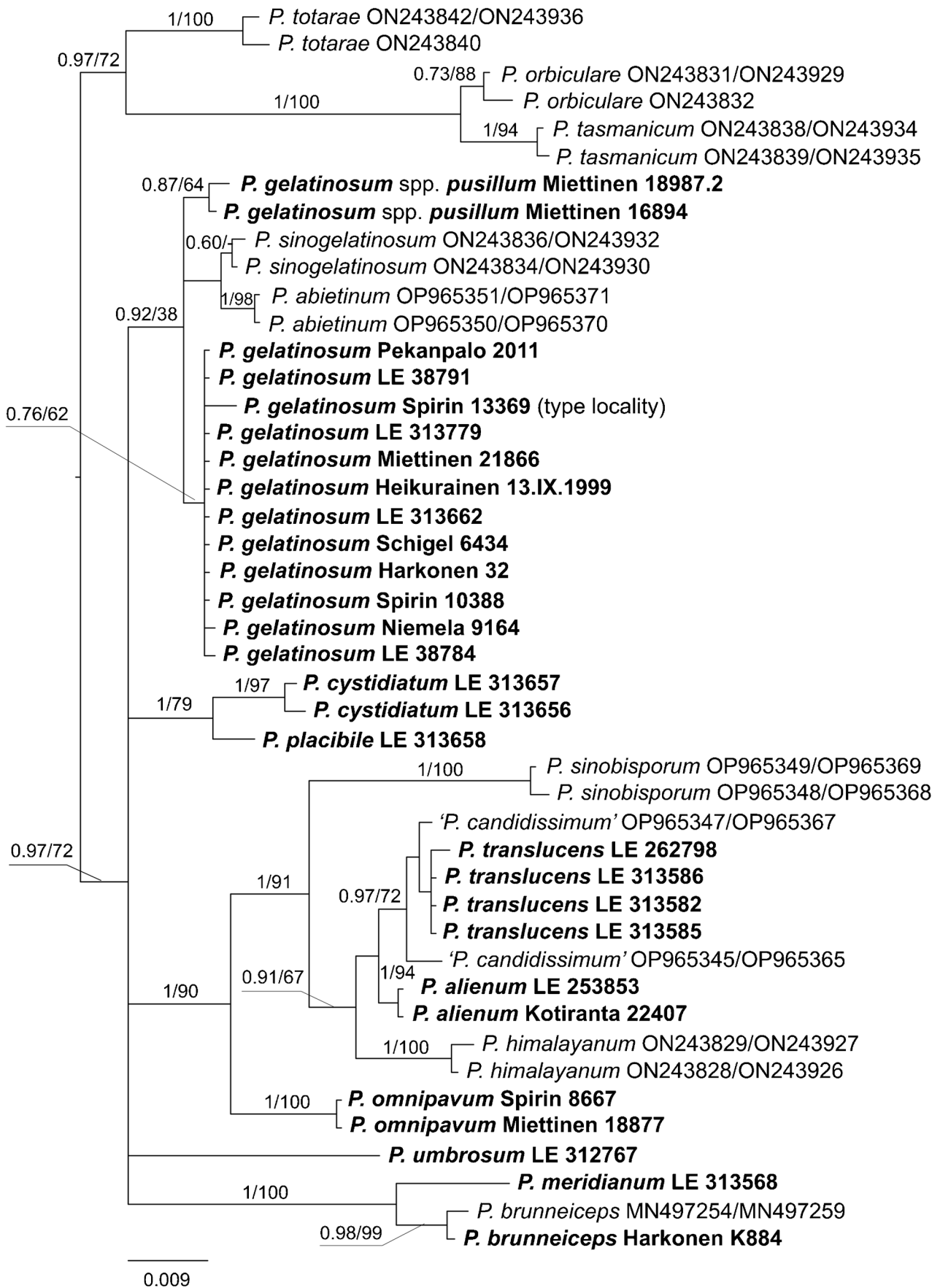
Bank accession numbers are given for all additional sequences. Support values (pp/bs) are given above the branches. Scale bar shows expected changes per site

species are discussed in taxonomic section (see under *P. translucens*).

The ITS dataset of *P. translucens* complex indicates that there seems to be yet more species in this complex. Two highly similar sequences (GenBank KC152166, KT875091) originated from Mexico; however, it is impossible to decide from ITS region only if they belong to one or two species. Four sequences from the northwestern part of North America (UDB034836, UDB0778273, GenBank MF954690, HM488590) have 4–5 unique positions versus *P. alienum*

and *P. translucens* and show 1–3 bp difference from each other. As in the case of the Mexican sequences, more genetic markers and proper morphological study are necessary to understand how many species they could represent.

(6) This single-species lineage subclade is represented by the newly described *P. umbrosum* from temperate East Asia. The three-marker phylogeny places this species as a sister to the fifth subclade around *P. translucens* (Fig. 3). Morphologically, *P. umbrosum* is distinguishable from other species



**Fig. 2** Combined phylogenetic ITS–nc LSU rDNA topology from Bayesian analysis for *Pseudohydnum* spp. All sequences generated for this study are indicated in bold. GenBank accession numbers are given for all additional sequences. Support values (pp/bs) are given on the branches. Scale bar shows expected changes per site

due to dwarf-sized, dark-coloured basidiocarps with a rudimentary stipe and long, ellipsoid basidiospores.

(7) The last subclade encompasses *P. brunneiceps* Y.L. Chen, M.S. Su & L.P. Zhang recently described from the southern part of China and a new species, *P. meridianum* from Vietnam. They both have substantial, dark-coloured basidiocarps with a pronounced, long stipe differentiating them from other members of the genus.

The *TEF1* phylogeny (Fig. 5) makes the whole picture more complicated. *TEF1* sequences of *P. gelatinosum* are divided among three clades, and each of them reveals strong inner variation. All but two *TEF1* sequences of *P. gelatinosum* (all originated from Eurasian specimens) belong to two related clades; however, genetic distance between them is comparable to other sister species within the genus. The larger clade covers Eurasia from the northern part of Slovenia up to Kuril Islands, while the smaller clade embraces an epitype of *P. gelatinosum* from the western part of Slovenia (*Spirin 13369*) and another specimen from the southern part of the country, as well as three other collections from very distant areas (i.e., Finland, South Ural, and Central Siberia) (Fig. 5). This certainly points at the lack of a geographic pattern reflecting these two genetic groups. No morphological or ecological data differentiate them either. The single *TEF1* sequence from the North American specimen of *P. gelatinosum* (*Miettinen 19671*) clearly deviates from the Eurasian ones although it forms a strongly supported lineage with *TEF1* sequence of *P. gelatinosum* from Kunashir, Kuril Islands (LE 313565). ITS sequence of the latter specimen shows no differences versus other *P. gelatinosum* sequences from Eurasia. Therefore, we are unwilling to interpret the high divergence among *TEF1* sequences of *P. gelatinosum* s. lato as an argument for splitting it into several species. Nevertheless, we redescribe the North American specimens of *P. gelatinosum* as belonging to ssp. *pusillum*, in anticipation of better solution in the future. In the combined ITS–LSU–*RPB1* phylogeny, *P. gelatinosum* from Eurasia and ssp. *pusillum* from North America form one highly supported clade (pp = 1, bs = 98%) (Fig. 3). The taxonomic status of *P. abietinum* and *P. sinogelatinosum* as separate species deserves further clarification with the use of *RPB1* and *TEF1* sequences. To conclude, we can only recognize one species in this

lineage, *P. gelatinosum*, with high certainty, while one to two further species (including *P. sinogelatinosum*) might also be recognized pending better genetic data.

## Taxonomy

*Pseudohydnum alienum* Spirin & V. Malysheva, sp. nov.  
— Figs. 6, 9, and 10

MycoBank MB846386.

Holotype. Russia. Karachay-Cherkessia: Karachayevsk Dist, Teberda Nat. Res., Khadzhibey, 43.37889N 41.68360E, *Picea orientalis*, 8.VIII.2009 V. Malysheva (LE 253853\*, isotype — H 7200585).

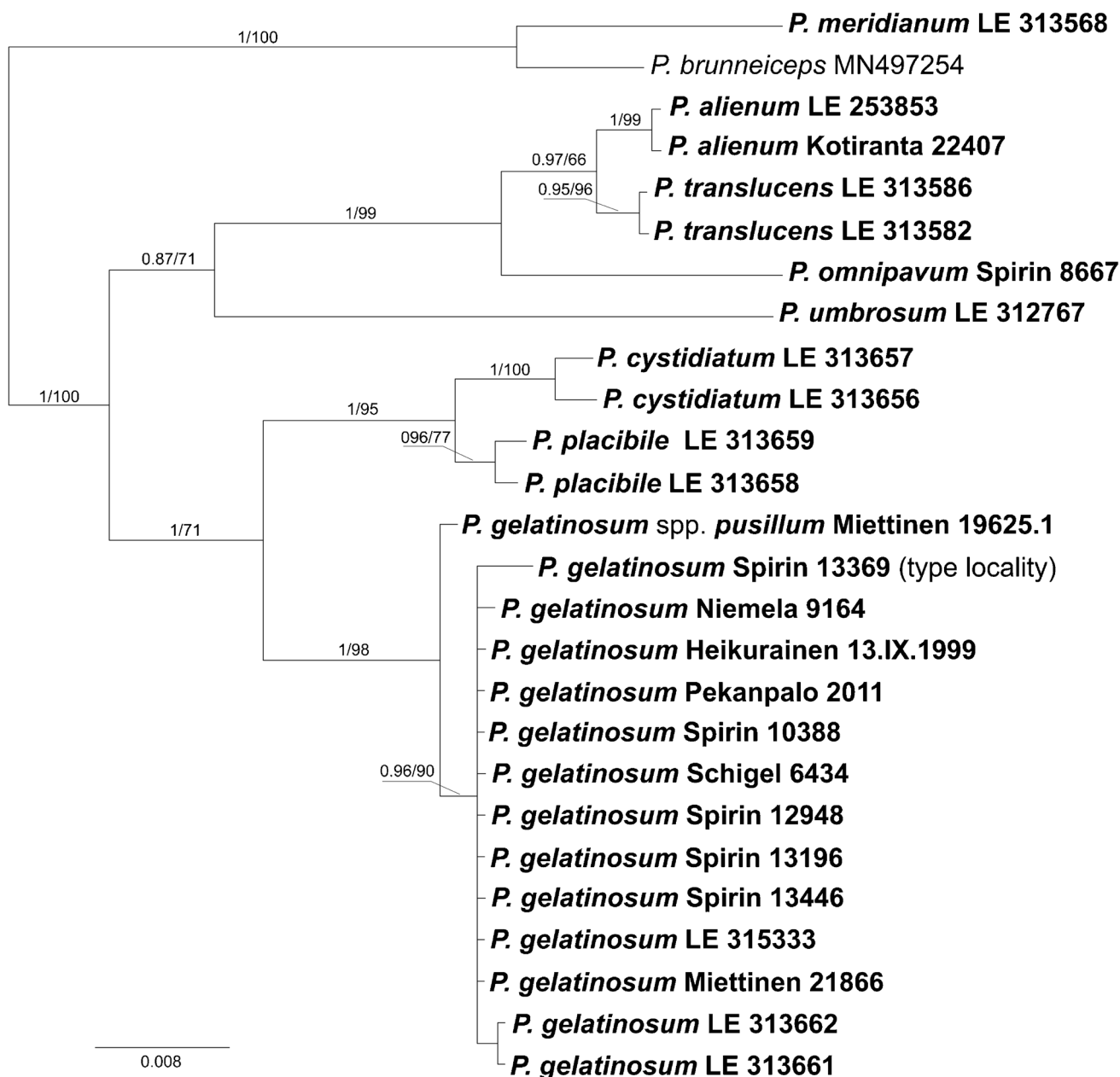
Etymology: alienus (Lat., adj.) – alien, unfamiliar.

Basidiocarps up to 2 cm in widest dimension and 2–3 mm thick, pileate, laterally stipitate, gelatinous. Pileal surface strigose, watery-greyish, sometimes with faint reddish-brownish stains, pale ochraceous or greyish-brownish in dry condition. Pileal edge rather blunt, fertile. Spines sharp-tipped, white to greyish, 0.5–1 mm long, 6–8 per mm. Stipe a few millimeter long, watery-greyish, usually covered by spines up to the very base.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline, thin- or slightly thick-walled, subparallel or ascending (hairs), some short-celled and slightly inflated, 3–7  $\mu\text{m}$  in diam. Tramal hyphae hyaline, thin-walled, interwoven and rather loosely arranged, occasionally anastomosing, (2.2–) 2.3–4.8 (–5.0)  $\mu\text{m}$  in diam. ( $n = 80/4$ ). Subhymenial hyphae hyaline, thin-walled, predominantly ascending, (1.8–) 1.9–3.3 (–3.5)  $\mu\text{m}$  in diam. ( $n = 80/4$ ). Hyphidia abundant, occasionally branched, 0.8–1.2  $\mu\text{m}$  in diam. at the apex, covering basidial cells or projecting above hymenial layer up to 25  $\mu\text{m}$ . Basidia four-celled, (10.2–) 10.9–14.2 (–14.8)  $\times$  (8.2–) 8.3–10.4 (–11.0)  $\mu\text{m}$  ( $n = 80/4$ ), often arranged in a dense palisade and covering spines up to the very top, stalk up to 25  $\times$  2–4  $\mu\text{m}$ , sterigmata up to 28  $\times$  2.5–3  $\mu\text{m}$ . Basidiospores ellipsoid to broadly ellipsoid, more rarely subglobose, (6.0–) 6.1–7.9 (–8.2)  $\times$  (5.0–) 5.1–6.7 (–6.9)  $\mu\text{m}$  ( $n = 120/4$ ),  $L = 6.61$ –6.98,  $W = 5.48$ –6.11,  $Q' = (1.0$ –) 1.1–1.4 (–1.5),  $Q = 1.14$ –1.22.

Distribution and ecology. Europe (Finland, Georgia, Russian Caucasus); fallen logs and branches of conifers (*Abies nordmanniana*, *Picea orientalis*, *Pinus sylvestris*, *Thuja* sp.).

Remarks. *Pseudohydnum alienum* is one of two representatives of the genus distributed in Europe. From another European species, *P. gelatinosum*, it differs in having smaller basidiocarps, distinctly narrower tramal and subhymenial hyphae, as well as slenderer hyphidia. In addition, subhymenial hyphae of *P. alienum* are more regularly packed, predominantly ascending, and basidia are normally arranged in



**Fig. 3** Combined phylogenetic ITS–nc LSU rDNA–*RPB1* topology from Bayesian analysis for *Pseudohydnum* spp. All sequences generated for this study are indicated in bold. GenBank accession number

is given for additional sequence. Support values (pp/bs) are given on the branches. Scale bar shows expected changes per site

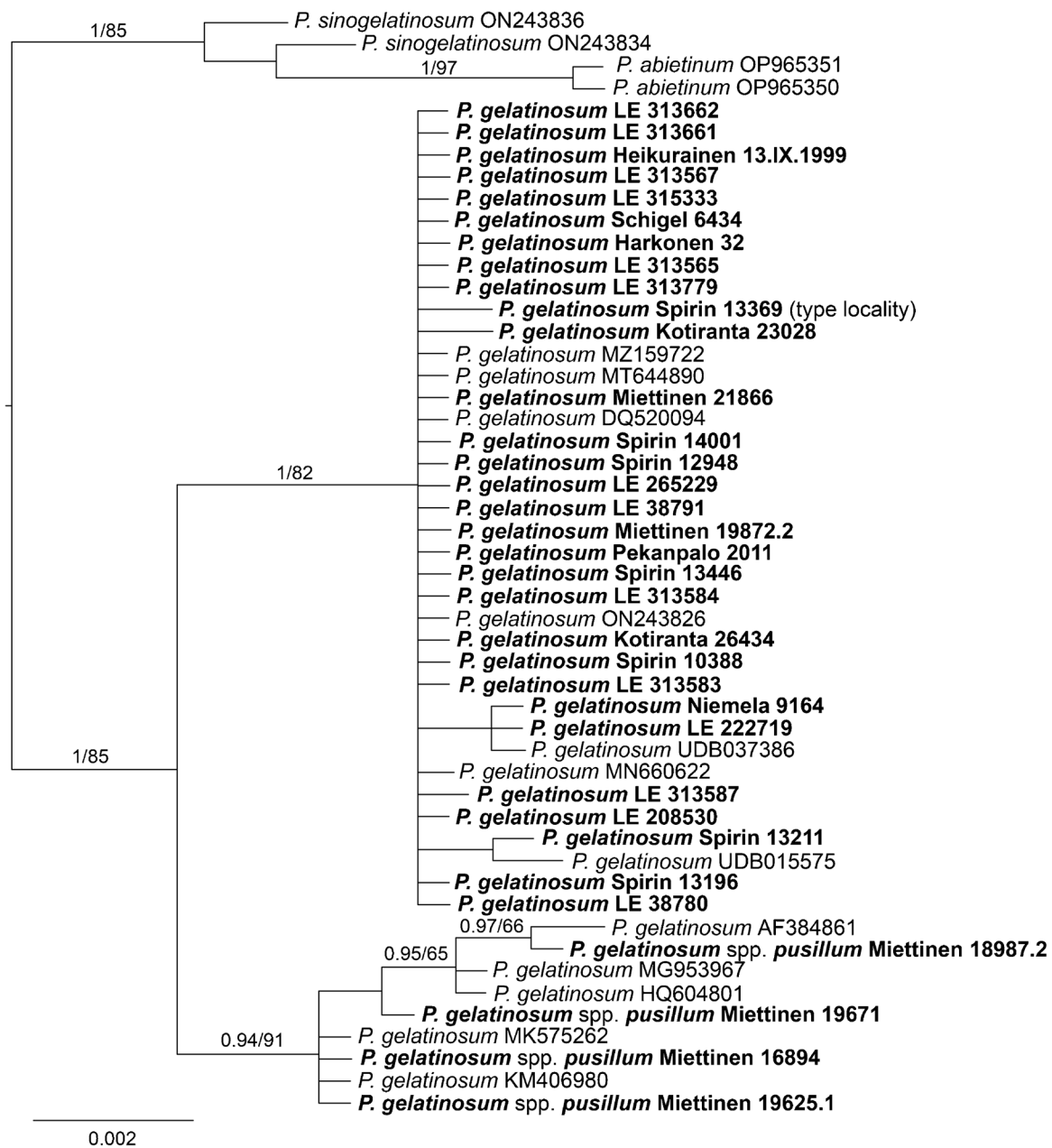
a palisade manner. On the contrary, the subhymenial structure of *P. gelatinosum* looks much more disorderly, with hyphae mostly oriented in a random way. Differences of *P. alienum* from the phylogenetically close *P. omnipavum* and *P. translucens* are discussed under these species.

*Pseudohydnum alienum* is a poorly sampled species known from two collections from the Caucasus and two specimens from the southwestern Finland. One of the latter specimens was collected from remains of a cultivated

*Thuja* tree. DNA sequences of the Finnish and Caucasian specimens are identical.

Specimens examined. Finland. Varsinais-suomi: Raasepori, Lökudden Nat. Res., *Thuja* sp. (fallen decorticated branch), 16.IX.2008 Kotiranta 22407\* (H), Tjurberget, *Pinus sylvestris* (cut bolt), 6.XI.2021 Miettinen 25013 (H). Georgia. Imereti: Tqibuli, Kharistvali, *Abies nordmanniana* (fallen log), 18.X.1963 Parmasto (TAAM 015898). Russia. Karachay-Cherkessia (holotype, see above).





**Fig. 4** Bayesian phylogram for ITS dataset of *P. gelatinosum* complex. All sequences generated for this study are indicated in bold. GenBank/UNITE accession numbers are given for all additional

sequences. Support values (pp/bs) are given on the branches. Scale bar shows expected changes per site

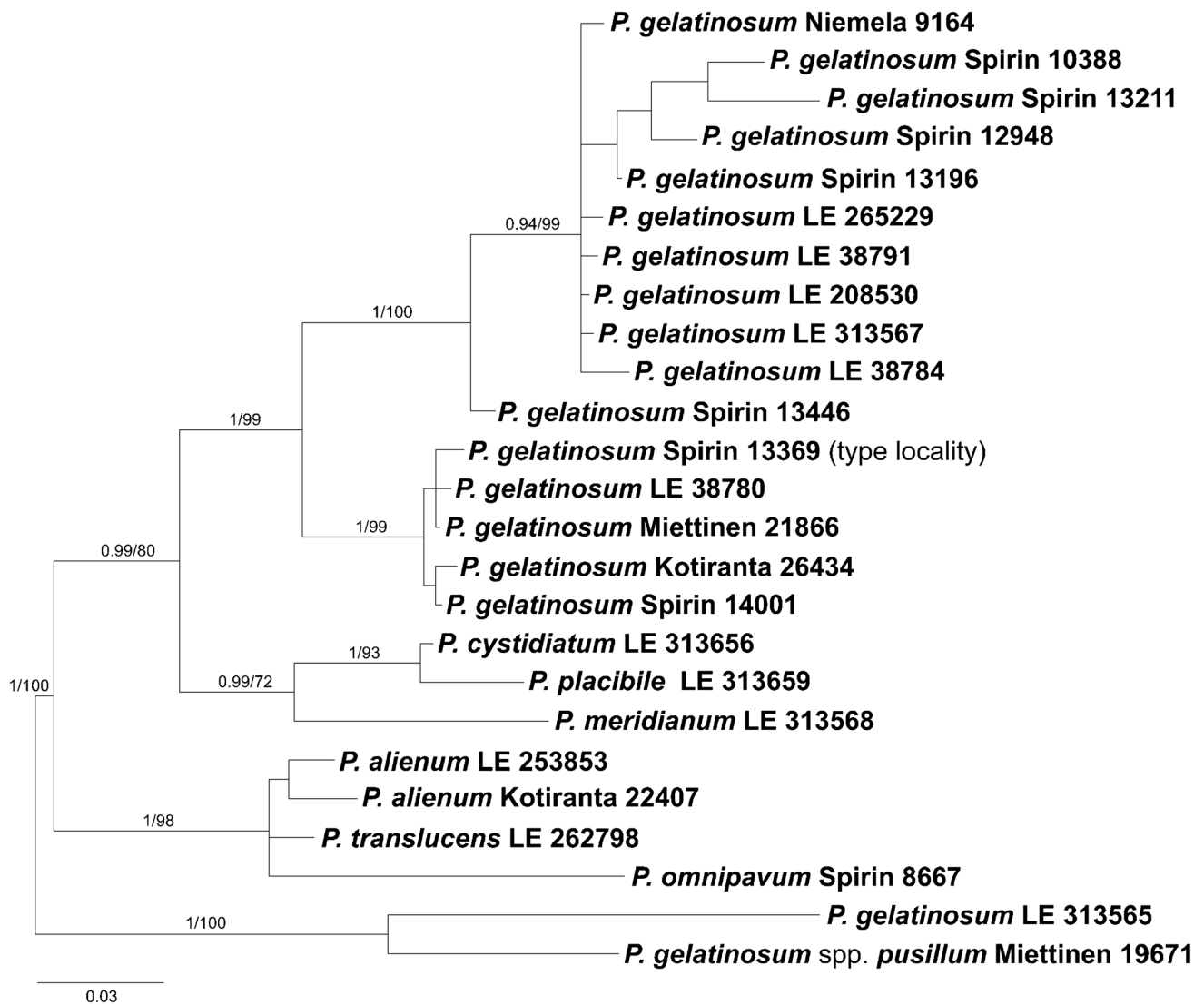
***Pseudohydnum brunneiceps*** Y.L. Chen, M.S. Su & L.P. Zhang, Phytotaxa 441: 91, 2020. — Fig. 10

Holotype. China. Jiangxi: Jiujiang Co., Lushan Nat. Res., coniferous wood, 26.VI.2018 Zhang (JXSB0967).

Basidiocarps up to 3 cm in widest dimension and 2–3 mm thick, pileate, laterally stipitate, gelatinous. Pileal surface strigose, reddish-brownish to brown. Pileal edge sharp, fertile. Spines sharp-tipped, white to cream-coloured, 0.5–2 mm long, 4–5 per mm. Stipe up to 3 cm long and 5 mm in diam.,

equally thickened along the whole length, greyish- or reddish-brown, strigose or partly covered by spines.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface greyish or brownish, thin- or slightly thick-walled, subparallel or ascending (hairs), some short-celled and inflated, 2–8  $\mu$ m in diam. Tramal hyphae hyaline to greyish or brownish, thin-walled, interwoven, occasionally anastomosing, (2.3–) 2.9–5.4 (–6.0)  $\mu$ m in diam. ( $n = 60/3$ ). Subhymenial hyphae hyaline, thin-walled, interwoven, (2.1–) 2.2–3.3 (–3.6)  $\mu$ m in diam.



**Fig. 5** Bayesian phylogram for the *TEF1* dataset, showing phylogenetic relationships of *Pseudohydnum* spp. All sequences generated for this study are indicated in bold. GenBank accession number is

given for additional sequence. Support values (pp/bs) are given on the branches. Scale bar shows expected changes per site

( $n = 20/1$ ). Hyphidia abundant, richly branched, 1.5–2  $\mu\text{m}$  in diam. at the apex, covering basidial cells. Basidia four-celled, predominantly obliquely septate, (10.2–) 10.8–12.8 (–13.3)  $\times$  (7.0–) 7.2–8.4 (–8.8)  $\mu\text{m}$  ( $n = 30/1$ ), scattered and embedded in masses of hyphidia, stalk up to 15  $\times$  2.5–4  $\mu\text{m}$ , sterigmata up to 17  $\times$  2–2.5  $\mu\text{m}$ . Basidiospores ellipsoid to broadly ellipsoid, rarely subglobose, (6.8–) 6.9–8.9 (–9.2)  $\times$  (6.0–) 6.1–7.1 (–8.0)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 7.76$ ,  $W = 6.66$ ,  $Q' = (1.0\text{--}) 1.1\text{--}1.3$  (–1.4),  $Q = 1.17$ .

**Distribution and ecology.** Southeast Asia (China — Hunan, Jiangxi); rotten wood of conifers.

**Remarks.** Dark-coloured basidiocarps with strigose upper surface and a well-developed stipe differentiate *P.*

*brunneiceps* from all other species described here. Microscopically, large, broadly ellipsoid basidiospores and predominantly obliquely septate basidia are characteristic for the species. *Pseudohydnum brunneiceps* was introduced based on collections from Jiangxi, Southeast China, where it inhabits decayed wood of conifers, mainly *Cryptomeria japonica* (Chen et al. 2020). Here, we report it from Hunan.

**Specimen examined.** China. Hunan: Liu Yang Co., Daweishan Nat. Park Forest, fallen log, 28.IX.2000 *Härkönen K884\** (H).

*Pseudohydnum cystidiatum* V. Malysheva & V. Dudka, sp. nov. — Figs. 6, 9, and 10

Mycobank MB846387.

Holotype. Vietnam. Cao Bằng Province: Nguyễn Bình Dist., Thành Công, 22.60695N 105.87303E, decayed wood, 10.IV.2021 *Dudka* (LE 313656\*).

Etymology: *cystidiatus* (Lat., adj.) — bearing cystidia.

Basidiocarps up to 1 cm in widest dimension and 1–1.5 mm thick, pileate, sessile, gelatinous. Pileal surface papillate, pale ochraceous when fresh, greyish-brownish in dry condition. Pileal edge sharp, somewhat undulating, fertile. Spines sharp-tipped, white to cream-coloured, up to 0.5 mm long, 3–4 per mm. Stipe rudimentary, very short, or absent.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline, thin- or slightly thick-walled, subparallel, some short-celled and slightly inflated, 2–7  $\mu\text{m}$  in diam. Tramal hyphae hyaline, thin-walled, interwoven, frequently anastomosing, (1.5–) 2.0–5.0 (–4.5)  $\mu\text{m}$  in diam. ( $n = 20/2$ ), accidentally inflated (up to 6  $\mu\text{m}$  in diam.) at septa, in uppermost layers hyaline and with a distinct wall. Subhymenial hyphae hyaline, thin-walled, interwoven, (1.0–) 1.2–2.0 (–2.3)  $\mu\text{m}$  in diam. ( $n = 20/2$ ). Hyphidia abundant, occasionally branched, 1–1.5  $\mu\text{m}$  in diam. at the apex, covering basidial cells. Cystidia hyaline, rather rare, tapering, projecting above hymenial layer, (27–) 27.2–43 (–58)  $\times$  (11.5–) 15.5–16.7 (–18.0)  $\mu\text{m}$  ( $n = 6/2$ ). Basidia four-celled, (10.1–) 10.5–12.9 (–13.1)  $\times$  (8.0–) 8.9–10.2 (–10.6)  $\mu\text{m}$  ( $n = 20/2$ ), scattered and mostly embedded in masses of hyphidia, stalk up to 48  $\times$  2–2.5  $\mu\text{m}$ , sterigmata up to 30  $\times$  2–3  $\mu\text{m}$ . Basidiospores broadly ellipsoid to subglobose, (6.6–) 6.8–9.5 (–9.6)  $\times$  (4.9–) 5.6–7.6 (–8.1)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 8.10$ ,  $W = 6.38$ ,  $Q' = 1.1–1.5$  (–1.6),  $Q = 1.27$ .

Distribution and ecology. Southeast Asia (Vietnam); decayed wood in lowland evergreen mixed forest.

Remarks. The presence of hymenial cystidia differentiate *P. cystidiatum* from other species described in the present paper. From two other Vietnamese species (*P. meridianum* and *P. placibile*) described here, *P. cystidiatum* differs in having small basidiocarps with a rudimentary stipe and larger, broadly ellipsoid basidiospores. The species is so far known only from two localities in Vietnam.

Specimens examined. Vietnam. Cao Bằng Province: Nguyễn Bình Dist., Thành Công, 10.IV.2021 *Dudka* (holotype, see above), National Park Phia Oac–Phia Den, decayed wood, 15.IV.2021 *Dudka* (LE 313657\*).

***Pseudohydnum gelatinosum*** (Scop.) P. Karst., Not. Sällsk. Fauna Flora Fennica Förh. 9: 374, 1868. — Figs. 7, 9, and 10

$\equiv$  *Hydnum gelatinosum* Scop., Flora Carniolica 2: 472, 1772. Lectotype. Table 9 (p. 239) in Jacquin, Miscellanea Austriaca ad Botanicam, Chemiam et Historiam Naturalem Spectantia 1, 1778 (designated here, MBT10010097). Epitype. Slovenia. Idrija: Idrija, 45.992E 14.017N, *Picea abies*

(old cut stump), 27.IX.2019 *Grebenc & Spirin 13369\** (LJF, dupl. H 7200586 and LE) (designated here, MBT10010098).

$\equiv$  *Hydnum crystallinum* O.F. Müll., Flora Danica 4 (12): 6, 1777. Lectotype. Figure 717 in Müller, op. cit. (designated here, MBT10010099).

$\equiv$  *Hydnum clandestinum* Batsch, Elenchus Fungorum: 113, 1783. Lectotype. Figure 44 (Table X) in Batsch, op. cit. (designated here, MBT10010100).

Basidiocarps rarely exceeding 4 cm in widest dimension, 2–4 mm thick, pileate, laterally stipitate, gelatinous. Pileal surface first strigose, watery-greyish or greyish-brownish, then almost smooth, grey to brown, pale ochraceous or greyish-brownish to dark brown in dry condition. Pileal edge sharp to rather blunt, fertile. Spines sharp-tipped, white to greyish, 1–3 mm long, 5–8 per mm. Stipe up to 1 cm long (rarely longer), watery-greyish, usually covered by spines up to the very base, in some specimens rudimentary.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline or greyish, thin- or slightly thick-walled, subparallel or ascending (hairs), 3–10  $\mu\text{m}$  in diam., some short-celled and inflated up to 16  $\mu\text{m}$ . Tramal hyphae hyaline or greyish, thin-walled, interwoven, occasionally anastomosing, (1.7–) 1.9–9.2 (–9.7)  $\mu\text{m}$  in diam. ( $n = 140/7$ ), accidentally inflated (up to 12  $\mu\text{m}$  in diam.) at septa. Subhymenial hyphae hyaline or greyish, thin-walled, interwoven, (1.9–) 2.0–4.3 (–4.6)  $\mu\text{m}$  in diam. ( $n = 140/7$ ). Hyphidia abundant, occasionally branched, 1–2.5  $\mu\text{m}$  in diam. at the apex, scattered among basidial cells or partly covering them, sometimes projecting above hymenial layer up to 40  $\mu\text{m}$ . Basidia four-celled, (8.8–) 9.8–14.4 (–14.8)  $\times$  (7.0–) 7.4–10.9 (–11.2)  $\mu\text{m}$  ( $n = 160/8$ ), arranged in a dense palisade or scattered among hyphidia, stalk up to 35  $\times$  2–3  $\mu\text{m}$ , sterigmata up to 25  $\times$  2–3  $\mu\text{m}$ . Sterile spine tips up to 200  $\mu\text{m}$  long. Basidiospores ellipsoid to broadly ellipsoid, (5.2–) 5.3–9.0 (–9.2)  $\times$  (4.6–) 4.9–7.6 (–8.2)  $\mu\text{m}$  ( $n = 690/23$ ),  $L = 6.02–7.67$ ,  $W = 5.11–6.61$ ,  $Q' = (1.0–) 1.1–1.5$  (–1.6),  $Q = 1.09–1.28$ .

Distribution and ecology. Europe, Asia (Ural, Siberia, Russian Far East); various wood remnants of conifers.

Remarks. *Hydnum gelatinosum* was described by Scopoli (1772) from the present-day Slovenia, and the name was subsequently sanctioned by Fries (1821: 407). No authentic material of *H. gelatinosum* survives except Scopoli's oil painting stored in the National Museum of Natural History, Paris (A. Piltvater, pers. comm. 13.XII.2020). However, we see no strong reasons to designate this illustration as a lectotype of *H. gelatinosum*. First, there is no reference to the oil painting (or any other illustrative material) in the protologue. Second, Scopoli's oil paintings have a formal status of copyright material, and therefore, they are currently not available for a broader audience. The current version of the Code allows us to select a lectotype from the



**Fig. 6** Basidiocarps of *Pseudohydnum* spp.: **a** *P. alienum* (holotype); **b** *P. meridianum* (LE F-347447); **c** *P. cystidiatum* (holotype); **d** *P. cystidiatum* (LE 313657); **e, f** *P. placibile* (holotype). Scale bar = 1 cm

sanctioning treatment, i.e., Fries' *Systema Mycologicum* (1821). Therein, Fries referred to a colour figure of *H. gelatinosum* by Jacquin (1778); this book is available online and can be easily accessed by researchers. We designate the latter illustration as a lectotype (iconotype) of *H. gelatinosum*. Additionally, a recent sequenced specimen of *P. gelatinosum* from Idrija (Slovenia), the place where Scopoli lived and collected many of his species, is selected as epitype (see above).

Fries (1821) mentioned *Hydnum crystallinum* O.F. Müll. (described from Denmark) and *H. clandestinum* Batsch (described from Germany, presumably Thuringia) under synonyms of *H. gelatinosum*. No original specimens exist for either of them but illustrations are available (Müller 1777; Batsch 1783), and we use them for lectotypification of these taxa. In both cases, distinct brownish coloration of the pileal surface was depicted: this feature certainly refers to *P. gelatinosum* as redefined here and rules out another European species, *P. alienum* (see description above). Donk (1966) treated *H. auriculatum* Fr. as one more synonym of *P. gelatinosum*. The protologue (Fries 1838) seemingly refers to *P. gelatinosum*. The single specimen of *H. auriculatum* in Fries' herbarium (UPS F-117034) consists of two pieces with different labels (Å. Kruys, pers. comm. 19.IV.2023). Unfortunately, it is impossible to decide whether they were collected before 1838. Buxbaum's illustration cited by Fries in the protologue of *H. auriculatum* makes the idea of this species even more obscure. This illustration (Buxbaum 1728: Table 56; Fig. 2) is almost incomprehensible, and the accompanying description (as "Agaricus gelatinosus, parte prona erinaceus," p. 36) refers to a hydroid fungus with bluish or light-violet fructifications growing on wood of *Alnus* ("dilute coeruleus aut purpurascens, antiquarum Alnorum truncis adnascitur," *ibid.*). These indications are certainly at odds with Fries's own description of *H. auriculatum* ("pileis ... murinis, aculeis teretibus brevibus albis... In truncis Pini" — Fries, *op. cit.*, p. 513). At the moment, we leave this problem unresolved.

Bourdot and Galzin (1927) introduced *Tremellodon crystallinum* var. *exidiodon* as a taxon deviating from *P. gelatinosum* (treated by them as *T. crystallinum* (O.F. Müll.) Quél.) due to its globose basidiocarps and a peculiar host (*Populus*). This variety was even suggested to represent a separate species (Pilát 1957) although never formally raised to the species rank. We studied the single authentic collection of *T. crystallinum* var. *exidiodon* (Aveyron, Crouzette, 15.XII.1913 Galzin 14918 (herb. Bourdot 12384, PC)) and concluded it shows no morphological differences from typical specimens of *P. gelatinosum*. However, we are unaware

of other collections of this species from deciduous trees. Newly collected material from the southern part of France is highly desirable for settling taxonomic status of this variety.

*Pseudohydnum gelatinosum* is the most common representative of the genus in temperate–boreal forests of Eurasia. Morphologically, it is a highly diverse species, and its recognition versus sister taxa demands a meticulous microscopic study. The variation range of basidiospores in *P. gelatinosum* is huge, and it covers the variation range of all other temperate–boreal species except *P. umbrosum* (Fig. 11). Therefore, *P. gelatinosum* can be confidently distinguished from *P. alienum* in Europe, *P. translucens* in Asia, and *P. omnipavum* in North America due to distinctly wider tramal hyphae and hyphidia (Table 2). The North-American collections of *P. gelatinosum* are described below as *P. gelatinosum* ssp. *pusillum*.

Specimens examined. Belarus. Minsk Reg.: Borisov Dist., Kischino Sloboda, *Picea abies*, 20.VIII.1934 Nikolaeva (LE 38784\*). Finland. Uusimaa: Helsinki, Puotila, Juurumäki, *P. abies*, 13.IX.1999 Heikurainen\* (H), Veräjämäki, *P. abies*, 6.XII.2015 Miettinen 19872.2\* (H); Sipoo, Pilvijärvi, *P. abies*, 4.X.2011 Pekanpalo\* (H). Pohjois-Karjala: Lieksa, Koli Nat. Park, *P. abies*, 13.IX.2011 Härkönen 32\* (H). Satakunta: Ylöjärvi, Inkula, *P. abies*, 10.IX.2014 Niemelä 9164\* (H). Perä-Pohjanmaa: Rovaniemi, Pisavaara, *P. abies*, 15.VIII.2009 Kinnunen 5242 (H). Kainuu: Puolanka, Paljakka Strict Nat. Res., *P. abies*, 29.IX.2018 Miettinen 21866\* (H). Poland. Podlesie: Hajnówka Dist., Białowieża Primateval Forest, *P. abies*, 10.IX.2009 Schigel 6434\* (H). Russia. Altai Rep.: Ulagan Dist., Altai Nat. Res., Atkichu, decayed coniferous wood, 15.VIII.2008 Psurtseva (LE 265229\*). Bashkortostan: Beloretsk Dist., Bashkirsky Nat. Res., Ural-Tau, *Larix sibirica*, 30.VIII.1945 Selivanova (LE 38780\*). Irkutsk Reg.: Ust'-Kut Dist., Orlenga, *L. sibirica*, 8.IX.1967 Bondartseva (LE 38791\*). Khakassia: Abakan, Erkagi, *Picea obovata*, 11.VIII.2011 Kotiranta 23028\* (H). Krasnoyarsk Reg.: Ermakovskoe Dist., Sayano-Shushensky Nat. Res., Talovka, *Picea* sp., 8.VIII.2020 V. Malysheva (LE 313583\*), 9.VIII.2020 Kiyashko (LE 313584\*), Bol'shaya Golaya, *Abies sibirica*, 24.VIII.2020 V. Malysheva (LE 313587\*); Turukhansk Dist., Lebed', *P. obovata*, 23.VIII.2013 Kotiranta 26434\* (H). Leningrad Reg.: Boksitogorsk Dist., Kolp', *P. abies*, 27.VII.2016 Spirin 10388\* (H); Kirishi Dist., Shariya, *P. abies*, 11.VIII.2019 Spirin 12948\* (H); Luga Dist., Natalino, *P. abies*, 4.X.2015 Volobuev (LE 313779\*); Tosno Dist., *P. abies*, 20.VIII.1999 Morozova (LE 208530\*). Moscow Reg.: Krasnogorsk Dist., Opalikha, *Pinus sylvestris*, 26.IX.2017 Matershev (LE 315333\*). Primorie: Shkotovo Dist., Anisimovka, rotten wood, 31.VIII.2001 Diakov (LE 313661\*, 313662\*). Pskov Reg.: Loknya Dist., Bashovo, *P. sylvestris*, 1.VII.1998 Popov (LE 222719\*). Sakhalin Reg.: Kunashir, Yuzhno-Kuril'sk, rotten wood, 10.IX.1989 Kovalenko (LE



**Fig. 7** Basidiocarps of *Pseudohydnum gelatinosum*: **a** epitype (Slovenia); **b** Spirin 12948 (Northwest Russia); **c** Spirin 13196 (Slovenia); **d** Spirin 13211 (Slovenia); **e** LE 313583 (Siberia); **f** LE 313584 (Siberia); **g** LE 313587 (Siberia); **h** LE 313661 (Far East Asia). Scale bar = 1 cm

313565\*), Tretyakova River, rotten log, 15.VIII.2017 *Bulakh* (LE 313567\*). Slovenia. Jesenice: Mojstrana, Triglavsko Bistrica, *P. abies*, 28.IX.2019 *Grebenc & Spirin\* 13446* (H, LJF). Kočevje: Rajhenav, *Abies alba*, 30.VII.2020 *Grebenc & Spirin 14001\** (H). Radovljica: Bohinj, Mrežce, *P. abies*, 26.IX.2019 *Spirin 13196\**, *13198*, *13211\** (H, LJF). Sweden. Bohuslän: Hjärtum, Valdalen, *P. abies*, 27.IX.1974 *Jeppson 900* (GB-0185577). Halland: Fjärås, Bräckan, coniferous wood, 10.X.1968 *Karlvall 13227* (GB-0185571); Halmstad, Biskopstorps Nat. Res., *P. abies*, 28.IX.2012 *Schigel 7414* (GB-0130727). Småland: Rumskulla, Norra Kvill Nat. Park, *P. abies*, 8.X.1966 *Eriksson* (GB-0185570). Västmanland: Vikar, Sjöändan, coniferous wood, 29.VIII.1981 *Jeppson 2061* (GB-0185595).

*Pseudohydnum gelatinosum* ssp. *pusillum* (Ellis & Everh.) Miettinen & Viner, comb. nov. — Figs. 8 and 10  
Mycobank MB846388.

≡ *Tremellodon pusillus* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 46: 323, 1894. Neotype. USA. Washington: Jefferson Co., Hoh River, 47.86417N 123.92826W, *Tsuga heterophylla* (fallen tree crown), 20.X.2014 *Miettinen 18987.2\** (H 7200192) (designated here, MBT10010101).

Basidiocarps up to 5 cm in widest dimension and 1–3 mm thick, pileate, laterally stipitate, gelatinous. Pileal surface first strigose, watery-greyish or greyish-brownish, then almost smooth, brown, pale ochraceous or greyish-brownish in dry condition. Pileal edge sharp to rather blunt, fertile. Spines sharp-tipped, white to greyish, 1–3 mm long, 6–8 per mm. Stipe up to 0.5 cm long, watery-greyish, usually covered by spines up to the very base, sometimes rudimentary.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline or greyish, thin- or slightly thick-walled, subparallel or ascending (hairs), some short-celled and inflated, 3–12 µm in diam. Tramal hyphae hyaline or greyish, thin-walled or with a distinct wall, subparallel to interwoven, occasionally anastomosing, (2.9–) 3.0–8.2 (–9.0) µm in diam. ( $n = 100/5$ ), accidentally inflated (up to 10 µm in diam.) at septa. Subhymenial hyphae hyaline or greyish, thin- or slightly thick-walled, interwoven or ascending, (2.0–) 2.1–4.0 (–4.2) µm in diam. ( $n = 100/5$ ). Hyphidia abundant, occasionally branched, 1–2 µm in diam. at the apex, partly covering basidial cells or projecting up to 20 µm. Basidia four-celled, (10.4–) 10.6–14.5 (–15.2) × (8.0–) 8.1–11.1 (–12.8) µm ( $n = 100/5$ ), scattered among hyphidia, stalk up to 32 × 3–3.5 µm, sterigmata up to

25 × 2–3 µm. Sterile spine tips up to 150 µm long. Basidiospores broadly ellipsoid to subglobose, (6.0–) 6.1–7.3 (–7.6) × (5.1–) 5.2–6.7 (–6.8) µm ( $n = 150/5$ ),  $L = 6.62–6.90$ ,  $W = 5.65–6.04$ ,  $Q' = 1.0–1.3$ ,  $Q = 1.10–1.21$ .

Distribution and ecology. North America (USA – New York, North Carolina, Tennessee, Washington); fallen logs of conifers.

Remarks. *Tremellodon pusillus* was described from the Olympic Peninsula, the northwestern part of the USA (Ellis & Everhart 1894). The species quickly became forgotten, most likely because of the lack of the surviving type material. The single specimen (a presumable type) was cited in the protologue. We could not trace this collection in the contemporary public herbaria and thus consider it lost. Therefore, the only remaining source for understanding of *T. pusillus* is the original description. Ellis and Everhart described their species as having smoky-brown upper surface with sparse hairs and producing a rather long (up to 1 cm) stipe. These features preclude *P. omnipavum* (see description below) distributed in the same geographic region but fit well to the North-American subspecies of *P. gelatinosum* (henceforth treated as *P. gelatinosum* ssp. *pusillum*). A neotype for *T. pusillus* from the Olympic Peninsula is selected here to support our viewpoint.

*Pseudohydnum gelatinosum* ssp. *pusillum* normally produces somewhat larger and darker basidiocarps than *P. gelatinosum* s. str. from Eurasia. Its basidiospores are not so variable as in the latter taxon; nevertheless, their dimensions totally fall within the range limits of *P. gelatinosum* s. str. No reliable anatomical traits were detected by us to distinguish these two taxa, and *P. gelatinosum* ssp. *pusillum* is treated here as a separate entity mainly because of its small genetic differences from *P. gelatinosum* s. str. Further studies with the use of additional markers may provide better interpretation of *P. gelatinosum* ssp. *pusillum*.

Specimens examined. USA. New York: Essex Co., Huntington Wildlife Forest, rotten wood, 16.VIII.2012 *Sjökvist* (H), *Picea rubens*, 17.VIII.2012 *Miettinen 15646* (H), *Tsuga canadensis* (?), 16.IX.2013 *Miettinen 16888* (H), snag (*Tsuga* or *Picea*), 17.IX.2013 *Miettinen 16894\** (H); Hamilton, Huntington Wildlife Forest, *T. canadensis*, 19.IX.2013 *Miettinen 17010* (H). North Carolina: Swain Co., Clingmans Dome, *Abies fraseri/Picea rubens*, 1.X.2015 *Miettinen 19625.1\** (H). Tennessee: Cocke Co., Cosby Creek, *Tsuga canadensis*, 2.X.2015 *Miettinen 19671\** (H). Washington (neotype of *T. pusillus*, see above).

*Pseudohydnum meridianum* V. Malysheva & Spirin, sp. nov. — Figs. 6 and 12

Mycobank MB846389.

Holotype. Vietnam. Gia Lai Province: K'Bang Dist., Son Lang, Kon Chu Rang Nature Reserve, 14.51805N 108.55376E, decayed wood, 31.V.2016 *Morozova* (LE 313568\*, isotype – H 7200587).

**Table 2** A comparison of *Pseudohydnum* spp. found in temperate–boreal Northern hemisphere

Species	Distribution	Tramal hyphae, diameter ( $\mu\text{m}$ )	Subhymenial hyphae, diameter ( $\mu\text{m}$ )	Hyphidia, diameter ( $\mu\text{m}$ )	Basidia, size ( $\mu\text{m}$ )	Basidiospores, size ( $\mu\text{m}$ )	Special characters
<i>P. alienum</i>	Europe (incl. Caucasus)	2.5–5	2–3.5	0.8–1.2	11–14 $\times$ 8.5–10.5	(6.0–) 6.1–7.9 (–8.2) $\times$ (5.0–) 5.1–6.7 (–6.9)	Hyphae hyaline; basidia tending to a palisade arrangement
<i>P. gelatinosum</i>	Eurasia	2–9	2–4.5	1–2.5	10–14.5 $\times$ 7.5–11	(5.2–) 5.3–9.0 (–9.2) $\times$ (4.6–) 4.9–7.6 (–8.2)	At least some hyphae greyish
<i>P. gelatinosum</i> ssp. <i>pusillum</i>	North America	3–8	2–4	1–2	10.5–14.5 $\times$ 8–11	(6.0–) 6.1–7.3 (–7.6) $\times$ (5.1–) 5.2–6.7 (–6.8)	At least some hyphae greyish
<i>P. omnipavum</i>	North America (Rocky Mts.)	3–4	2–3.5	1–1.5	10–12 $\times$ 8–10	(5.2–) 5.8–7.3 (–7.6) $\times$ (4.8–) 5.1–6.2 (–7.2)	Hyphae hyaline
<i>P. translucens</i>	East Asia	1.5–5	1–3	1–2	10–13 $\times$ 8.5–10.5	(5.3–) 5.4–7.4 (–8.0) $\times$ (4.1–) 4.2–6.9 (–7.0)	Hyphae hyaline
<i>P. umbrosum</i>	East Asia	3.5–7.5	2–4	1.5–2	12–16 $\times$ 9–12	(7.1–) 7.6–9.8 (–10.2) $\times$ (5.4–) 6.0–7.1 (–7.3)	Basidiocarps brown or brownish-black when dry; basidiospores ellipsoid

We had no opportunity to study *P. abietinum* and *P. sinobisporum* recently described from temperate East Asia. For their descriptions, see Zhou et al. (2023)

**Etymology:** meridianus (Lat., adj.) – southern.

Basidiocarps up to 4 cm in widest dimension and 1–2 mm thick, pileate, laterally stipitate, gelatinous. Pileal surface papillate or smooth, greyish-brown when fresh, dark brown to almost black in dry condition. Pileal edge sharp, somewhat undulating, fertile. Spines sharp-tipped, white to cream-coloured, 0.5–1 mm long, 3–4 per mm. Stipe up to 2 cm long and 5 mm in diam., gradually tapering to the base, concolorous with pileal surface, finely tomentose to almost smooth.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline or greyish, thin- or slightly thick-walled, subparallel or ascending (hairs), some short-celled and slightly inflated, 3–10  $\mu\text{m}$  in diam. Tramal hyphae hyaline, thin-walled, interwoven, frequently anastomosing, (2.0–) 2.8–7.2 (–7.3)  $\mu\text{m}$  in diam. ( $n = 20/1$ ), accidentally inflated (up to 9  $\mu\text{m}$  in diam.) at septa, in uppermost layers greyish and with a distinct wall. Subhymenial hyphae hyaline, thin-walled, interwoven, (1.8–) 1.9–2.7 (–2.8)  $\mu\text{m}$  in diam. ( $n = 20/1$ ). Hyphidia abundant, occasionally branched, 1–1.5  $\mu\text{m}$  in diam. at the apex, covering basidial cells. Basidia four-celled, (10.3–) 10.7–13.0 (–13.2)  $\times$  (7.8–) 8.0–10.3 (–10.4)  $\mu\text{m}$  ( $n = 20/1$ ), scattered and mostly embedded in masses of hyphidia, stalk up to 25  $\times$  2–2.5  $\mu\text{m}$ , sterigmata up to 30  $\times$  2–3  $\mu\text{m}$ .

Sterile spine tips up to 120  $\mu\text{m}$  long. Basidiospores subglobose to globose, rarely broadly ellipsoid, (5.0–) 5.1–6.2 (–6.3)  $\times$  (4.8–) 4.9–5.8 (–6.0)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 5.65$ ,  $W = 5.26$ ,  $Q' = 1.0$ –1.1 (–1.2),  $Q = 1.07$ .

**Distribution and ecology.** Southeast Asia (Vietnam); decayed wood in lowland evergreen mixed forest.

**Remarks.** Dark-coloured basidiocarps with a pronounced stipe and nearly smooth pileal surface, as well as small, predominantly subglobose basidiospores differentiate *P. meridianum* from other species distributed in the Southeast Asia. The species is so far known from a few localities in Vietnam.

**Specimens examined.** Vietnam. Gia Lai Province: K' Bang Dist., Son Lang, Kon Chu Rang Nature Reserve, decayed wood, 24.X.2022 *Dudka* (LE F-347479\*, LE F-347480\*), 27.X.2022 *Dudka* (LE F-347478\*). Dak Nong Province, Dak Glong District, Ta Dung National Park, decayed wood, 11.X.2022 *Dudka* (LE F-347477\*).

***Pseudohydnum omnipavum*** Spirin & Miettinen, sp. nov.  
— Figs. 8 and 12  
Mycobank MB846390.

**Holotype.** USA. Idaho: Boundary Co., Upper Priest River, 48.927N 117.333W, *Pseudotsuga menziesii* (fallen partly corticated log), 16.X.2014 *Spirin 8667\** (H 7200588, isotype – LE).



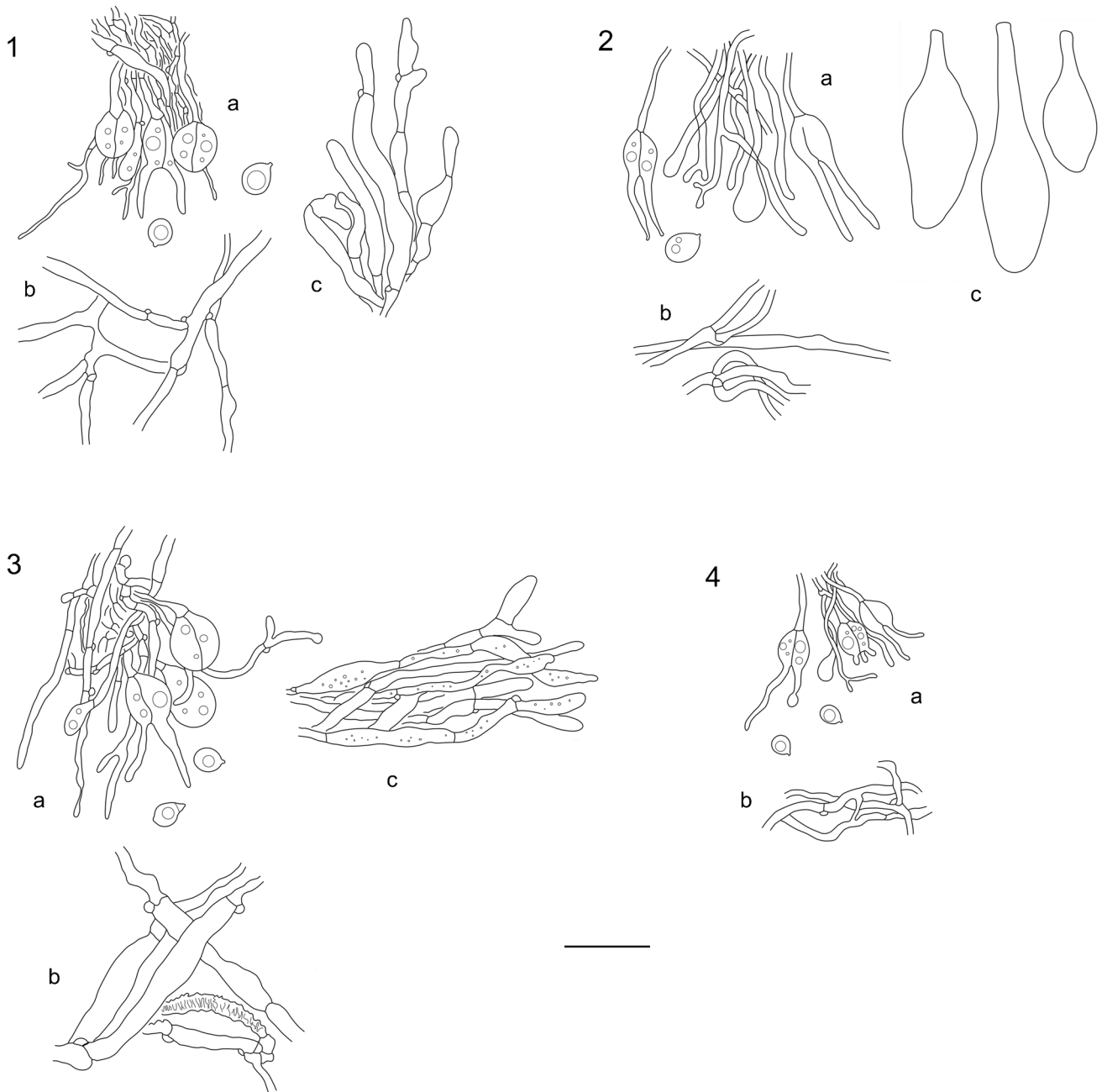


**Fig. 8** Basidiocarps of *Pseudohydnum* spp.: **a** *P. gelatinosum* spp. *pusillum* (neotype); **b** *P. omnipavum* (Miettinen 18877); **c** *P. translucens* (LE 313582); **d** *P. translucens* (LE 313585); **e** *P. translucens* (LE 313586); **f** *P. umbrosum* (holotype). Scale bar = 1 cm

Etymology: *omnipavus* (Lat., adj.) — trembling.

Basidiocarps up to 2 cm in widest dimension and 1–2 mm thick, pileate, laterally stipitate, gelatinous. Pileal surface finely tomentose to strigose, first watery-greyish, then greyish, pale ochraceous or

greyish-brownish in dry condition. Pileal edge sharp, fertile. Spines sharp-tipped, white to cream-coloured, 0.5–1.5 mm long, 4–6 per mm. Stipe up to 0.5 cm long, watery-greyish, finely tomentose or more or less smooth and covered by spines.

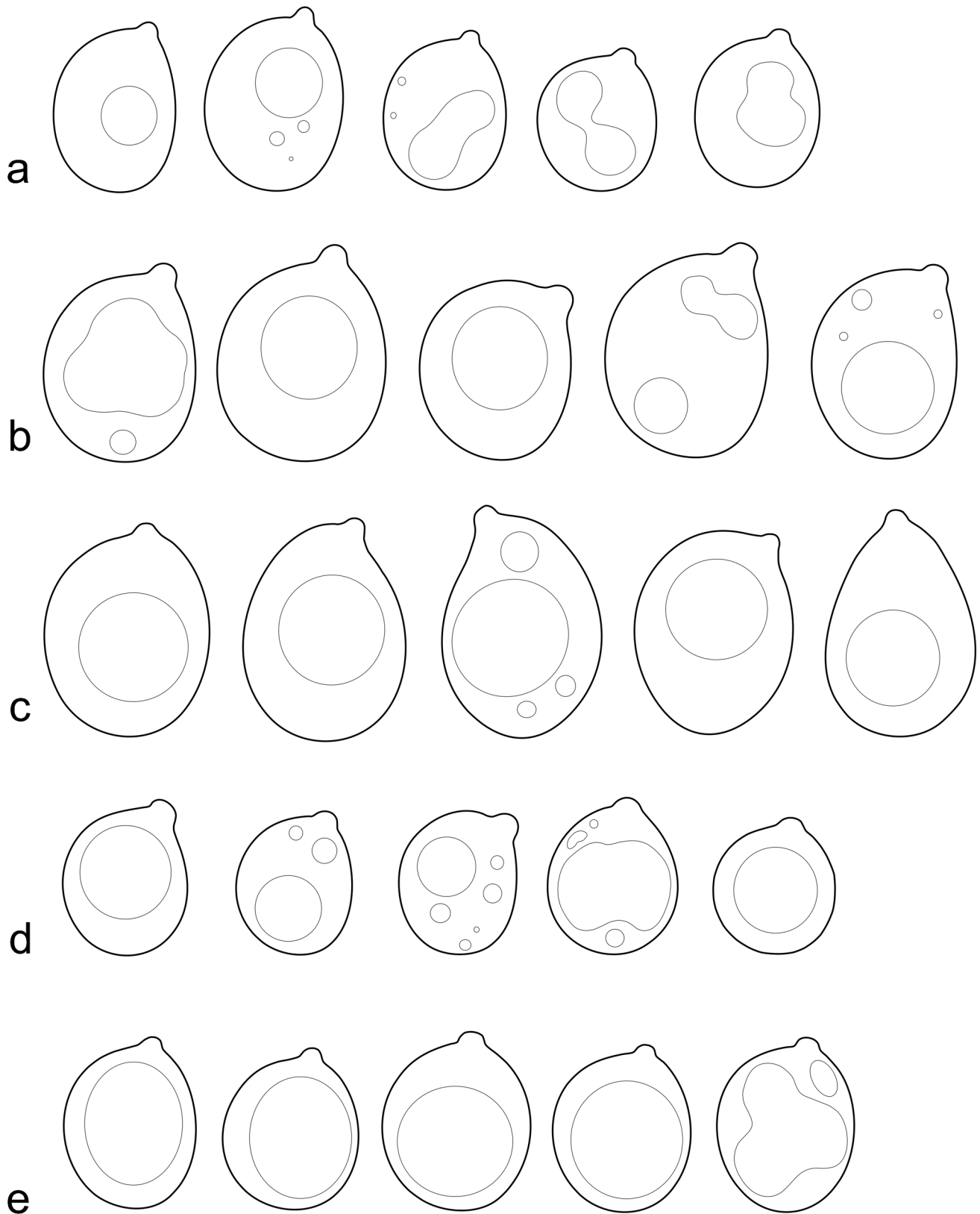


**Fig. 9** Anatomical structures of *Pseudohydnum* spp.: 1 — *P. alienum* (holotype): a — basidia, hyphidia, subhymenial hyphae; b — tramal hyphae; c — hyphae of pileal surface; 2 — *P. cystidiatum* (holotype): a — basidia, hyphidia, subhymenial hyphae; b — tramal hyphae; c

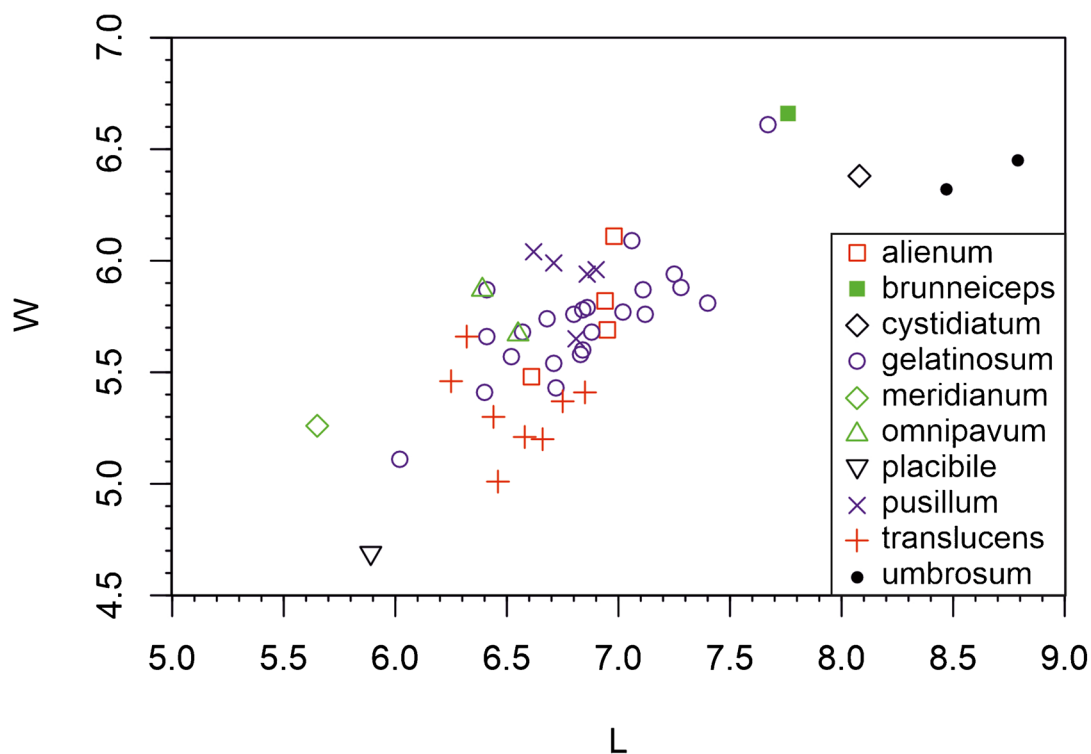
— cystidia; 3 — *P. gelatinosum* (epitype): a — basidia, hyphidia, subhymenial hyphae; b — tramal hyphae; c — hyphae of pileal surface; 4 — *P. placibile* (holotype): a — basidia, hyphidia, subhymenial hyphae; b — tramal hyphae. Scale bar = 10  $\mu$ m

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline, thin-walled, subparallel or ascending (hairs), some short-celled and inflated, 3–9  $\mu$ m in diam. Tramal hyphae hyaline, thin-walled, interwoven, occasionally anastomosing, (2.8–) 2.9–4.2 (–4.3)  $\mu$ m in diam. ( $n=40/2$ ), in some parts tightly glued by gelatinous matter. Subhymenial hyphae hyaline, thin-walled, interwoven, (2.0–) 2.1–3.3 (–3.8)

$\mu$ m in diam. ( $n=40/2$ ). Hyphidia abundant, richly branched, 1–1.5  $\mu$ m in diam. at the apex, partly covering basidial cells. Basidia four-celled, (9.8–) 9.9–12.2 (–12.3)  $\times$  (7.0–) 7.8–10.1 (–10.2)  $\mu$ m ( $n=40/2$ ), scattered among hyphidia and covering spines up to the very top, stalk up to 30  $\times$  2–3  $\mu$ m, sterigmata up to 20  $\times$  2–3  $\mu$ m. Basidiospores broadly ellipsoid to subglobose, rarely globose, (5.2–) 5.8–7.3 (–7.6)  $\times$  (4.8–)



**Fig. 10** Basidiospores of *Pseudohydnum* spp.: **a** *P. alienum* (holotype); **b** *P. brunneiceps* (Härkönen K884); **c** *P. cystidiatum* (holotype); **d** *P. gelatinosum* (epitype); **e** *P. gelatinosum* ssp. *pusillum* (neotype). Scale bar = 10  $\mu$ m



**Fig. 11** The average basidiospore size in *Pseudohydnum* spp

5.1–6.2 (–7.2)  $\mu\text{m}$  ( $n=60/2$ ),  $L=6.39\text{--}6.55$ ,  $W=5.67\text{--}5.87$ ,  $Q'=1.0\text{--}1.2$  (–1.4),  $Q=1.09\text{--}1.16$ .

Distribution and ecology. North America (USA–Idaho, Canada–British Columbia); fallen logs of conifers (*Pseudotsuga*, *Tsuga*).

Remarks. Phylogenetically and morphologically, *P. omnipavum* is closest to *P. alienum* and *P. translucens*. These three species possess narrow tramal hyphae and slender hyphidia. From the latter two species, *P. omnipavum* can be distinguished mainly due to a better-differentiated stipe and a lesser number of spines per mm, as well as different distribution area (North America vs. Eurasia). The species is so far known from two localities in Rocky Mts.

Specimens examined. Canada. British Columbia: Columbia — Shuswap Regional Dist., Glacier Nat. Park, fallen coniferous log, 24.VIII.1982 *Hallenberg 6817* (GB-0185596). USA. Idaho: Boundary Co., Upper Priest River, *Tsuga heterophylla* (fallen tree crown), 16.X.2014 *Miettinen 18877\** (H).

***Pseudohydnum placibile*** V. Malysheva & V. Dudka, sp. nov. — Figs. 6, 9, and 12

Mycobank MB846391.

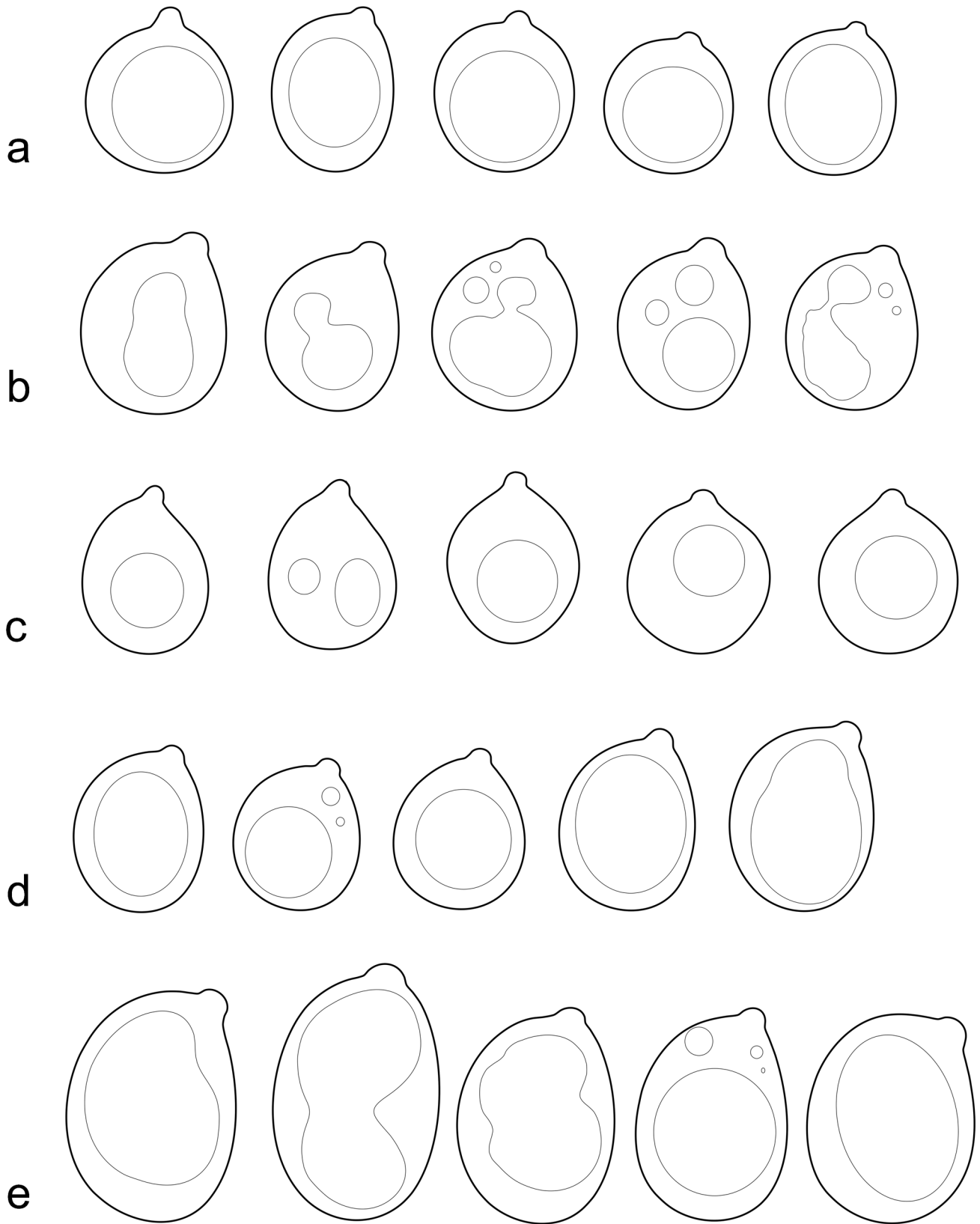
Holotype. Vietnam. Cao Bằng Province: Nguyễn Bình Dist., Thành Công, National Park Phia Oac — Phia Den,

22.60661N 105.87346E, decayed wood, 15.IV.2021 *Do & Dudka* (LE 313658\*).

Etymology: *placibilis* (Lat., adj.) – pleasant, attractive.

Basidiocarps up to 1.5 cm in widest dimension and 1–1.5 mm thick, pileate, stipitate, gelatinous. Pileal surface papillate, pale ochraceous when fresh, greyish-brownish in dry condition. Pileal edge sharp, somewhat undulating, fertile. Spines sharp-tipped, white to cream-coloured, up to 0.5 cm long, 2–3 per mm. Stipe up to 1 cm long, watery-greyish, usually covered by spines up to the very base.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline, thin- or slightly thick-walled, sub-parallel, some short-celled and slightly inflated, 2–5  $\mu\text{m}$  in diam. Tramal hyphae hyaline, thin-walled, rare interwoven, frequently anastomosing, (1.0–) 1.5–2.5 (–4.0)  $\mu\text{m}$  in diam. ( $n=20/2$ ), accidentally inflated (up to 5  $\mu\text{m}$  in diam.) at septa, in uppermost layers hyaline and with a distinct wall. Subhymenial hyphae hyaline, thin-walled, interwoven, (1.0–) 1.2–1.5 (–2.0)  $\mu\text{m}$  in diam. ( $n=20/2$ ). Hyphidia abundant, occasionally branched, 1–1.5  $\mu\text{m}$  in diam. at the apex, covering basidial cells. Basidia four-celled, (9.5–) 10.1–11.4 (–12.0)  $\times$  (7.5–) 7.6–9.3 (–9.6)  $\mu\text{m}$  ( $n=20/2$ ), scattered and mostly embedded in masses of hyphidia, stalk up to  $45 \times 2\text{--}2.5$   $\mu\text{m}$ , sterigmata up to  $25 \times 2\text{--}3$   $\mu\text{m}$ . Basidiospores subglobose to globose, rarely



**Fig. 12** Basidiospores of *Pseudohydnum* spp.: **a** *P. meridianum* (holotype); **b** *P. omnipavum* (holotype); **c** *P. placibile* (holotype); **d** *P. translucens* (LE 313586); **e** *P. umbrosum* (holotype). Scale bar = 10  $\mu$ m

broadly ellipsoid, (5.3–) 5.4–6.4 × (3.7–) 4.1–5.1 (–5.4) μm ( $n = 30/1$ ),  $L = 5.89$ ,  $W = 4.69$ ,  $Q' = (1.1–) 1.2–1.4 (–1.5)$ ,  $Q = 1.26$ .

Distribution and ecology. Southeast Asia (Vietnam); decayed wood in lowland evergreen mixed forest.

Remarks. The absence of hairs on pileal surface and relatively small, predominantly subglobose basidiospores make *P. placibile* similar to another Southeast Asian species, *P. meridianum*. Nevertheless, *P. placibile* can be differentiated from *P. meridianum* due to much paler basidiocarps and distinctly narrower tramal hyphae. The species is so far known from two collections in the type locality (Vietnam).

Specimens examined. Vietnam. Cao Bằng Province: Nguyễn Bình Dist., Thành Công, National Park Phia Oac — Phia Den, decayed wood, 7.IV.2021 *Dudka* (LE 313659\*), 15.IV.2021 *Do & Dudka* (holotype, see above).

***Pseudohydnum translucens*** Lloyd, Mycological Writings 7: 1357, 1925. — Figs. 8 and 12

Holotype. Japan. Kansai: Hyōgo, Kobe, [no collecting date] *Lewis* (BPI 0324962, studied).

= *Pseudohydnum candidissimum* H.M. Zhou, T. Bau & Jing Si, *Frontiers in Cellular and Infection Microbiology* 13:1139449: 5, 2023.

Basidiocarps up to 2 cm in widest dimension and 1–2 mm thick, pileate, laterally stipitate, gelatinous. Pileal surface first strigose, watery-greyish, then almost smooth, greyish-brownish, pale ochraceous or greyish-brownish in dry condition. Pileal edge sharp to rather blunt, fertile. Spines sharp-tipped, white to greyish, 1–1.5 mm long, 6–8 per mm. Stipe up to 0.5 cm long, watery-greyish, usually covered by spines up to the very base.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline, thin- or slightly thick-walled, subparallel or ascending (hairs), some short-celled and slightly inflated, 2–9 μm in diam. Tramal hyphae hyaline, thin-walled, interwoven, occasionally anastomosing, (1.1–) 1.4–5.2 (–5.4) μm in diam. ( $n = 160/8$ ), accidentally inflated (up to 6.5 μm in diam.) at septa. Subhymenial hyphae hyaline, thin-walled, mostly ascending, (1.0–) 1.1–3.0 (–3.2) μm in diam. ( $n = 140/7$ ). Hyphidia abundant, occasionally branched, 1–2 μm in diam. at the apex, covering basidial cells. Basidia four-celled, (9.3–) 9.8–13.2 (–13.5) × (8.2–) 8.3–10.4 (–11.2) μm ( $n = 150/8$ ), scattered and embedded in masses of hyphidia, stalk up to 35 × 2–3 μm, sterigmata up to 20 × 2–3 μm. Sterile spine tips up to 150 μm long. Basidiospores ellipsoid to ovoid or subglobose, (5.3–) 5.4–7.4 (–8.0) × (4.1–) 4.2–6.9 (–7.0) μm ( $n = 240/8$ ),  $L = 6.24–6.85$ ,  $W = 5.01–5.66$ ,  $Q' = (1.0–) 1.1–1.5 (–1.7)$ ,  $Q = 1.12–1.29$ .

Distribution and ecology. East Asia (China, Japan, Siberia, Russian Far East); fallen logs and branches of conifers (predominantly *Abies* spp.).

Remarks. *Pseudohydnum translucens* is the East Asian relative of *P. alienum*. The latter species is distributed in Europe and it differs from *P. translucens* in having on average wider basidiospores and narrower hyphidia (Table 2). Moreover, basidia of *P. translucens* are intermixed with hyphidia in a highly irregular manner, while they tend to be arranged in a dense palisade layer in *P. alienum*. Two other *Pseudohydnum* species distributed in the same geographic area, *P. gelatinosum* and *P. umbrosum*, have more robust basidiocarps with more intensively coloured, grey to brownish-black upper surface, as well as wider hyphae and larger basidiospores.

Specimens examined. Japan. Kansai (holotype, see above). Russia. Jewish Autonomous Reg.: Obluchensky Dist., Yadrino, fallen coniferous log, 10.VIII.1961 *Raitviir* (TAAM 042211). Krasnoyarsk Reg.: Ermakovskoe Dist., Sayano-Shushensky Nat. Res., Talovka, *Abies sibirica*, 7–8.VIII.2020 V. *Malysheva* (LE 313582\*, LE 313585\*, 313586\*). Primorie. Terney Dist.: Sikhote-Alin Nat. Res., Maisa, strongly decayed log, 21.VIII.1996 *Morozova* (LE 262798\*). Sakhalin Reg.: Kunashir, Goryachii Plyazh, *Abies sachalinensis* (fallen branch), 2.X.1960 *Parmasto* (TAAM 012200); Nevel'sky Dist., *A. sachalinensis* (fallen branch), 12.IX.1979 *Parmasto* (TAAM 102447).

***Pseudohydnum umbrosum*** V. Malysheva & Spirin, sp. nov. — Figs. 8 and 12

Mycobank MB846392.

Holotype. Russia. Krasnoyarsk Reg.: Ermakovskoe Dist., Sayano-Shushensky Nat. Res., 2 km upstream of the Bol'shaya Golaya River, 52.56388N 92.12777E, rotten coniferous log, 15.VIII.2015 V. *Malysheva* (LE 312767\*, isotype – H 7200589).

Etymology: umbrosus (Lat., adj.) – dark-coloured.

Basidiocarps up to 2 cm in widest dimension and 1–2 mm thick, pileate, sessile, gelatinous. Pileal surface strigose, greyish-brown when fresh, brown to brownish-black in dry condition. Pileal edge rather blunt, fertile. Spines sharp-tipped, white to greyish, 0.5–2 mm long, 5–7 per mm. Stipe rudimentary, very short, or absent.

Hyphal structure monomitic, hyphae clamped. Hyphae of pileal surface hyaline to brownish, thin- or slightly thick-walled, subparallel or ascending (hairs), densely glued together and mostly hardly discernible, some short-celled and inflated, 3–8 μm in diam. Tramal hyphae hyaline, thin-walled, interwoven, occasionally anastomosing, (3.0–) 3.4–7.6 (–8.7) μm in diam. ( $n = 40/2$ ), accidentally inflated (up to 14 μm in diam.) at septa. Subhymenial hyphae hyaline, thin-walled, ascending or interwoven, (2.0–) 2.1–4.2 (–4.8) μm in diam. ( $n = 40/2$ ). Hyphidia present, sparsely branched, 1.5–2 μm in diam. at the apex. Basidia four-celled, (12.0–) 12.2–15.8 (–16.2) × (9.0–) 9.1–12.2 (–12.8) μm ( $n = 40/2$ ), openly and loosely arranged, usually covering spines up to the very top, stalk up to 50 × 3–3.5 μm, sterigmata up to 25 × 2–3 μm. Basidiospores

narrowly to broadly ellipsoid, (7.1–) 7.6–9.8 (–10.2) × (5.4–) 6.0–7.1 (–7.3) μm ( $n=60/2$ ), L=8.47–8.79, W=6.32–6.45, Q'=(1.1–) 1.2–1.5 (–1.6), Q=1.34–1.36.

Distribution and ecology. East Asia (Siberia, Russian Far East); decayed wood of conifers.

Remarks. Of the temperate–boreal species treated here, *P. umbrosum* is morphologically most distinctive due to a dark-coloured, fuscous-brown upper surface of pilei covered by short hairs. In addition, it possesses the largest spores in the genus; they are more or less regularly ellipsoid and have highest Q values comparing to other *Pseudohydnum* species.

Specimens examined. Russia. Krasnoyarsk Reg. (holotype, see above). Primorie: Khasan Dist., Kedrovaya Pad' Nat. Res., decayed wood, 18.IX.1961 *Parmasto* (TAAM 015358).

## Discussion

In the present study, we re-established identity of *P. gelatinosum* and described six new *Pseudohydnum* species from Eurasia and North America, in addition to eight species previously introduced by Chen et al. (2020) and Zhou et al. (2022, 2023). However, the species diversity in the genus seems to be much higher, as we could judge from the already existing data. Descriptions of *P. gelatinosum* s. lato from the neotropics provided by Möller (1895) and Lowy (1971) do not fit to any of the species treated here, likely referring to species yet to be described. Future taxonomic studies of the genus outside Europe and boreal North America should carefully reconsider already existing older names associated with *P. gelatinosum*, e.g. *Hydnum hirneoloides* Berk. & M.A. Curtis from Cuba.

The species concepts advocated above have been based on combined morphological and DNA evidence. The main obstacle for morphological definition of *Pseudohydnum* spp. is the large variability of basidiospores in the most common species, *P. gelatinosum*. Therefore, we propose to pay attention to other morphological traits for introducing new species. Among macroscopic characters, the pileal surface, basidiocarp colour(s), and a presence of stipe are the most important. Species-specific microscopic traits are the width of contextual and tramal hyphae, shape, and width of hyphidia and dimensions of basidia. Combined, these features provide a comprehensive background for the species delimitation. However, we cannot preclude an existence of morphologically indistinguishable *Pseudohydnum* species which could be identified via DNA tools only.

Of four generic markers used in this study, ITS, nc LSU rDNA, and to a lesser extent, *RPB1* sequences allow of species recognition. The large divergence of *TEF1* detected in *P. gelatinosum* deserves further investigations. Intraspecific variation of *TEF1* is higher in this complex than interspecific

variation of some other species, and phylogenetic signal is also mixed, placing some *TEF1* copies far outside of the core *P. gelatinosum* clade (Fig. 5). Our previous studies of the *Auriculariales* (Spirin et al. 2018, 2019, 2020, 2021) revealed no conflicts between ITS–LSU- and *TEF1*-based phylogenies. Therefore, *Pseudohydnum* is the first documented case of obvious discordance between these markers. Among the *Auriculariales*, an unnamed *Auricularia* species was shown to have multiple copies of *TEF1* region (Matheny et al. 2007). Further studies are needed to understand whether *Pseudohydnum* represents the same case.

Data on geographic distribution of most *Pseudohydnum* spp. remain rather fragmentary. Four species, *P. brunnei-ceps*, *P. cystidiatum*, *P. meridianum*, and *P. placibile*, seem to have a subtropical–tropical distribution in East and Southeast Asia; however, they all are known from a few records only. The rest of species are distributed in temperate–boreal forests of the northern hemisphere. Of them, *P. gelatinosum* is the most common Eurasian species, occurring on various wood remains of (almost exclusively) coniferous trees. *Pseudohydnum translucens* is seemingly restricted to East Asia, predominantly inhabiting remnants of *Abies* spp. Its closest relative, *P. alienum*, was so far found in Finland and Caucasus although it surely has a wider distribution. Therefore, much denser sampling of jelly fungi even in Europe is highly desirable.

The existence of two *Pseudohydnum* species in Europe made it necessary to collect the epitype material in the *locus classicus* of *P. gelatinosum* (Ildrija, Slovenia). Although fulfilling minimal requirements for solid epitypification, re-collecting specimens in the type locality should consider changes of forest types in the targeted area. The Norway spruce (*Picea abies*) is currently the most common coniferous tree in the type locality of *P. gelatinosum*. In Scopoli's time, the dominating tree species was evidently *Abies alba*. Additional sampling in the intact fir-dominated forest in Slovenia and sequencing this material for four markers confirmed that it is identical with our specimen of *P. gelatinosum* from the type locality, thus validating designation of the latter collection as an epitype of this species.

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**Author contribution** All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Viacheslav Spirin, Vera Malysheva, Ilya Viner, and Otto Miettinen. The first draft of the manuscript was written by Viacheslav Spirin, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data availability** DNA sequences used in the present study are available in GenBank. Alignments were deposited in PlutoF (<https://doi.plutof.ut.ee/doi/10.15156/BIO/2912106>). Fungal specimens are stored in public herbaria (as indicated under Specimens examined).

## Declarations

**Ethics approval and consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Competing interests** The authors declare no competing interests.

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