Persoonia 55, 2025: 141–157
https://www.persoonia.org

RESEARCH ARTICLE

ISSN (Online) 1878-9080
https://doi.org/10.3114/persoonia.2025.55.04

A multilocus phylogeny of *Hericium* (*Hericiaceae, Russulales*)

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Key words:
biogeography
erinacines
hericenones
new taxa
systematics

Abstract: Clear distinction of the species of *Hericium* will aid in natural products discovery, medicinal applications, and breeding for commercial cultivation of these edible and medicinally valuable mushrooms. A phylogeny of *Hericium* species from North America, together with key taxa from Europe, was accomplished using sequence data from the nuclear ribosomal internal transcribed spacer (ITS) region and adjacent large ribosomal subunit (LSU), translation elongation factor 1-alpha (*TEF-1α*), and RNA polymerase second largest subunit (*RPB2*) gene sequences. Compared to previous unresolved phylogenies based solely on ITS data, the species of *Hericium* were resolved as monophyletic groups, including the type species *H. coralloides* (synonyms *H. flagellum* and *H. ramosum*; Europe and North America), *H. alpestre* (Europe to central Asia), *H. americanum* (eastern North America), *H. abietis* (western North America), *H. cirrhatum* (Europe and boreal-montane North America), *H. erinaceus* (Europe), two recently described species of the *H. erinaceus* species complex, *H. asiaticum* (Eastern Asia) and *H. carolinense* (eastern United States), and a third new species in this complex from western North America, *H. oregonense*, described herein. All taxa, including the newly described species within the *H. erinaceus* complex, were strongly supported in maximum likelihood analyses.

Citation: Koga J, Thorn RG, Langer E (2025). A multilocus phylogeny of *Hericium* (*Hericiaceae, Russulales*). *Persoonia* **55**: 141–157. doi: 10.3114/persoonia.2025.55.04

Received: 28 October 2024; **Accepted:** 18 June 2025; **Effectively published online:** 31 July 2025

Corresponding editor: J. Nuytinck

INTRODUCTION

Species of *Hericium* are wood-decomposing basidiomycetes that produce large, white basidiocarps with a toothed hymenophore or fertile surface. In nature, *Hericium* is found on wood of deciduous trees (hardwoods), and to a lesser extent, that of conifers (softwoods), causing a white rot (Ginns 1985, Das *et al*. 2011). Considered both a highly prized edible mushroom as well as a valuable medicinal resource, *H. erinaceus* has a long history of use in the treatment of gastric ailments in East Asia, where *H. erinaceus* is known as the monkey head mushroom (Houtou) in China and as Yamabushitake in Japan (Bhandari *et al*. 2014). Analyses over the past three decades of the compounds present in *H. erinaceus* fruit body and mycelium, which include erinacines, hericenones, pyrones, sterols, and polysaccharides, suggest that these mushrooms, and their secondary metabolites in particular, do indeed possess medicinal qualities by modern standards (Kawagishi *et al*. 1994, 1996a, b, Chen *et al*. 2017, Corana et al. 2019). Evidence of their bioactivity by in vitro and in vivo studies have demonstrated that isolated compounds as well as whole extracts possess various bioactivity profiles including anti-inflammatory (Chiu *et al*. 2018, Wang *et al*. 2019), antimicrobial (Kim *et al*. 2000, Wong *et al*. 2009), anti-cancer (Li *et al*. 2014), and neuroprotective (Suruga *et al*. 2015, Chen *et al*. 2016) properties. Because of these potential health-promoting properties, together with its culinary value as an edible mushroom, the demand for *H. erinaceus* has extended beyond East Asia into Europe and North America in culinary and nutraceutical markets (Thongbai *et al*. 2015).

Since the description of *Hericium* by Persoon (1794), with *H. coralloides* as the type and only species, nomenclature of *Hericium*, and of *H. coralloides* in particular, has been controversial, as no original specimen is available for a holotype (Jumbam *et al*. 2019). Approximately 17 species of *Hericium* are currently recognized globally, with five occurring in North America (Harrison 1984, Ginns 1985, Van Der Merwe *et al*. 2023). Harrison (1973b) treated the four species then known to occur in North America as *H. erinaceus*, *H. abietis*, *H. ramosum*., and *H. coralloides*, of which all but *H. abietis* were originally described from Europe. Neotypification of *H. coralloides* by Hallenberg (1983) placed *H. ramosum* in synonymy with *H. coralloides*, confirming the synonymy indicated by Bulliard (1791) and Fries (1821). Subsequently, Ginns (1985) used mating intercompatibility tests to show that cultures of the species in North America that Harrison (1973b) and others referred to as *H. ramosum* were compatible with European *H. coralloides*, whereas cultures of the species known by Harrison (1973b) and others in North America as *H. coralloides* were not. Based on preliminary results of these studies, Ginns (1984) proposed the name *H. americanum* for this North American species, and the published mating tests (Ginns 1985) supported the redescription of *H. coralloides* sensu auct. N. Amer. as *H. americanum*. The fifth *Hericium* species in North America is *Hericium cirrhatum*, known for many years as *Creolophus cirrhatus* (Harrison 1984). Analyses of sequences of the internal transcribed spacer (ITS) region by Hallenberg *et al*. (2013) support the concept of *H. coralloides* sensu lato as a species complex, within which collections of *H. coralloides* sensu stricto from Europe were placed on a separate branch from those of North American origin. The use of the name *H. coralloides* in North America was therefore considered uncertain by these authors. Additionally, several authors have shown that ITS sequences of *H. erinaceus* of Asian origin cluster separately from those of North American and European origin (Hallenberg *et al*. 2013, Cesaroni *et al*. 2019, Jumbam *et al*. 2019). The interpretation of *Hericium* species is complicated by the high frequency of misidentified specimens and their subsequent deposit as mislabelled sequences in public databases, as well as the high number of sequences from commercial strains of *H. erinaceus* for which voucher specimens are unknown or unavailable.

Despite the progress made in our understanding of *Hericium* taxonomy by ITS sequence analysis, polymorphisms at this locus are minimal in *Hericium,* and phylogenies produced using ITS alone have provided unsatisfactory species delimitations with little resolution to interspecific relationships (Das *et al*. 2013, Hallenberg *et al*. 2013, Cesaroni *et al*. 2019, Ouali *et al*. 2020). Combination of ITS and the large subunit (LSU) of nuclear rDNA regions with protein-coding genes *RPB2* and *TEF-1α* have provided stronger phylogenetic signals to delimit species in other groups, such as *Trametes* (Carlson *et al*. 2014) and *Tolypocladium* (Dong *et al*. 2022), where ITS alone provides little resolution. Here, we present the first multilocus phylogenetic study of the genus *Hericium,* with a particular focus on species occurring in North America and Europe. The first major objective of the present work is to provide a higher resolution to the interspecific relationships of *Hericium* species known from North America using ITS, LSU, *RPB2*, and *TEF-1α*, and to position these species in relation to global *Hericium* diversity. Secondly, to help stabilize the nomenclature of *Hericium*, we designate lectotypes and epitypes, where possible, for critical European species, *H. coralloides*, *H. erinaceus*, *H. flagellum* and *H. clathroides*.

MATERIALS AND METHODS

Sampling and collecting

From September 2022 to August 2023, specimens of *H. americanum* and *H. coralloides* basidiocarps were collected from forests in Southern Ontario, and mycelial cultures were isolated by transferring clean internal tissue of basidiocarps to malt extract (ME) agar containing 50 mg/L chloramphenicol (Nobles 1948) as sources of genomic DNA for sequence analysis. Basidiocarps of collected specimens were dried at 45 ºC for 48 h to serve as voucher specimens and were deposited in the Dr. Laurie L. Consaul Herbarium, London, Canada (UWO). Cultures of other *Hericium* species were obtained from the Canadian Collection of Fungal Cultures (CCFC) (Table 1) to extend the breadth and depth of our taxon sample for DNA analysis. With the exception of DAOMC 195739 (as *H. erinaceus*, Japan), DAOMC 172297 (*H. alpestre*, France), and DAOMC 251013 (as *H. clathroides*, Czech Republic), which were included for assessment of geographic diversity in relation to North American *Hericium* species, all cultures obtained from CCFC were those used by Ginns (1985) in his treatment of the genus in North America and are therefore formally representative of *H. erinaceus, H. americanum, H. coralloides,* and *H. abietis* as they are currently understood. Cultures were maintained on ME agar at room temperature in the dark and transferred as needed. Additional voucher specimens identified as *H. erinaceus* from British Columbia (DAOM 193896, DAOM 193728, DAOM 185101) and Ontario (DAOM 241459) were obtained from the National Mycological Herbarium of Canada (DAOM), along with a specimen of *H. cirrhatum* obtained from Stacey Scorda, a naturalist in northern Alberta (UWO-F1892).

Phylogenetic analysis

For each strain, mycelium was grown in liquid culture by transferring 5 × 5 mm sections of colonized ME agar at the leading edge of the mycelium into autoclaved liquid V8 medium (20 % V8 vegetable juice, 80 % deionized H_2O) and grown at room temperature on a rotary shaker to obtain biomass for DNA extractions. Small portions of dried basidiocarps of voucher specimens for which no cultures were available were ground in liquid nitrogen, and genomic DNA from these and of mycelial cultures was obtained using a CTAB and chloroform extraction and ethanol precipitation (Lee *et al.* 1988, Bainbridge *et al.* 1990, Möller *et al.* 1992). The ITS and LSU regions of nuclear rDNA were amplified as a single ~1200 bp amplicon using primers ITS1F/LR3 (Gardes & Bruns 1993, Hopple & Vilgalys 1994). Protein coding genes *TEF-1α* (~600 bp) and *RPB2* (~800 bp) were amplified using primers RR.EF1-983F (5'-GCY CCY GGH CAY CGY GAY TTY AT-3')/RR.EF1-1567R (5'-ACH GTR CCR ATA CCR CCR ATC TT-3', both modified from Rehner & Buckley 2005) and bRPB2-6F/bRPB2-7.1R (Liu *et al.* 1999, Matheny *et al.* 2007), respectively. Successful PCR products were cleaned using the Bio Basic EZ-10 Spin Column PCR Products Purification Kit and sequenced by Sanger sequencing at the London Regional Genomics Centre. Sequence files were cleaned and assembled in SeqEd v. 1.03 (ABI Software) and BLAST searches of ITS–LSU, *RPB2,* and *TEF-1α* were used to select reference sequences for inclusion in the analyses. Forty-three strains of *Hericium* from the present study were sequenced for ITS–LSU (OR793913–OR793952, PP786302–PP786306), *TEF-1α* (OR829812–OR829851, PP793770–PP793774), and *RPB2* (OR829852–OR829891, PP793774–PP793777), and 10 strains from GenBank for which all three loci were available and one of *Hericium cirrhatum* for which only ITS–LSU data were available were added to the analysis (Table 1). Most sequences of *Hericium* that were available on GenBank could not be included in our analyses because they included only ITS or LSU regions, which are largely uninformative for *Hericium* taxonomy (Hallenberg *et al*. 2013), and no *TEF-1α* or *RPB2* sequences were available for the same samples. In addition, several sequences are apparently obtained from commercial strains for which the natural origins are unknown.

Datasets for each locus were aligned individually with MAFFT (Multiple Alignment using Fast Fourier Transform) software v. 7 (Katoh & Standley 2013) with the options for

Table 1. Sequences included in the multilocus phylogeny, including taxon names as identified in this study, geographic origin, voucher or culture number, and GenBank accession numbers.

			Accession Number[3]			
Species	**Origin**	**Voucher**	**ITS**	**LSU**	***TEF-1α***	***RPB2***
Amylostereum areolatum	China	HG-01[1]	SAXG01000196	SAXG01000196	SAXG01000196	SAXG01000196
Auriscalpium vulgare	IN, USA	FP105234-sp[1]	JAFLMV010000061	JAFLMV010000061	JAFLMV010000061	JAFLMV010000061
Auriscalpium vulgare	Netherlands	CBS 236.39[1]	JAHBBC010000018	JAHBBC010000018	JAHBBC010000018	JAHBBC010000018
Dentipellis fragilis	Germany	DSM 105465[1]	SEOQ01000808.1	SEOQ01000808.1	SEOQ01000031.1	SEOQ01000005.1
Dentipellis sp.	South Korea	KUC8613[1]	OL898488	OL898488	NSJX01000003.1	NSJX01000003.1
Hericium abietis (HB1)[2]	BC, Canada	DAOMC17054	*OR793932*	*OR793932*	*OR829831*	*OR829871*
H. abietis (HB2)	BC, Canada	DAOMC251004	*OR793933*	*OR793933*	*OR829832*	*OR829872*
H. abietis (HB3)	BC, Canada	DAOMC196447	*OR793934*	*OR793934*	*OR829833*	*OR829873*
H. abietis (HB4)	BC, Canada	DAOMC22748	*OR793935*	*OR793935*	*OR829834*	*OR829874*
H. abietis (HB5)	BC, Canada	DAOMC16601	*OR793936*	*OR793936*	*OR829835*	*OR829875*
H. abietis (HB6)	BC, Canada	DAOMC251005	*OR793937*	*OR793937*	*OR829836*	*OR829876*
H. abietis (HB7)	BC, Canada	DAOMC251006	*OR793938*	*OR793938*	*OR829837*	*OR829877*
Hericium alpestre	Germany	DSM 108284[1]	SFCI01000210	SFCI01000210	SFCI01000210	SFCI01000210
H. alpestre (HL1)	France	DAOMC172297	*OR793952*	*OR793952*	*OR829851*	*OR829891*
Hericium americanum	MA, USA	AFTOL-ID 469	DQ206987	DQ411538	DQ028585	DQ408127
H. americanum (HA1)	ON, Canada	UWO-F1485	*OR793913*	*OR793913*	*OR829812*	*OR829852*
H. americanum (HA2)	ON, Canada	—	*OR793914*	*OR793914*	*OR829813*	*OR829853*
H. americanum (HA3)	ON, Canada	UWO-F1487	*OR793915*	*OR793915*	*OR829814*	*OR829854*
H. americanum (HA5)	ON, Canada	UWO-F1488	*OR793916*	*OR793916*	*OR829815*	*OR829855*
H. americanum (HA6)	ON, Canada	UWO-F1489	*OR793917*	*OR793917*	*OR829816*	*OR829856*
H. americanum (HA8)	ON, Canada	UWO-F1490	*OR793918*	*OR793918*	*OR829817*	*OR829857*
H. americanum (HA9)	ON, Canada	—	*OR793919*	*OR793919*	*OR829818*	*OR829858*
H. americanum (HA10)	ON, Canada	UWO-F1492	*OR793920*	*OR793920*	*OR829819*	*OR829859*
H. americanum (HA11)	ON, Canada	UWO-F1493	*OR793921*	*OR793921*	*OR829820*	*OR829860*
H. americanum (HAX1)	ON, Canada	DAOMC21467	*OR793928*	*OR793928*	*OR829827*	*OR829867*
H. americanum (HAX2)	PA, USA	DAOMC251011	*OR793929*	*OR793929*	*OR829828*	*OR829868*
H. americanum (HC3)	ON, Canada	UWO-F1482	*OR793925*	*OR793925*	*OR829824*	*OR829864*
H. americanum (HC4)	ON, Canada	UWO-F1483	*OR793926*	*OR793926*	*OR829825*	*OR829865*
H. americanum (HC5)	ON, Canada	UWO-F1484	*OR793927*	*OR793927*	*OR829826*	*OR829866*

Table 1. (Continued).

Species	Origin	Voucher	Accession Number[3]			
			ITS	LSU	*TEF-1α*	*RPB2*
H. americanum (WCHA)	ON, Canada	—	*OR793922*	*OR793922*	*OR829821*	*OR829861*
H. americanum (EON1)	ON, Canada	DAOM 241459	*PP786302*	*PP786302*	*PP793770*	*PP793775*
Hericium asiaticum	China	CS-4[1]	SZZO02000036	SZZO02000036	SZZO02000036	SZZO02000036
H. asiaticum	Taiwan	Strain 0605[1]	—	—	JABWEG010000004	JABWEG010000004
H. asiaticum (HE9)	Japan	DAOMC195739	*OR793950*	*OR793950*	*OR829849*	*OR829889*
Hericium carolinense (HE1)	PA, USA	DAOMC251029	*OR793939*	*OR793939*	*OR829838*	*OR829878*
H. carolinense (HE2)	MD, USA	DAOMC251034	*OR793940*	*OR793940*	*OR829839*	*OR829879*
H. carolinense (HE3)	MD, USA	DAOMC251033	*OR793941*	*OR793941*	*OR829840*	*OR829880*
H. carolinense (HE4)	GA, USA	DAOMC251031	*OR793942*	*OR793942*	*OR829841*	*OR829881*
H. carolinense (HE6)	PA, USA	DAOMC251030	*OR793943*	*OR793943*	*OR829842*	*OR829882*
Hericium cirrhatum	Germany	TUB F794	AF506385	AF506385	—	—
H. cirrhatum (HCi1)	AB, Canada	UWO-F1892	*PP786306*	*PP786306*	*PP793774*	*PP793777*
Hericium coralloides	China	tvtc0002[1]	QUOP01000211	QUOP01000211	QUOP01000211	QUOP01000211
H. coralloides (HC2)	ON, Canada	UWO-F1481	*OR793924*	*OR793924*	*OR829823*	*OR829863*
H. coralloides (HC6)	ON, Canada	RGT 230902/02	*OR793947*	*OR793947*	*OR829846*	*OR829886*
H. coralloides (HCNB)	NB, Canada	RGT 220816/29	*OR793944*	*OR793944*	*OR829843*	*OR829883*
H. coralloides (HCX1)	MI, USA	DAOMC251025	*OR793930*	*OR793930*	*OR829829*	*OR829869*
H. coralloides (HCX3)	VA, USA	DAOMC251017	*OR793931*	*OR793931*	*OR829830*	*OR829870*
H. coralloides (HCX4)	England	DAOMC22531	*OR793946*	*OR793946*	*OR829845*	*OR829885*
H. coralloides (HCX5)	ON, Canada	DAOMC251022	*OR793945*	*OR793945*	*OR829844*	*OR829884*
H. coralloides (HD1)	Czech Republic	DAOMC251013	*OR793951*	*OR793951*	*OR829850*	*OR829890*
Hericium erinaceus (HE7)	Netherlands	CBS 202.31	*OR793948*	*OR793948*	*OR829847*	*OR829887*
H. erinaceus (HE8)	England	DAOMC251032	*OR793949*	*OR793949*	*OR829848*	*OR829888*
H. erinaceus (WCHE)	N/A	Commercial strain	*OR793923*	*OR793923*	*OR829822*	*OR829862*
Hericium oregonense (EBC1)	BC, Canada	DAOM 193728	*PP786303*	*PP786303*	*PP793771*	*PP793776*
H. oregonense (EBC2)	BC, Canada	DAOM 193896	*PP786304*	*PP786304*	*PP793772*	—
H. oregonense (EBC3)	BC, Canada	DAOM 185101	*PP786305*	*PP786305*	*PP793773*	—

[1] Whole genome sequence (WGS) data.
[2] Koga & Thorn culture code.
[3] Accession numbers in *italics* for sequences generated in the present study.

iterative G-INSi algorithm and aligning gappy regions invoked. Alignments were manually improved and forward and reverse primers trimmed in MEGA v. 11 (Tamura *et al.* 2021). Maximum likelihood analyses of each gene region were conducted individually using IQ-TREE v. 3 (Wong *et al.* 2025) with 10000 ultrafast bootstrap replicates (Hoang *et al*. 2018), with the best evolutionary model chosen using ModelFinder (Kalyaanamoorthy *et al*. 2017) (Figs S2–S5). The trimmed and aligned sequences of ITS–LSU, *RPB2*, and *TEF-1α* were concatenated and used to generate a phylogenetic tree using Maximum Likelihood with 10000 ultrafast bootstrap replicates and optimal partition merging (MF+Merge; Chernomor *et al.* 2016) in IQ-TREE v. 3 (Fig. 1). Genetic distances (base substitutions per site) within and between species across the ITS, LSU, *TEF-1α* and *RPB2* dataset were calculated in MEGA v. 11 and summarized in Table 2.

A separate analysis of just the ITS region, using every *Hericium* sequence available in GenBank and UNITE databases, was conducted to determine if any previously named sequences matched any of our proposed new taxa. Name queries in Entrez (https://www.ncbi.nlm.nih.gov/nuccore) and UNITE (https://unite.ut.ee/search.php) were supplemented with Blastn searches of each dataset to obtain all available matching sequences, which were then aligned in MAFFT, and maximum likelihood analyses conducted as described above (Fig. S1). All alignments and trees have been uploaded to Figshare (doi: 10.6084/m9.figshare.29295407).

Phylogenetic trees from IQ-TREE v. 3 were imported into Treeviewer (Bianchini & Sánchez-Baracaldo 2024), exported as pdf files and brought into Adobe Acrobat Pro 2020 to add italic font and labels, then brought into Adobe CS3 to set image size and resolution. Historic illustrations (all in the public domain except Fig. 2C; specific sources cited below) were acquired into Photos v. 8 to adjust brightness and contrast, then these and photographs of specimens in the field were brought into Adobe Photoshop CS3 to set the image size and resolution and apply figure dividing lines and labels.

RESULTS

Phylogeny of *Hericium*

A comprehensive phylogenetic analysis of all available ITS sequences (Fig. S1) provided strong support for the *Hericiaceae* (100 %) and the monophyly of the genera *Dentipellis* (99 %) and *Hericium* (99 %) as well as for some named and unnamed species-level clades within these genera: *H. abietis* (99 %, mostly from Canada: BC, plus MK463636 as *H. erinaceus* from USA: CA; and a distinct sister clade with 99 % support, apparently from China), *H. bembedjaense* (99 %), *H. cirrhatum* (100 %), *H. novaezealandeae* (98 %, including JQ716934 from Argentina and OP558598 from Chile), *H. opheliae* (97 %), *H. rajchenbergii* (100 %), and *H. yumthangense* (96 %, from China and India). In contrast, the type species *H. coralloides* was not supported as monophyletic but formed a paraphyletic grade that included the sequence of the epitype specimen near the base of *Hericium*, but an unnamed sister clade (100 %) included sequences identified as *H. coralloides* from Canada (NB, BC), USA (AZ, AK), Russia, Sweden, Ukraine, and several

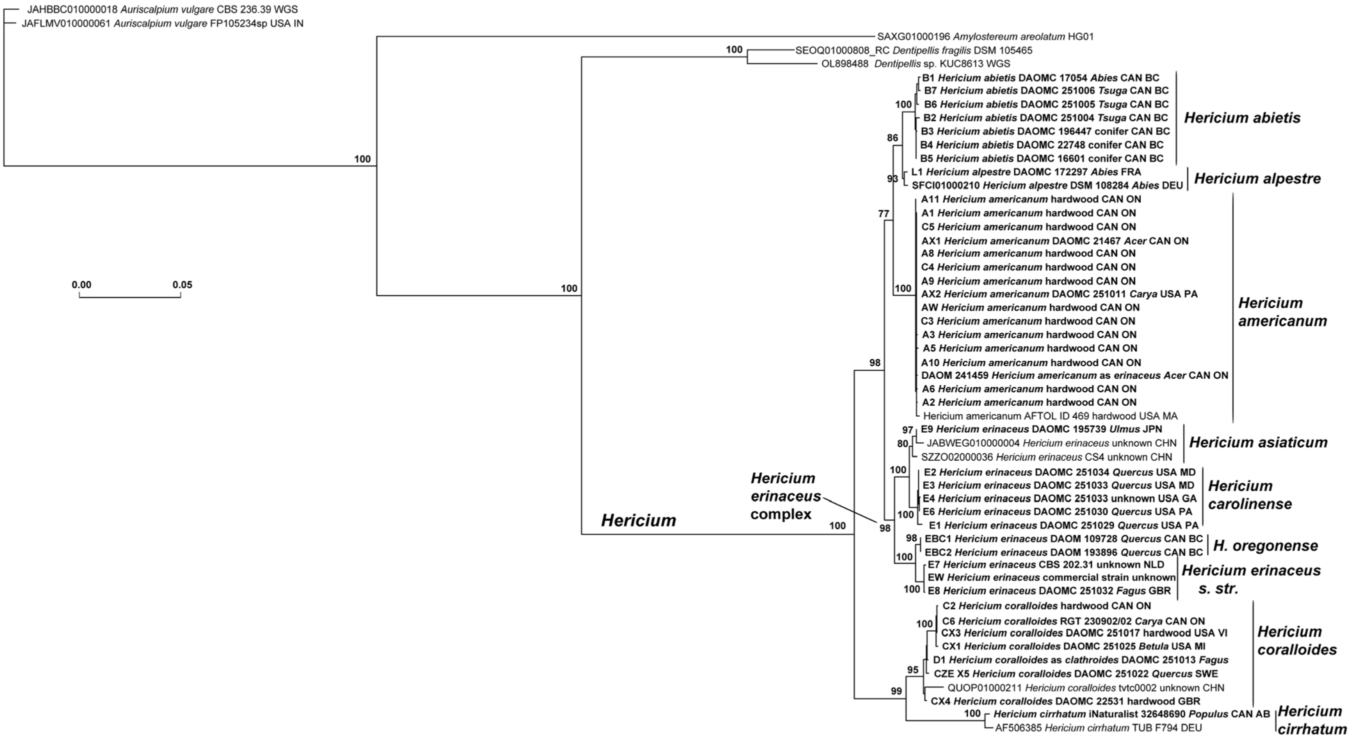

Fig. 1. Maximum likelihood tree based on concatenated sequences of the nuclear ribosomal internal transcribed spacer region (ITS), adjacent 3'-end of the large ribosomal subunit (LSU), and portions of the translation elongation factor 1-alpha (*TEF-1α*), and the RNA polymerase second largest subunit (*RPB2*). Numbers at nodes represent support from 10000 ultrafast bootstrap replications run in IQ-TREE v. 3 (Wong *et al.* 2025). *Auriscalpium vulgare* was used as the outgroup. Ingroup taxa are labelled with lab code or GenBank accession, species name, voucher or culture number, host, three-letter country code, and two-letter state or province code for the United States and Canada; **bold** font indicates sequences determined in this study.

sequences without locality data. The species *H. alpestre* formed a grade at the base of the branch (93 %) leading to *H. abietis*, *H. americanum*, *H. yumthangense* and the *H. erinaceus* complex. Sequences labelled *H. americanum* were recovered as a grade at the base of the poorly supported branch leading to *H. abietis*, *H. yumthangense* and the *H. erinaceus* complex. The *H. erinaceus* complex was weakly supported (55 %) as monophyletic, but included several well-supported clades within it, including *H. erinaceus* sensu stricto (64 %) from Great Britain, Iran, Italy, Netherlands, Russia, Spain, and Tunisia as well as many without locality data, *H. bharengense* (100 %), an unnamed clade (100 %) from New Zealand, and what we refer to as *H. carolinense* (98 %) from Mexico and the USA (AR, AZ, GA, OH, MD, MO, PA, TN, VA, WI). Within *Dentipellis*, a number of species-level clades were well supported, including *D. fragilis* (100 %, Austria, China, Germany, and Russia), *D. parmastoi* (100 %, Thailand), *D. rhizomorpha* (93 %, China), *D. tasmanica*

L'HYDNE RAMEUX.

Hydnum ramoſum. Cette superbe espece est très rare; elle m'a été apportée deux fois du bois de Boulogne par M. Thuillier; elle vient sur la fin de l'automne dans les trous des plus vieux arbres... sa base charnue et pleine se divise et se subdivise en une quantité prodigieuse de rameaux diversement entrelacés et garnis dans presque toute leur longeur de pointes pendantes et plus ou moins alongées, les plus longues pointes se trouvent aux extrémités de chaque ramification; elles y sont réunies en forme de pinceau ou par petits paquets étagés et d'un très joli effet; sa poussiere seminale est blanche et extrêmement fine, elle s'echappe de tous les points de la superficie de chaque pointe C... la direction de ses rameaux est dabord verticale, mais ils prennent une certaine courbure à mesure quils se developpent

NB. Ce champignon est representé de grandeur naturelle fig. A. on voit fig. B une partie de rameau representée à la loupe ainsi qu'une pointe dessinée séparément fig. C.

L'HYDNE HERISSON.

Hydnum paraſiticum, acaulon, candido-flavicans, aculeis gradatim dependentibus, longiusculis.

Hydnum erinaceus. ce beau champignon nait des cicatrices des vieux chênes, est toujours dans une situation pendante, affecte le plus souvent une forme convexe, a dabord une couleur blanche et prend ensuite une teinte jaunâtre, il est composé d'une substance médullaire qui s'enfonce plus ou moins dans les cicatrices, d'une chair ferme qui donne naissance à une très grande quantité de piquans assés longs, amincis insensiblemt. en pointe, pendans tous parallelemt. et par gradation.

N. B. la fig. A le répresente dans son état de jeunesse la fig. B le répresente dans son plus bel état, il a quelque-fois 6 a 7 pouces de diametre.

Cette belle espece ma été communiqué par Mr. RICHARD qui en a fait la description.

Fig. 2. Lectotypes and other historic illustrations helping to establish the identities of key species in *Hericium*. **A.** The lectotype of *Hydnum coralloides* Scop., tab. 142 in Schaeffer (1763). **B.** The lectotype of *Manina flagellum* Scop., tab. 11 in Scopoli (1772a). **C.** *Hericium coralloides* (photo by A.H. Smith in The Michigan Botanist 12: 187; Harrison 1973b, fig. 5, as *H. ramosum*) – note the similarity in form to B. **D.** Tab. 64, fig. 2 from Micheli (1729), cited by Scopoli (1772b) and Fries (1821) as *Hydnum coralloides*. **E.** The lectotype of *Hydnum clathroides* Pall., plate K, fig. 3 (Pallas 1773). **F.** The lectotype of *Hydnum ramosum* Bull., Plate 390 in Herbier de la France, vol. 9 (Bulliard 1789). **G.** The lectotype of *Hydnum erinaceus* Bull., plate 34 in Herbier de la France, vol. 1 (Bulliard 1780).

(100 %, Australia), *Dentipellicula leptodon* (100 %, China and New Zealand), and two unnamed clades (100 % and 99 %) of sequences variously identified as *Dentipellis* sp., *Hericium* sp., or *H. alpestre* (South Korea, Taiwan, Vietnam, and without locality data).

Single-gene trees for the small group of isolates and taxa for which we were able to obtain ITS, LSU, *RPB2* and *TEF-1α* data are presented as Figs S2–S5. All provide strong support for *Dentipellis* (97–99 %) and *Hericium* (92–100 %). The type species, *H. coralloides*, is moderately supported (70–85 %) or forms a basal grade (LSU). *Hericium abietis* is consistently strongly supported as monophyletic (91–100 %), as is *H. americanum* (86–100 %). The *H. erinaceus* complex is supported as monophyletic by ITS (90 %) and *TEF-1α* (91 %) but is paraphyletic in LSU and *RPB2*. Within the *H. erinaceus* complex, ITS supports *H. erinaceus* sensu stricto (79 %) and *H. carolinense* (97 %) but unites *H. asiaticum* and *H. oregonense* (93 %); LSU similarly supports *H. erinaceus* s. str. (86 %) and *H. carolinense* (85 %) but leaves *H. asiaticum* and *H. oregonense* as paraphyletic; *RPB2* supports *H. carolinense* (98 %), weakly supports *H. asiaticum* (56 %), and unites *H. erinaceus* s. str. and the one strain of *H. oregonense* for which data were obtained (99 %); and *TEF-1α* supports *H. erinaceus* s. str. (100 %), *H. carolinense* (100 %), *H. asiaticum* (74 %) and *H. oregonense* (75 %).

The concatenated multigene tree yielded a well-supported *Hericiaceae* and *Hericium,* each with 100 % bootstrap support (bss) (Fig. 1). Seventeen representatives of *H. americanum* (including one identified as *H. erinaceus*), all of which originated from specimens growing on hardwood (*Fagus*, *Acer*, *Carya*) in eastern North America, formed a well-supported (100 % bss) clade that is sister to a branch (86 % bss) that includes the European conifer-dwelling species *H. alpestre* (93 % bss) and the conifer-dwelling species from western North America, *H. abietis* (100 % bss). Sister to all of these is a clade representing the *H. erinaceus* complex (98 % bss), subdivided into strains from Europe (100 % bss), western North America (98 % bss), Asia (80 % bss), and eastern North America (100 % bss). A collection of *H. cirrhatum* from Alberta clustered with the single ITS–LSU sequence of this species from Germany (100 % bss) and sister to *H. coralloides* from Europe, Asia, and North America (95 % bss), and both as sister to the remainder of the genus. Eight representatives of *H. coralloides* from Europe, Asia, and North America formed a clade with some internal geographic structure, with a clade of four isolates from Ontario and the eastern United States (100 % bss) subtended by a grade of isolates from Sweden, Czech Republic, China, and Great Britain. Genetic distances within the sequences we are calling *H. coralloides* had a broader range than intraspecific variation seen within other species of *Hericium*, namely up to 0.82 % compared to 0.00–0.22 % (Table 2). Interspecific distances ranged from lows of 0.31–0.48 % (*H. erinaceus* compared with *H. oregonense*), 0.46–0.54 % (*H. abietis* compared with *H. alpestre*), and 0.36–0.60 % (*H. asiaticum* compared with *H. carolinense*) to 3.01–3.64 % (*H. coralloides* s.l. compared with *H. erinaceus* s.str.) or 1.33–4.12 % (*H. americanum* compared with *H. cirrhatum*), with most species differing by approximately 1 %. The two species of *Dentipellis* included differed by 2.55 % and from all *Hericium* species by 3.41–9.47 % (Table 2).

Table 2. Interspecific and intraspecific genetic distances (%) in *Hericium* and *Dentipellis* for combined ITS, LSU, *TEF-1α* and *RPB2* markers, for isolates and sequences listed in Table 1.

Name (n)	*H. abietis*	*H. alpestre*	*H. americanum*	*H. asiaticum*	*H. carolinense*	*H. cirrhatum*	*H. coralloides*	*H. erinaceus*	*H. oregonense*	*Dentipellis* spp.
H. abietis (7)	0.02–0.22									
H. alpestre (2)	0.46–0.54	0.14								
H. americanum (17)	1.04–1.21	0.72–0.90	0.00–0.09							
H. asiaticum (3)	1.34–1.68	1.13–1.40	1.29–1.57	0.14–0.30						
H. carolinense (5)	1.40–1.56	1.25–1.34	1.31–1.50	0.36–0.60	0.00–0.16					
H. cirrhatum (2)	1.49–3.89	1.33–3.66	1.33–4.12	1.23–4.10	1.43–4.07	0.15				
H. coralloides (8)	2.64–3.09	2.49–2.90	2.74–3.40	2.79–3.47	2.84–3.32	1.10–2.82	0.00–0.82			
H. erinaceus (3)	1.48–1.60	1.35–1.38	1.20–1.33	1.10–1.43	1.20–1.31	1.38–3.94	3.01–3.64	0.02–0.06		
H. oregonense (2)	0.94–1.58	0.57–1.27	0.68–1.25	0.28–1.26	0.37–1.18	1.33–3.89	1.82–3.45	0.31–0.48	0	
Dentipellis spp. (2)	8.22–8.50	8.08–8.18	7.67–8.54	8.03–8.78	8.19–8.73	3.41–9.02	8.11–9.47	8.15–8.43	4.99–8.37	2.55

Taxonomy

Hericium abietis (Weir ex Hubert) K.A. Harrison, *Canad. J. Bot*. **32**: 1208. 1964. MB 331940. Fig. 3C, D.
Basionym: *Hydnum abietis* Weir ex Hubert, *Outline of Forest Pathology*: 305. 1931.

Typus: Holotype none; **USA**, Priest River, Idaho, on *Abies grandis*, 19 Sep. 1916, *R.J. Weir 9964* (**lectotype** BPI 261825, designated by Maas Geesteranus 1960); dupl. S-F15316.

Notes: Maas Geesteranus (1959, 1960) was uncertain whether this species was a synonym of *H. americanum* (as *H. coralloides*) or *H. coralloides* (as *H. ramosum*) but settled on the former. However, sequence data support *H. abietis* as a good species, closely related to *H. alpestre* of Europe and *H. americanum* of North America (Fig. 1). Detailed descriptions were provided by Harrison (1964, 1973b), and the species has been illustrated by Smith (1963, as *Hericium weirii*, nom. inval.), Bandoni & Szczawinski (1976, as *H. coralloides*), Tylutki (1979), Arora (1986), Trudell & Ammirati (2009), Desjardin *et al*. (2015), and MacKinnon & Luther (2021). This species occurs on coniferous wood, both of standing trees and fallen logs, in the Pacific Northwest, causing a heart rot of living trees (Hubert 1931). Observations from central and eastern Canada posted to iNaturalist.ca appear to be misidentifications of *H. americanum* or *H. coralloides*.

Hericium alpestre Pers., *Mycol. Eur*. (Erlanga) **2**: 151. 1825. MB 224021.

Typus: **Holotype** none; **neotype** designated by Hallenberg *et al*. 2013: **Romania**, Suceava region, Codrul Secular Slatioara, on a dead standing tree of *Abies*, 16 Oct. 1985, *N. Hallenberg*, NH 9161 (GB), GenBank accession JQ716936 (ITS).

Fig. 3. North American species of *Hericium*. **A.** *Hericium americanum*, on hardwood log, Point Pelee National Park, Ontario, RGT 230830/s.n. (UWO). **B.** *Hericium coralloides*, on fallen bitternut hickory (*Carya cordiformis*), London, Ontario, RGT 230902/02 (UWO). **C.** *Hericium abietis*, habitat, near Needle Peak, British Columbia, iNaturalist 176674507 (photo by D. Brayshaw). **D.** *Hericium abietis*, on standing conifer, near Needle Peak, British Columbia, iNaturalist 176674507 (photo by D. Brayshaw). **E.** Possibly *Hericium carolinense*, on standing soft maple (*Acer* sect. *Rubra*), near Caledonia, Ontario, iNaturalist 138570613 (photo by J. Brodeur). Another Ontario specimen on the same host that looked very similar and was tentatively identified by J.H. Ginns as *H. erinaceus* (DAOM 241459) proved to be *H. americanum* by sequence data (Fig. 1).

Notes: Hallenberg (1983, Hallenberg *et al*. 2013) mentioned the presence of what is possibly original material of the species in the Persoon herbarium in Leiden (L 910256–1300), but the packet has no other label data beyond the name. In the absence of original material or an illustration cited in the original description, the neotype designated by Hallenberg is compliant with the Code (Turland *et al*. 2018). Of the names that have been applied to this species, which is restricted to growing on fir (*Abies alba*) in southern and central Europe north to the Netherlands (Laessoe & Petersen 2019), *H. alpestre* is the only one that can reliably be associated with this conifer-dwelling species, as previously indicated by Hallenberg (1983, Hallenberg *et al*. 2013). The basionyms of both *H. clathroides* and *H. flagellum* are more likely to apply to the hardwood inhabiting species correctly known as *H. coralloides*, as suggested by their original descriptions and illustrations, discussed below, highlighting short spines on long, open branches. *Hericium alpestre* is well-supported in our multilocus phylogeny (Fig. 1) as a sister taxon to *H. abietis*, the conifer-dwelling species of the Pacific Northwest (above), and these two as sister to the North American, mostly hardwood-dwelling species *H. americanum*. Basidiospores of all three species are larger than those of *H. coralloides*, and the basidiocarps are more compact or densely branched, with shorter branches with longer spines at their tips. Basidiocarps of *H. alpestre* develop pinkish staining in age, as do *H. americanum* and *H. abietis*, whereas tips of *H. coralloides* turn brown in age. *Hericium yumthangense* is a member of this species group, of which six sequences including that of the type formed a distinct and well-supported clade (96 % bss) in our comprehensive ITS tree (Fig. S1).

Hericium americanum Ginns, *Mycotaxon* **20**(1): 43. 1984. MB 106862. Fig. 3A.
Misapplication: *Hericium coralloides* auct. N. Amer. (e.g., Harrison 1973b, Smith & Smith 1973).

Typus: **USA**, Pennsylvania, on *Platanus*, 5 Nov. 1931, *J.W. Sinden*, L.O. Overholts 14844 (**holotype** PAC), ex-type culture preserved as DAOMC 2167.

Notes: The species was briefly described by Ginns (1984) when differentiated from *H. coralloides* by mating tests, and described in full by Harrison (1973b, as *H. coralloides*). It occurs on wood of diverse hardwoods, and rarely on wood of conifers (*Tsuga*), mostly in eastern North America, east to Nova Scotia (Harrison 1973b, Pomerleau 1980, as *H. coralloides* and *H. abietis*, Ginns 1984); records on iNaturalist from the West appear to be misidentifications of *H. coralloides*. It is certainly the most common species in Ontario. *Hericium botryoides*, growing on living trunks of *Quercus myrsinifolia* in Nara, Japan, was described as cauliflower-like, with 5–10 mm spines covering the surface of multiple globular outgrowths of a solid core, salmon pink or light orange yellow in colour, with non-amyloid basidiospores 4.5–6.5 × 4.5–6.0 µm (Otani 1957). The type collection and recent collections should be examined and sequenced to determine the correct disposition of this species, which seems most like *H. americanum* but might be quite unrelated. Harrison (1973a) has similarly raised the possibility that two species of the "*H. coralloides*" group occur on hardwood substrates in Europe as they do in North America, citing a specimen from *Fagus* in Hungary with spores 5.0–6.2(–6.8) × 4.8–5.6(–6.4) µm, matching the spore size of what Harrison knew as *H. coralloides* (now *H. americanum*). It is hard to imagine how a vicariant of *H. americanum* could have been overlooked in both Europe and Asia, except perhaps because the mature, undisturbed deciduous forests supporting their growth and fruiting are now rare (Harrison 1973b).

Hericium asiaticum Koga & Thorn, *Index Fungorum* **569**: 1. 2023. MB 850907.

Typus: **Japan**, Horoiwayama, Saroma-cho, Tokoro-gun, Hokkaido, on fallen hardwood log, 27 Sep. 1984, *I. Ohira, N. Maekawa & E. Nagasawa* (**holotype** TMI-8380). A culture derived from this collection (TMIC-30293) was sent to Ottawa for study by J.H. Ginns and is maintained there as DAOMC 195739.

Basidiomata ovate to globose, 5–10 cm broad, white at first, yellowing with age and becoming brown when dried, the upper surface roughened-hispid, the lower surface composed of spines 1–5 cm long, 1–2 mm thick at their base and tapering to needle tips, with solid, spongy white flesh. *Gloeocystidia* present, up to 7.5 µm broad. *Basidiospores* subglobose, smooth, amyloid, 6.5–7.5 × 5.0–5.5 µm. On beech, oak, and chestnut, causing a white rot (Teng 1963, Imazeki *et al*. 1988, Imazeki & Hongo 1989).

Notes: We are not aware of any characters of macro- or micromorphology that differentiate the members of the *H. erinaceus* species complex, which includes *H. erinaceus* s. str., *H. asiaticum*, *H. carolinense*, and now *H. oregonense*, and mating tests by Ginns (1985) indicated that strains which he identified as *H. erinaceus* from Europe, eastern North America and Asia were all interfertile. Unfortunately, neither we nor Ginns (1985) had living material available of the population of *Hericium erinaceus* occurring on the West Coast of North America, which we describe as *H. oregonense*. Nonetheless, since sequences from the four geographic regions form mutually monophyletic clades, we feel that it is worthwhile distinguishing all these entities at the species level to allow precise designation of the subjects of study by mushroom cultivators, biochemists, and medical researchers. Only ITS sequences are available for *Hericium rajendrae*, described from a living tree of *Quercus* in Uttarakhand state in northern India (Singh & Das 2019) and *H. bharengense*, described from *Tsuga* in the Sikkim region of northern India (Das *et al*. 2011) and these are placed in the *H. erinaceus* complex without strong resolution (Fig. S1). Multilocus sequence data from type or authentic material of these species are desirable.

Hericium carolinense Koga & Thorn, *Index Fungorum* **569**: 1. 2023. MB 850975. Fig. 3E.

Typus: **USA**, Laurel, Maryland, on *Quercus* in oak stand, 21 Nov. 1965, *J. Lindsay*, O.K. Miller, Jr 3766 (**holotype** VPI-F-0001744). A culture derived from this collection (OKM 3766-S) was sent to Ottawa for study by J.H. Ginns and is maintained there as DAOMC 251033.

Basidiomata ovate to globose, sometimes lobed, up to 25 cm broad, white at first, then yellowing in age and browning when dry, the upper surface a coarsely matted tangle of mycelial strands, the lower portion composed of spines up to 4 cm long, tapering to needle tips, with soft, solid to porous white flesh. *Gloeocystidia* arising in subhymenium, up to 7 µm broad. *Basidiospores* subglobose, amyloid, smooth to finely roughened (finely ridged under SEM, Pegler & Young 1972, referring to *H. erinaceus* s. str.), 5.5–6.8 × 4.5–5.6 µm. Usually growing from cracks or knot holes in living trees, recorded on *Quercus*, *Fagus*, *Platanus*, and *Acer* (Harrison 1973b).

Notes: Neither Harrison (1973b) nor Ginns (1985) knew of any confirmed records of this species from Canada. Some recent observations from southern Ontario posted to iNaturalist.ca appear plausible (e.g., Fig. 3E), but none are substantiated with a specimen or by DNA sequence data. One specimen in DAOM from Ontario annotated by Ginns as *H. erinaceus* was sequenced in this study and proved to be *H. americanum*. Below, we describe another vicariant of the *H. erinaceus* complex, on *Quercus garryana* from southern British Columbia, as a new species *H. oregonense*. Phylogenetic analyses of available ITS sequence data yielded a clade corresponding to *H. carolinense* (98 % bss) from Mexico and the USA (AR, AZ, GA, OH, MD, MO, PA, TN, VA, WI).

Hericium cirrhatum (Pers.) Nikol., *Acta Inst. Bot. Acad. Sci. USSR Plant. Crypt*., Ser. II **6**: 343. 1950. MB 298405. Fig. 4.
Basionym: *Hydnum cirrhatum* Pers. [as ‘*cirratum*’], *Neues Mag. Bot*. **1**: 109. 1794, nom. sanct., Fr., *Syst. Mycol*. **1**: 411. 1821.
Synonym: *Creolophus cirrhatus* (Pers.) P. Karst., *Meddn. Soc. Fauna Flora Fenn*. **5**: 42. 1879.

Fig. 4. *Hericium cirrhatum*, on dead standing *Populus tremuloides*, near Last Lepine, Saskatchewan, iNaturalist 95907531 (photo by M. Delorme). Note the fine spines on the upper surface of the dimidiate-imbricate basidiocarps, as well as the longer spore-bearing spines on the underside.

Typus: Holotype none; no material or plates were cited that could be available for lectotypification. A well-documented recent specimen from the collecting areas of Fries or Persoon should be designated as neotype.

Description (microscopic details from Harrison 1984): *Pilei* uniformly white to cream when fresh, drying grey to brown, compound, imbricate, segments broadly triquetrous to applanate, 3–10 cm broad by 1–4 cm thick at the base, surface dry and rough, usually with distinct fine spines at least toward the acute margin; lower surface covered with fine to coarse spines, terete to flattened and sometimes branched; context soft and white, sometimes drawn out into a pseudostipe to 5 × 3 cm. *Basidiospores* white, amyloid, broadly ellipsoid to oval, smooth, 4.0–4.5(–4.8) × 3.2–3.5(–4.0) µm; context and hymenium inamyloid, hymenium mostly of gloeocystidia that originate deep in the context, 6–8 µm broad.

Notes: This species, which in Europe is known mostly from *Fagus*, occurs rarely in boreal and montane North America on *Populus* (Harrison 1984; records from iNaturalist.ca), but until now there were no sequences from any North American material. Whether this is the same as the European species remains an open question with our small sample size. We were fortunate to receive a voucher of an observation published on iNaturalist.ca from northern Alberta (iNaturalist 32648690), from which we were able to get high-quality ITS-LSU, *TEF-1α* and *RPB2* sequence data, making this the first sequence-confirmed record of the species from North America and the first published record of the species in Canada. Good quality photographs of this highly distinctive species support additional observations from New Brunswick (iNaturalist 89219181, 142821513), Saskatchewan (iNaturalist 95907531, 124501128), and Alberta (iNaturalist 175651143, 179090349, 183457588, 184213002).

Hericium coralloides (Scop.) Pers., *Neues Mag. Bot*. **1**: 109. 1794. MB 120231. Fig. 2A, C, D, 3B.
Basionym: *Hydnum coralloides* Scop., *Fl. Carniol*., Edn. 2 (Wien) **2**: 472. 1772, nom sanct., Fr., *Syst. Mycol.* **1**: 408. 1821.

Typus: **Holotype** none; **lectotype** designated here (MBT 10016573): Schaeffer, Fung. Bavar. Palat. Nasc. (Ratisbonae) 2: tab. 142 (1763), specifically, the copy in the Bayerische Staatsbibliothek München, posted online as https://commons.wikimedia.org/wiki/File:Hericium_coralloides_(Schaeffer,_1763).jpg (Fig. 2A). A neotype designated by Hallenberg (1983) is not Code compliant because of the existence of original icons. We hereby designate as **epitype** (MBT 10016816) the collection NW-FVA 2023-90-2, **Germany**, Ederseerandstrasse, 34513 Waldeck, Hesse, 51.20110° N, 9.06083° E, on rotten log of *Fagus sylvatica*, in mixed old growth forest with *Fagus sylvatica, Quercus petraea,* and *Carpinus betulus*, 28 Aug. 2023, *G. & E. Langer* (TUB).

The highly branched basidiocarps with fine short spines lining the lower sides of the branches, and the small basidiospores are diagnostic for this species. Micheli (1729) illustrated this species (as tab. 64, fig. 2; Fig. 2D), and was perhaps the first to introduce the confusion among the branched species of *Hericium* occurring in Europe on hardwoods (this species) and fir (*H. alpestre*), since he listed the hosts of the species illustrated in tab. 64, fig. 2 as *Ilex, Morus, Fagus,* and *Abies*. This confusion was not solved for over 250 years (Hallenberg 1983). This species is most common on hardwoods, but collections from coniferous wood in Europe are known. The distribution extends across Eurasia and in North America extends from the island of Newfoundland west to the Yukon, British Columbia and California (Harrison 1973b, Tylutki 1979, Pomerleau 1980, Ginns 1984, 1985, Arora 1986, Schalkwijk-Barendsen 1991, Hallenberg *et al*. 2013, Desjardin *et al*. 2015, this study), although some distinct taxa may be included as suggested by ITS sequence data (Fig. S1).

Possible synonym: ***Hericium clathroides*** (Pall.) Pers., *Comm. Fung. Clav*. (Lipsiae): 23. 1797. MB 438438. Fig. 2E.
Basionym: *Hydnum clathroides* Pall., *Reise Prov. Russ. Reichs* **2**(2): 744. 1773, nom. sanct., Fr., *Syst. Mycol*. **1**: 409. 1821.

Typus: Holotype none; **lectotype** designated here (MBT 10016572): Pallas, Reise Prov. Russ. Reichs 2(2): tab. K, fig. 3 (1773) (Fig. 2E).

Notes: *Hericium clathroides* has been listed in the synonymy of *H. coralloides* (Stalpers 1996), or as the correct name for that species (Maas Geesteranus 1959, 1971). Pallas' specimen was found on wood in coniferous forest ("*in Pineto*") near the Ob River in central Siberia (Pallas 1773). However, there are multiple observations on iNaturalist of typical *H. coralloides*, often on *Betula*, from this region and the only observation on iNaturalist from Russia labelled *H. alpestre* is on *Abies* in the Ussuri region of far eastern Siberia. The illustration by Pallas (1773, Fig. 2E) is a better match for *H. coralloides* than *H. alpestre*. A collection from the Tomsk or southern Krasnoyarsk regions of Russia should be selected as epitype. Although the basionyms of both *H. coralloides* and *H. clathroides* were sanctioned by Fries (1821), *Hydnum coralloides* Scop. (1772b) is one year older than *Hydnum clathroides* Pall. (1773), so it has priority if the two are synonyms. However, a comprehensive phylogeny based on ITS data (Fig. S1) indicates considerable variation within *H. coralloides* as we are recognizing it. There is a well-supported, basal subclade (100 %) that includes sequences identified as *H. coralloides* from Canada (NB, BC), USA (AZ, AK), Russia, Sweden, Ukraine, and several sequences without locality data; should this prove to be specifically distinct through further study, the name *Hericium clathroides* may be suitable for it.

Synonym: ***Hericium flagellum*** (Scop.) Pers., *Comm. Fung. Clav*. (Lipsiae): 25. 1797. MB 469436. Fig. 2B.
Basionym: *Manina flagellum* Scop., *Diss. Sci. Nat., Edn*. **1**: 97 (1772a) (not sanctioned by Fries).

Typus: Holotype none; **lectotype** designated here (MBT 10016818) Scop., Diss. Sci. Nat., Edn 1: tab. XI (1772a) (Fig. 2B); **epitype** designated here (MBT 10016819): **Germany**, Ederseerandstrasse, 34513 Waldeck, Hesse, 51.20110° N, 9.06083° E, on rotten log of *Fagus sylvatica*, in mixed old growth forest with *Fagus sylvatica*, *Quercus petraea*, and *Carpinus betulus*, 28 Aug. 2023, *G. & E. Langer*, NW-FVA 2023-90-2 (TUB).

Notes: The original description and illustration emphasized the highly branched nature of the basidiocarp, with spines lining the undersides of the branches, characteristics of *H. coralloides* (Fig. 2C), not *H. alpestre*. The choice of epitype, above, fixes this name as an obligate synonym (typonym) of *H. coralloides*.

Synonym: ***Hericium ramosum*** (Bull.) Letell., *Hist. Descr. Champ*. (Paris): 43. 1826. MB 356813. Fig. 2F.
Basionym: *Hydnum ramosum* Bull., *Herb. Fr.* **9**: pl. 390. 1789.

Typus: Holotype none; **lectotype** Bulliard, Herb. Fr. 9: pl. 390, 1789 (designated by Harrison 1973b) (Fig. 2F).

Notes: Bulliard (1791) expressly stated that *H. ramosum* was a synonym of *H. coralloides*, citing the same plate by Schaeffer as had Scopoli (1772b), and Fries (1821) agreed, thus designation of an epitype to settle the application of the name is unnecessary, since this same plate is now the lectotype of *H. coralloides*.

Hericium erinaceus (Bull.) Pers., *Comm. Fung. Clav*. (Lipsiae): 27. 1797. MB 356812. Fig. 2G.
Basionym: *Hydnum erinaceus* Bull., *Herb. Fr*. (Paris) 1: pl. 34. 1780, nom. sanct., Fr., *Syst. Mycol.* **1**: 407. 1821.

Typus: Holotype none; **lectotype** designated here (MBT 10016574): Bulliard, Herb. Fr. (Paris) 1: pl. 34 (1780) (Fig. 2G). A neotype designated by Hallenberg (1983) is not Code compliant because of the existence of an original icon, but the same or another specimen could be designated as epitype if desired.

Notes: This species appears to be restricted to Western Europe, where it occurs on *Fagus* and *Quercus* (Hallenberg *et al*. 2013; this study). We recognize vicariants in eastern North America (*H. carolinense*), western North America (*H. oregonense*) and Asia (*H. asiaticum*) as distinct species, albeit morphologically indistinguishable and mating compatible (Ginns 1985).

Hericium oregonense Koga & Thorn, ***sp. nov***. MB 854007.

Etymology: (Latin) of the oregonian ecoregion where the host, *Quercus garryana* (and other *Quercus* species further south to California) lives.

Typus: **Canada**, Oak Bay, Vancouver Island, British Columbia, (approximately 48.45 N, 123.31 W), on *Quercus garryana*, 8 Nov. 1984, *R.S. Hunt & A. Funk* (**holotype** DAOM 193728), (**isotype** DAVP 23114), ITS-LSU sequence PP786303.

Basidiomata ungulate to globose, 5–20 cm broad, white at first, becoming creamy yellow, the upper surface roughly hairy and becoming brown in age, the lower surface composed of spines 1–6 cm long, 1–3 mm thick at their base and tapering to needle tips, white when young but discolouring yellow or orange brown, with solid, fibrous-spongy white flesh, especially tough towards base. *Gloeocystidia* present, up to 7 µm broad. *Basidiospores* broadly elliptical to subglobose, smooth to finely roughened, amyloid, 5.0–6.5 × 4.0–5.5 µm.

Ecology and distribution: On *Quercus garryana*, presumably causing a white rot, coastal southern Vancouver Island, the Gulf Islands and dryer portions of the Lower Mainland of British Columbia, Canada, and apparently occurring on this and other species of *Quercus* as well as introduced *Eucalyptus* further south through coastal Washington, Oregon and California in the United States based on published and iNaturalist records as *H. erinaceus* (Harrison 1973b, Arora 1986, Desjardin *et al*. 2015, Siegel & Schwarz 2016, MacKinnon & Luther 2021). Good macroscopic illustrations of the species are included in the last four references listed, as well as on iNaturalist, e.g., https://inaturalist.ca/observations/159175505, https://inaturalist.ca/observations/15113648, and https://inaturalist.ca/observations/140082243.

Notes: We are not aware of any characters of macro- or micromorphology that reliably differentiate the members of the *H. erinaceus* species complex, which includes *H. erinaceus* s. str*., H. asiaticum*, *H. carolinense*, and *H. oregonense*. The spines of *H. oregonense* may be slightly longer than those of *H. carolinense*, and its spores slightly smaller than those of *H. asiaticum*, but these details should be confirmed on a larger sample. To our knowledge, there are no publicly available cultures of this species, nor studies of mating intercompatibility that have included strains of the *H. erinaceus* complex from western North America with strains from Europe, Asia or eastern North America. Nonetheless, since sequences (ITS, LSU, *TEF-1α*, and *RPB2*) from the four geographic regions form mutually monophyletic clades, we feel that it is important to distinguish these entities at the species level to allow precise designation of the subjects of study by mushroom cultivators, biochemists, and medical researchers. According to observations on iNaturalist, members of the *H. erinaceus* complex are relatively common across the southern United States, from Florida through Louisiana, Texas, Arizona, and California. A comprehensive analysis should be carried out of the genetic variation across the range of the complex in North America. Based on our small sample, the western *H. oregonense* is more closely related to European *H. erinaceus* s. str. than to *H. carolinense* of eastern North America.

DISCUSSION

The use of multiple loci in phylogenetic studies has become a valuable method for obtaining a stronger phylogenetic signal amongst closely related taxa where the use of the commonly used ITS region alone does not provide enough resolution to accurately delimit them to a satisfactory degree (Matheny 2005, Matheny *et al*. 2007, Carlson *et al*. 2014, Dong *et al*. 2022). Our comprehensive phylogeny of all available ITS sequences includes representatives of 13 named species and suggests several that may be undescribed, but lacks representation of the poorly known species *H. botryoides*, *H. clathroides*, *H. fimbriatum*, and *H. ptychogasteroides*, and multigene data are required to better place and distinguish species such as *H. bharengense*, *H. rajchenbergii*, *H. rajendrae*, and *H. yumthangense*. Such constraints have limited the understanding of global *Hericium* diversity as demonstrated by previous phylogenetic studies (Hallenberg *et al*. 2013, Jumbam *et al*. 2019, Cesaroni *et al*. 2019). The limited discrimination of species traditionally recognized through characters of morphology and mating compatibility (e.g., Hallenberg 1983, Ginns 1984, 1985), has raised concerns over accurate nomenclature and species delineation. The present multilocus analysis using sequence data from ITS, LSU, *TEF-1α* and *RPB2* provides a significant improvement in the resolution of interspecific variation of *Hericium* from North America, Europe, and Asia, and allows us to resolve some nomenclatural issues.

The maximum likelihood tree generated in this analysis resolves *Hericium* species into distinct, well-supported monophyletic clades and subclades. Sequences obtained from *Hericium americanum* are grouped together in a subclade with 100 % bss, consistent with Ginns' (1984, 1985) recognition of *H. americanum* based on interfertility tests using single-spore isolates. *Hericium abietis*, consisting of sequences obtained from specimens isolated from conifer wood (*Abies, Tsuga*) in western North America, is also well resolved with respect to the closely related *H. americanum* and *H. alpestre*. The name *Hericium alpestre* is used by some authors (Hallenberg 1983, Ginns 1985, Hallenberg *et al*. 2013), but others (Stalpers 1996, Laessoe & Petersen 2019, Kujawska *et al*. 2021, indexfungorum.org) place that name in synonymy with *H. flagellum*, an earlier name of very uncertain application. Above, we argue that the name *H. flagellum* applies to *H. coralloides*, not *H. alpestre*, and epitypification of both *H. coralloides* and *H. flagellum* with the same specimen makes it so. Several of these species are of conservation concern in Europe: in Great Britain, *H. coralloides* is listed as near threatened (Evans *et al*. 2006) or endangered (Smith *et al*. 2016), and in Czechia, *H. alpestre* (as *H. flagellum*) is listed as near threatened (Holec & Beran 2006, Kujawska *et al*. 2021).

Although the *H. coralloides* clade contains a relatively high degree of intraspecific variability with respect to other clades in our analysis, *H. coralloides* nevertheless forms a monophyletic grouping of sequences originating from specimens from North America, Europe, and Asia, all but one of which were isolated from hardwoods, consistent with the findings of Ginns (1985) of intercompatibility among isolates of *H. coralloides* from Europe and North America.

A collection of *Hericium cirrhatum* from Alberta clustered with the single available ITS-LSU sequence of *Hericium cirrhatum* from Germany and represents the first confirmed Canadian record of the species, previously known from Colorado and New Mexico in the United States (Harrison 1984). The Alberta collection also provides the first sequence data for North American material of this species, which is reported from boreal and montane regions of North America from New Brunswick to Alberta and south to New Mexico, and is associated with *Populus* (Harrison 1984, iNaturalist.com).

Our multilocus analysis clearly distinguishes four taxa within the *H. erinaceus* species complex delineated by geographic origin of the specimens. Prior works using single-gene sequence data (Hallenberg *et al*. 2013, Cesaroni *et al*. 2019) were suggestive of geographically isolated cryptic species within *H. erinaceus*. However, these studies did not display sufficient resolution of cryptic species from one another to formally establish novel species within the *H. erinaceus* complex. Although there are no apparent morphological differences between these four taxa that we are aware of, the mutually monophyletic clades obtained from multigene sequence data suggest a lack of genetic recombination among these populations (Taylor *et al*. 2000). This, together with the geographic separation, supports the recognition of four distinct species within the *H. erinaceus* species complex, two of which we recently proposed as new species, *H. carolinense* and *H. asiaticum* (Koga & Thorn 2023), and a third we describe here as *H. oregonense*.

Key to species of *Hericium* in North America, with comments on extralimital species

1a. Basidiocarps unbranched, either globular or dimidiate 2
1b. Basidiocarps branched 3

2a (1a). Basidiocarps ovate or globular, with coarsely hairy upper surface and lower surface with spines 1–5 cm long; basidiospores 5.5–6.8 × 4.5–5.6 µm .... *Hericium carolinense* (Fig. 3E)
[Morphologically identical species in western Europe, Asia and western North America are *H. erinaceus* s. str., *H. asiaticum*, and *H. oregonense*, respectively.]
2b. Basidiocarps dimidiate, often imbricate, thin-fleshed, with hispid to spinose upper surface and short spines on the lower surface; basidiospores 4.0–4.5(–4.8) × 3.2–3.5 (–4.0) µm (Harrison 1984); on dead aspens (*Populus*) in boreal-montane regions .... *Hericium cirrhatum* (Fig. 4)
[In Europe, this species is found primarily on *Fagus* and reported to have basidiospores 3.5–4.5 × 2.5–3.5 µm (Stalpers 1996).]

3a (1b). Basidiocarps massive, on wood of conifers (*Abies*, *Tsuga*) in the humid Pacific Northwest; basidiospores 4.5–5.5 × 4.0–4.5 µm (Harrison 1973b) .... *Hericium abietis* (Fig. 3C, D)
3b. Basidiocarps more highly branched, typically on hardwoods, widespread in North America 4

4a (3b). Basidiocarps with open, lacy branching, with short teeth (to 5 mm) along (beneath) the branches as well as at the tips; basidiospores 3.1–5.0 × 3.0–4.0 µm (Harrison 1973b) .... *Hericium coralloides* (Fig. 3B)
[This species also occurs across Eurasia, where it usually occurs on hardwoods, but rarely also on conifers.]
4b. Basidiocarps stockier, with short branches and longer teeth (to 1 cm); basidiospores 5.5–7.0 × 4.5–6.0 µm (Harrison 1973b) .... *Hericium americanum* (Fig. 3A)
[A similar and closely related species, *H. alpestre* (sometimes referred to as *H. clathroides* or *H. flagellum*) occurs on wood of conifers (*Abies*) in Europe; basidiospores are similarly (5.0–)5.5–6.5(–7.0) × 4.5–6.0(–6.5) µm (Stalpers 1996). For other similar species, see discussion above under *H. americanum*.]

Improved understanding of species delimitations and overall phylogeny in *Hericium* has potential economic consequences, especially with respect to the use of *H. erinaceus* s. l. in medicinal applications and in nutraceutical markets. In certain East Asian traditions, *H. asiaticum* (as *H. erinaceus*) is highly regarded as a medicinal mushroom and recent research evaluating specific bioactivity profiles of its secondary metabolites over the past thirty years has demonstrated a wide range of potential health promoting properties of these mushrooms (Kawagishi *et al*. 1994, 1996a, b, Suruga *et al*. 2015, Chen *et al*. 2017, Corana *et al*. 2019). These studies have increased research efforts in natural products discovery and have driven a growing demand for *H. erinaceus* s. l. supplement products globally (Thongbai *et al*. 2015). Additionally, several authors have discovered certain bioactive secondary metabolites originally isolated from *H. erinaceus* s. l. in other members of *Hericium* including *H. coralloides* (Saito *et al*. 1998, Wolters *et al*. 2015), *H. novazealandiae* (Chen *et al*. 2022), *H. alpestre* (Rupcic *et al*. 2018), and *Hericium* sp. WBSP8 (Song *et al*. 2020), which we determined as *H. americanum* according to ITS sequence data (Fig. S1). However, poorly defined species delineation in *Hericium* has led to misidentification of specimens used in biomedical and pharmacological studies, where researchers may characterize the biological effects of a specimen known to them by one name, but which is known to others as another. For example, Rupcic *et al*. (2018) evaluated the production of erinacines by *H. erinaceus* and *H. flagellum* but the latter name refers to *H. alpestre* or *H. coralloides,* depending on the species concept of the authors. Similarly, Suruga *et al*. (2015) evaluated the bioactivity of extracts of *H. erinaceus* and what they refer to as *H. ramosum*; again, the identity of the latter is uncertain although most likely *H. coralloides*. Multiple *Hericium* strains available from international culture collections are misidentified, listed under the identity provided by the supplier, just as is the case with sequences deposited to GenBank (Bidartondo 2008). For instance, CCBAS 654 and 837 are listed as *H. erinaceus*, but were collected on *Abies alba* and thus likely represent *H. alpestre*; whereas CCBAS 663 and 664 are listed as *H. coralloides* but are cultures of *H. abietis* (DAOMC 16601 and 22748), and CCBAS 662 is listed as *H. coralloides* but represents *H. americanum* (DAOMC 21467) (https://www.biomed.cas.cz/ccbas/fungi.htm). The problem is not new; in his studies of mating compatibility among *Hericium* strains, Ginns (1985) used two cultures sent to him by Nils Hallenberg as *H. alpestre* that later were identified as *Dentipellis fragilis* (Hallenberg *et al*. 2013). The origins of some *Hericium* strains for which sequences are available are not indicated in GenBank, with some appearing to be commercial strains from countries other than where the sequences were deposited from. We were fortunate that the majority of the strains we used in our phylogenetic analyses were wild-collected and assuredly native to the regions where they grew. However, in future, the phylogeography of *Hericium* species may be obscured if non-indigenous, cultivated strains escape into the wild, as has been documented recently for another cultivated mushroom, *Pleurotus citrinopileatus* (Bruce 2018). Given that there may not be barriers to interbreeding among closely related species from different continents, such escapes could also erode the genetic identities of indigenous species of *Hericium*. Evidently, misapplication of names of mushroom specimens used in pharmacological research may have consequences in future research and the present work seeks to firmly establish the nomenclatural status of *Hericium* species of high research interest. Additionally, discrimination of *H. erinaceus* s. str., *H. carolinense*, *H. oregonense*, and *H. asiaticum* may have potential consequences in supporting breeding programs for improved strain development, where mushroom growers may more accurately focus breeding strategies on certain lineages to achieve desirable phenotypes.

ACKNOWLEDGEMENTS

We thank T. Rintoul, Collection Manager, Canadian Collection of Fungal Cultures (Ottawa, Canada), for sending many of the cultures used in this study; J. Wilkinson, DAOM Fungarium Technician (Ottawa), for the loan of specimens; K. Mendola, Curatorial Assistant of UWO Herbarium, London, Canada, for managing these loans and new accessions; S. Dominick (Collections manager of BPI, Beltsville, MD, USA), I. Eichlerová (Curator of CCBAS, Prague, Czech Republic), S. Ekman (Uppsala University, Sweden), J. Holec (Herbarium PRM, Prague, Czech Republic), K.-H. Larsson (Natural History Museum, Oslo, Norway), and D.H. Pfister (Farlow Herbarium, Harvard, Boston, MA, USA), for email discussions of *Hericium* systematics, specimens, and icons; J. Brodeur, M. Delorme, and D. Brayshaw for permission to use their photos; and colleague R. Rajsp (University of Western Ontario) for the modification of *TEF-1α* primers (RR.EF1-983F and RR.EF1-1567R). RGT would especially like to thank N. Hallenberg and the late J.H. Ginns and K.A. Harrison, all of them mentors to him during his student years, and all of whom made great contributions to systematics of *Hericium*.

Data availability statement All new sequences generated in this work have been deposited to GenBank; ITS–LSU (OR793913–OR793952; PP786302–PP786306); *TEF-1α* (OR829812–OR829851; PP793770–PP793774); *RPB2* (OR829852–OR829891; PP793774–PP793777), and the trees and alignments were deposited in Figshare (doi: 10.6084/m9.figshare.29295407).

Declaration on conflict of interest The authors declare that there is no conflict of interest.

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SUPPLEMENTARY MATERIAL

Fig. S1. Comprehensive maximum likelihood tree of all available (Feb. 2025) ITS sequences of *Hericium* and close relatives. Numbers at nodes represent support from 10000 ultrafast bootstrap replications run in IQ-TREE v. 3 (Wong *et al*. 2025); highlighting indicates sequences obtained in this study and included in Fig 1.

Fig. S2. Maximum likelihood tree of ITS sequences of *Hericium* and close relatives, featuring just those individuals for which multigene data were available or obtained by us. Numbers at nodes represent support from 10000 ultrafast bootstrap replications run in IQ-TREE v. 3 (Wong *et al*. 2025); **bold** font indicates sequences determined in this study.

Fig. S3. Maximum likelihood tree of LSU sequences of *Hericium* and close relatives, featuring just those individuals for which multigene data were available or obtained by us. Numbers at nodes represent support from 10000 ultrafast bootstrap replications run in IQ-TREE v. 3 (Wong *et al*. 2025); **bold** font indicates sequences determined in this study.

Fig. S4. Maximum likelihood tree of *TEF-1α* sequences of *Hericium* and close relatives, featuring just those individuals for which multigene data were available or obtained by us. Numbers at nodes represent support from 10000 ultrafast bootstrap replications run in IQ-TREE v. 3 (Wong *et al*. 2025); **bold** font indicates sequences determined in this study.

Fig. S5. Maximum likelihood tree of *RPB2* sequences of *Hericium* and close relatives, featuring just those individuals for which multigene data were available or obtained by us. Numbers at nodes represent support from 10000 ultrafast bootstrap replications run in IQ-TREE v. 3 (Wong *et al*. 2025); **bold** font indicates sequences determined in this study.