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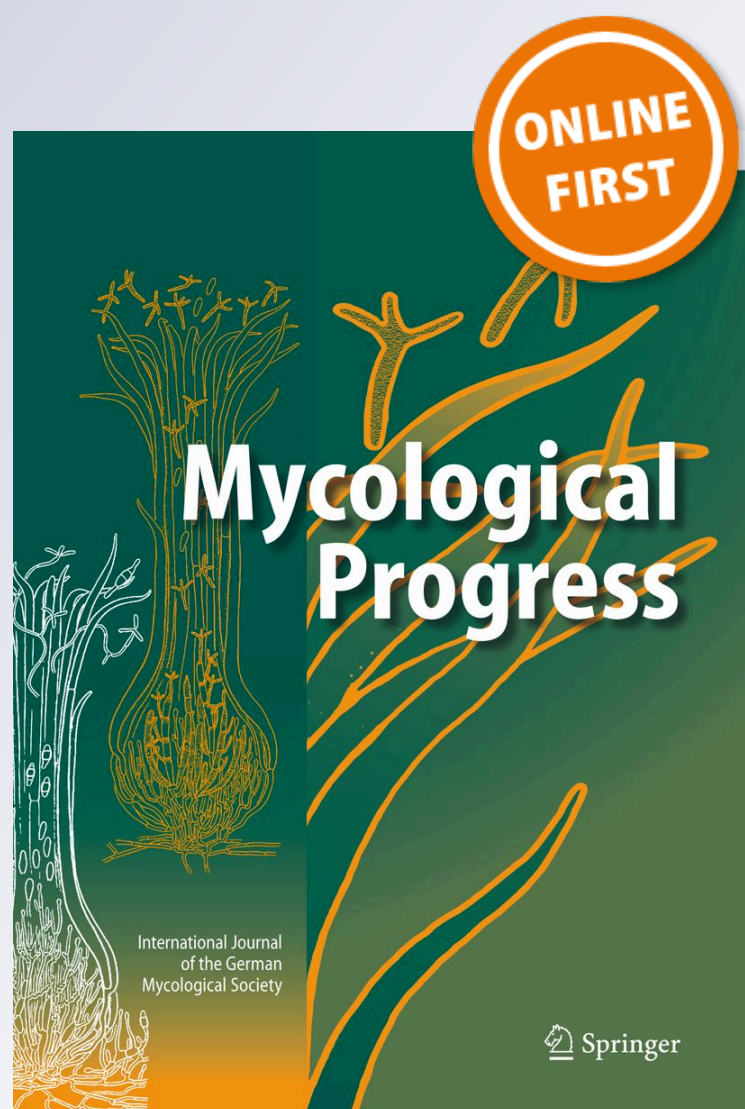
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Species complexes in *Hericium* (Russulales, Agaricomycota) and a new species - *Hericium rajchenbergii* - from southern South America

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Abstract Species of the genus *Hericium* are generally recognized by macro morphology of their basidiomes, while they are very similar in the microscope. As a result, species boundaries are not always clear, and many collections are subsumed under incorrect names. We report on a thorough phylogenetic analysis based on ITS sequences to clarify the application of the most common names in the genus. *H. alpestre*, *H. americanum*, and *H. erinaceus* cannot readily be distinguished by their ITS sequences alone, while they are kept separate by characters from substrate preferences, geographical distribution, and macro morphology. A neotype is selected for *H. alpestre*. A well supported clade includes *H. coralloides* together with other, unnamed taxa. One of these, *H. rajchenbergii* from Argentina, is here described as new to science.

Keywords *Hericium* · Cryptic species · ITS · Phylogeny · Morphology

Introduction

Hericium Pers. species have long attracted our attention because of their beautiful coral shaped basidiomes growing on wood. The species are edible but rare in nature and at

least one of them, *Hericium erinaceus* (Bull.) Pers., has been used for medical purposes (Pegler 2003; Mori et al. 2008).

The genus *Hericium* was described by Persoon (1794) with *Hericium coralloides* (Scop.) Pers. as the type, and only, species. The interpretation of *H. coralloides* has been under debate (Harrison 1973; Ginns 1985) because no original material was present and the only references were stylized icons. Hallenberg (1983) neotypified the species with material from Femsjö, Sweden, growing on *Fagus sylvatica* L., thus following the interpretation made by Fries, as a sanctioning author for name interpretations. A morphologically similar species is *H. alpestre* Pers., known from the European Alps and growing on *Abies* Mill. In their morphology the two species are similar but easily distinguished as *H. coralloides* has numerous teeth distributed over the surface of coralloid branches in a comb-like manner, while the teeth are grouped in bundles in *H. alpestre*. Moreover, the basidiospores are distinctly smaller in *H. coralloides*.

In North America, four species of the genus are known, but the species name *H. coralloides* has there been used for a different species, very similar to *H. alpestre*. After the neotypification of *H. coralloides*, the American counterpart was redescribed as *H. americanum* Ginns (Ginns 1984). No morphological differences could be found between *H. americanum* and *H. alpestre* but the former species is usually found on hardwood and seems to be restricted to NE North America (Ginns 1984).

Hericium species have been thoroughly investigated regarding morphology (Harrison 1973; Koski-Kotiranta and Niemelä 1988; Bernicchia and Gorjón 2010), incompatibility tests (Ginns 1985), DNA sequences (Larsson and Larsson 2003; Park et al. 2004), and ecology (reviewed in Boddy et al. 2010) but species delimitations are still far from being solved. The morphological differences between

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species are subtle, especially when the intraspecific variation is considered in light of specimens of different geographical origin and developmental stages. Several accessions reported to GenBank (Benson et al. 2012) seem to carry a wrong species name owing to incorrectly identified specimens.

The objectives of this study are to clarify species delimitations as far as possible in the genus *Hericium*, based on a phylogenetic analysis of ITS sequences, critical analysis of morphological characters, geographical distribution, and substrate preferences. The identity of *H. alpestre* is settled by neotypification, and a new taxon from Argentina is described.

Material and methods

Study and description of specimens Microscopic examinations and measurements were done in an Olympus BH2 phase contrast microscope, using Melzer's reagent and 3–5 % KOH as mounting media. Examined specimens are listed in Table 1 together with ITS sequences obtained for this study. An ITS sequence from the newly described species *Hericium bharengense* was kindly sent by Dr. U. Eberhardt, Utrecht. Herbarium acronyms are from Holmgren et al. (1990). In presenting the sizes of the microscopic elements of the new species, 5 % of the measurements were excluded from each end and are given in parentheses; \bar{x} = arithmetic mean of basidiospores; Q = the ratio of length/width of basidiospores; \bar{x}_Q = arithmetic mean of the ratio. Forty basidiospores were measured.

Molecular analysis Twelve new ITS sequences (nuclear r-DNA) were obtained from available FCUG-cultures (Fungal

Cultures of University of Gothenburg) as described in Hallenberg et al. (2006) and from CCC-cultures (Colección de Cultivos Córdoba) and herbarium material (CORD) at Laboratorio de Micología IMBIV-CONICET. For further details on the FCUG cultures, see Hallenberg (2011). In addition, 93 sequences from the species *Hericium abietis* (Weir ex Hubert) K.A. Harrison, *H. alpestre*, *H. americanum*, *H. coralloides*, *H. erinaceus*, *H. bharengense*, *Dentipellis fragilis* (Pers.) Donk, *D. leptodon* (Mont.) Maas Geest., and unclassified accessions found to belong to this group of species in BLAST searches (Altschul et al. 1997) in GenBank and *emerencia* (Nilsson et al. 2005) were included in the study. *Heterobasidion annosum* (Fr.) Bref. was used as outgroup given its proximity to *Hericium* in the Russulales (Larsson and Larsson 2003). The 105 sequences were aligned in MAFFT 6.864 (Katoh and Toh 2010), and the alignment was fine-tuned manually in SeaView 4.0 (Gouy et al. 2010). Bayesian phylogenetic analyses were carried out in MrBayes 3.0 (Ronquist and Huelsenbeck 2003), with a best-fit model of nucleotide evolution supplied by MrModeltest 2.2 (Nylander 2004). Eight default-setting Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains were run for 20 million generations with trees sampled every 10,000 generations and an initial burn-in of 50 %. After discarding the trees prior to the burn-in threshold, a 50 % majority-rule consensus phylogram was computed from the remaining 1,000 trees.

To get a better overview over the full phylogeny, 35 sequences from *H. erinaceus* were excluded, as this taxon was over-represented in the previous sampling. Using the same settings as in the full analysis we obtained a tree which did not differ in the topology and this reduced analysis is therefore presented here.

Table 1 List of specimens sequenced and examined. New accessions are given in bold typeface

Species	GenBank Accession N°	GenBank name	Collection N°-voucher/herb.	Origin	Substrate	Comments
<i>Hericium abietis</i>	JQ716938	<i>H. alpestre</i>	FCUG 2788-VC 63-12	Canada, BC	<i>Tsuga</i>	Can. For. Service
<i>H. abietis</i>	EU784259	<i>H. cf alpestre</i>	RGB K (M)107270-K	UK	<i>Pseudotsuga</i>	Sleeper wood
<i>H. alpestre</i>	JQ716936	<i>H. alpestre</i>	FCUG 1555-NH9161/GB	Romania	<i>Abies</i>	Selected neotype
<i>H. alpestre</i>	JQ716937	<i>H. alpestre</i>	FCUG 2408-NH12059/GB	Caucasus	<i>Abies</i>	
<i>H. alpestre</i>	JQ716930	<i>H. alpestre</i>	FCUG 2754-NH13240/GB	Caucasus	<i>Abies</i>	
<i>H. rajchenbergii</i>	JX403945	<i>H. rajchenbergii</i>	GR 1997-/CORD	Argentina	<i>Lithraea</i>	Holotype
<i>H. rajchenbergii</i>	JQ716939	<i>H. rajchenbergii</i>	GR 2041-/CORD	Argentina	<i>Lithraea</i>	
<i>H. coralloides</i>	JQ716934	<i>H. coralloides</i>	FCUG 3209-329/CIEFAP	Argentina	<i>Maytenus</i>	
<i>H. coralloides</i>	JQ716935	<i>H. coralloides</i>	FCUG 426-9923/LY	France	hardwood	
<i>Dentipellis leptodon</i>	JQ716932	<i>D. leptodon</i>	FCUG 2983-NH15350/GB	N. Zealand	hardwood	
<i>D. fragilis</i>	AY524580	<i>H. alpestre</i>	FCUG 407-NH4596/GB	Austria	<i>Abies</i>	
<i>D. fragilis</i>	JQ716931	<i>D. fragilis</i>	FCUG 2757-NH13243/GB	Caucasus	deciduous tree	
<i>D. fragilis</i>	JQ716933	<i>H. alpestre</i>	FCUG 392-NH4606/GB	Austria	<i>Abies</i>	
<i>D. fragilis</i>	JQ716929	<i>D. fragilis</i>	FCUG 2418-NH12031/GB	Caucasus	deciduous tree	

Results

The alignment consisted of 70 sequences and 626 base-pairs, 412 of which were constant, 66 variable but parsimony uninformative, and 148 (23 %) parsimony informative. As suggested by MrModeltest, the nucleotide evolution model HKY+G was used for the ITS1 and ITS2 spacers – and SYM+G for the intercalary 5.8S gene – in the Bayesian analysis. The MCMCMC analysis converged well in advance of the burn-in threshold and chain mixing was found to be satisfactory. The ingroup, identified as monophyletic with respect to the outgroup by the analysis, comprised two distinct, fully supported clades: *Hericium* and *Dentipellis* (Fig. 1). The *Hericium* clade features two subclades of very strong support: *H. coralloides* s.l. and *H. abietis*. In addition, *H. erinaceus* and *H. americanum* are found in several smaller subclades of weak to strong support. Eleven sequences, variously annotated as *H. alpestre*, *H. erinaceus*, and *H. americanum*, do not seem to belong in any of these three (Fig. 1). The origin of each accession has been traced regarding location and substrate as far as possible, but there are several uncertainties. Moreover, a few accessions quite obviously have been given an incorrect collection designation (indicated with “unknown origin” in Fig. 1).

The topology of the tree is discussed in relation to the most commonly used names in *Hericium*:

Hericium abietis

Hericium abietis constitutes a well supported clade (Fig. 1). The species produces big basidiomes on coniferous wood, and the spines are arranged in bundles like in *H. americanum* and *H. alpestre*. In the microscope it is distinguished by slightly smaller spores, 4.5–5.5×4–4.5 µm compared with 5.5–7×4.5–6 µm in *H. americanum*/*H. alpestre*. Its distribution seems to be confined to the NW parts of North America and NE China. One accession in GenBank, EU784259, was collected in UK on wood of *Pseudotsuga*, labelled *H. cf. alpestre*. It is conceivable that this wooden substrate (a sleeper) originated from Canada and that the wood was infected prior to its delivery to UK.

Hericium coralloides

The *H. coralloides* sensu lato species complex is strongly supported and comprises three taxa: *Hericium coralloides* sensu stricto, an unnamed but well-supported subclade with representatives from China and Canada, and a new species from Argentina. Morphologically, *H. coralloides* s. str. is recognized by having spines arranged singly on ventral and lateral sides of the

basidiome branches, like the teeth on a comb. Moreover, the spores are distinctly smaller than in other species in the genus (3.5–5×2.8–4 µm), and the basidia are narrower (3.5–5 µm). See Table 2 for comparisons.

In addition to the molecular differentiation (Fig. 1), the new species from Argentina also presents morphological differences that together with its particular substrate and distribution support the description of a new species:

Hericium rajchenbergii Robledo and Hallenb. **sp nov**
Fig. 2a, b, c, d and e

Mycobank: MB 564948

Holotype: Argentina, Córdoba province, Colón Department, Rio Ceballos, El cuadrado road, 31°7'30.8"S, 64°19'44.6"W, alt. 850 m a.s.l., on fallen log of *Lithraea molleoides*, 25. May.2009, leg. F. Quadri, *Robledo1997* (CORD).

Etymology: honouring the mycologist Dr. Mario Rajchenberg

Basidiome annual, solitary, repeatedly branched from a common base, laterally attached to the substrate, main branches 5–25 mm in diameter, fleshy, pale flesh-coloured pink when fresh, pale brown as dry or when bruised. Single spines are pending from the lower side of the branches in a comb-like manner, spines up to 10 mm long and up to 1 mm thick at the base, tapering. All basidiome more or less orbicular and coralloid, 10–12 cm; odor intense and pleasant when dry.

Hyphal system monomitic, generative hyphae clamped, up to 15 µm diam, thin- to thick-walled with walls up to 6 µm thick, occasionally solid, irregularly inflated. In the trama of spines hyphae are running parallel, amyloid in all parts of the basidiome. **Gloeocystidia** abundant, weakly sulfopositive, easily observed with phloxine, cylindrical to fusiform or acuminate, occasionally moniliform, terminating in the hymenium, variable in length, 3–5.0 µm wide and up to 65 µm in length. **Basidia** clavate, 17–22×4.5–5 µm, with four sterigmata and basal clamp. **Basidiospores** ellipsoid to broadly ellipsoid, with the ventral side slightly flattened, slightly thick-walled, minutely verrucose, (4.0)4.5–5.0(5.0)×(3.0)3.0–4.0(4.5) µm, $\bar{x} = 4.8 \times 3.7\mu\text{m}$, $Q = (1.1)1.1 - 1.5(1.7)$, $\bar{x}_Q = 1.3$, strongly amyloid.

Additional material ARGENTINA. Prov. Cordoba, Dpto. Punilla, Capilla del Monte, La higuera path, 30°51'32" S, 64°30'12"W, alt. 1,000 m a.s.l., on dead standing stem of *Lithraea molleoides*, 15. May.2010, leg. Robledo and Drechsler-Santos, *Robledo 2041* (CORD), Culture CCC70.

Ecology and distribution So far known growing on dead standing and fallen stems of *Lithraea molleoides* (Anacardiaceae), in the Chaco Serrano forests of central Argentina.

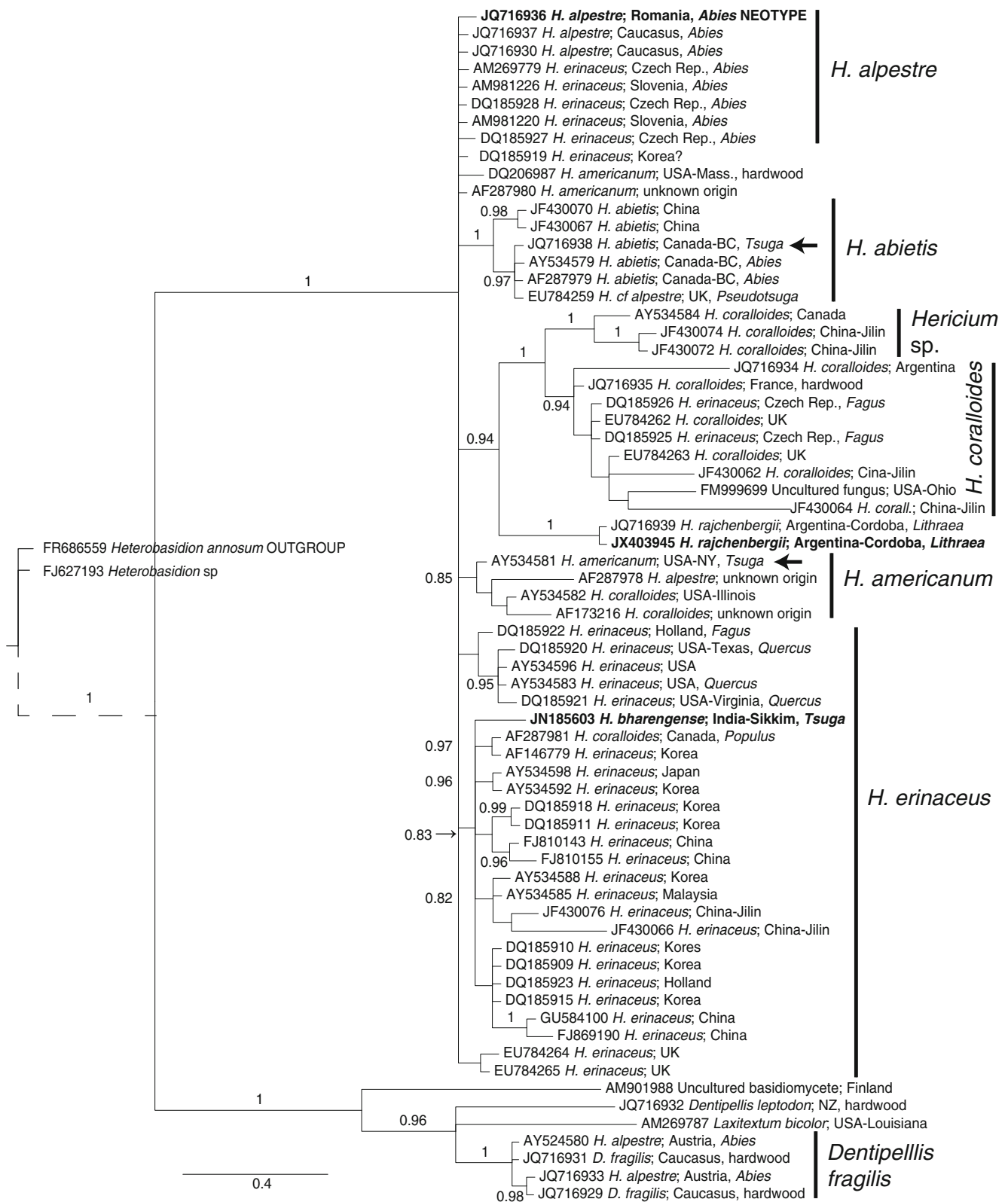


Fig. 1 Bayesian phylogram of the investigated samples. *Heterobasidion annosum* (GenBank FR686559) was used as outgroup. Bayesian Posterior Probabilities above 0.8 are given. The sequences indicated by an arrow in bold were used by Ginns (1985) for crossing tests

Culture characteristics Cultures growing at slow to medium rate, mats reaching 7 cm diam. at 6 weeks (Fig. 2c and

d). Mats plumose, downy, old mycelium velvety, with concentric growing zones and irregular margins; hyphae with

Table 2 A summary of diagnostic characteristics for *Hericium* species treated in this study

	<i>H. abietis</i>	<i>H. alpestre</i>	<i>H. americanum</i>	<i>H. bharengense</i>	<i>H. erinaceus</i>	<i>H. coralloides</i>	<i>H. rajchenbergii</i>
Arrangements of spines	Spines in bundles	Spines in bundles	Spines in bundles	Spines in bundles	Spines in bundles	Spines single, comblike	Spines single, comblike
Length of spines	<1 cm	<2 cm	0.5–1.5 cm	0.5–1.2 mm	1–4 cm	<1 cm	<1 cm
Spore size (µm)	4.5–5.5 × 4–4.5	5–6.5 × 4.5–5.5	5.5–7 × 4.5–6	4.3–5.5 × 3.6–4.4	5–6.5 × 4–5	3.5–5 × 2.8–4	4.5–5.0 × 3–4
Substrate preference	gymnosperms	<i>Abies</i>	hardwood	gymnosperms <i>Tsuga</i>	hardwood	hardwood	hardwood <i>Lithraea</i>
Geographical distribution	Pacific NW of North America, NE China	Central and Eastern Europe, Caucasus	NE parts of North America	NE India	Temperate North America, Eurasia	Temperate North America, Eurasia, Argentina, Australia	Argentina

clamps, ordinarily branched, 1.5–7 µm wide, with thin- to slightly thickened walls, some hyphae in strands; gloeoplerous hyphae 3–7 µm wide, mostly simple-septate, with an oily yellowish content, reacting negatively to sulfovanilline, sometimes apically enlarged to gloecystidium-like structures. Chlamydospores abundant, terminal (Fig. 2e), occasionally intercalary, regular in shape and size, globose to subglobose, 5–6 × 4–5 µm, yellowish and slightly thick-walled, smooth, IKI.

Remarks *H. rajchenbergii* is characterized by a basidiome morphology which is similar to *H. coralloides* but differs by slightly bigger spores (4.5–5.0 × 3–4 µm vs 3.5–5 × 2.8–4 µm in *H. coralloides*), the presence of terminal chlamydospores in culture, and the host substrate. In addition, most spines are distinctly thicker at the base and therefore more tapering and less cylindrical than in *H. coralloides*. The presence of chlamydospores in culture has earlier only been reported from *H. erinaceus* in the genus.

Hericium americanum

The name *H. americanum* is found in two different places in the tree, connected to an unresolved part dominated by *H. alpestre*, and in a small, well supported subclade of four sequences (Fig. 1). The species is well-known from eastern parts of North America, typically growing on hardwood, but at least one exception is known from *Tsuga* (AY534581). This specimen was used by Ginns in an extensive crossing tests and found to belong to *H. americanum* (Ginns 1985).

An extensive study based on incompatibility tests between single-spore isolates from all four North American species was done by Ginns (1984; 1985). He demonstrated compatibility in intraspecific crossings and incompatibility in crossings between these species, as well as between *H. americanum* and *H. alpestre*. Apart from the reported incompatibility, the only difference found between *H. americanum* and *H. alpestre* seemed to be the occurrence on hardwood and distribution limited to North America versus coniferous wood and Europe. Just two of the cultures which Ginns used in his crossing tests are available as accessions in GenBank (AY534581 – *H. americanum*; JQ716938 – *H. abietis*).

As representatives for *H. alpestre*, Ginns used cultures from Hallenberg (1983). It is here demonstrated that these cultures (FCUG 407, FCUG 392) are conspecific with *Dentipellis fragilis* (Fig. 1). Such a determination error may seem strange, but, in fact, this species is very similar to *H. alpestre* (and *H. americanum*, *H. erinaceum*) in the microscope. Hallenberg collected three specimens on cut, vertical surfaces of *Abies* in Austria, 1981. One of them was a branched and juvenile specimen of the typical *H. alpestre*

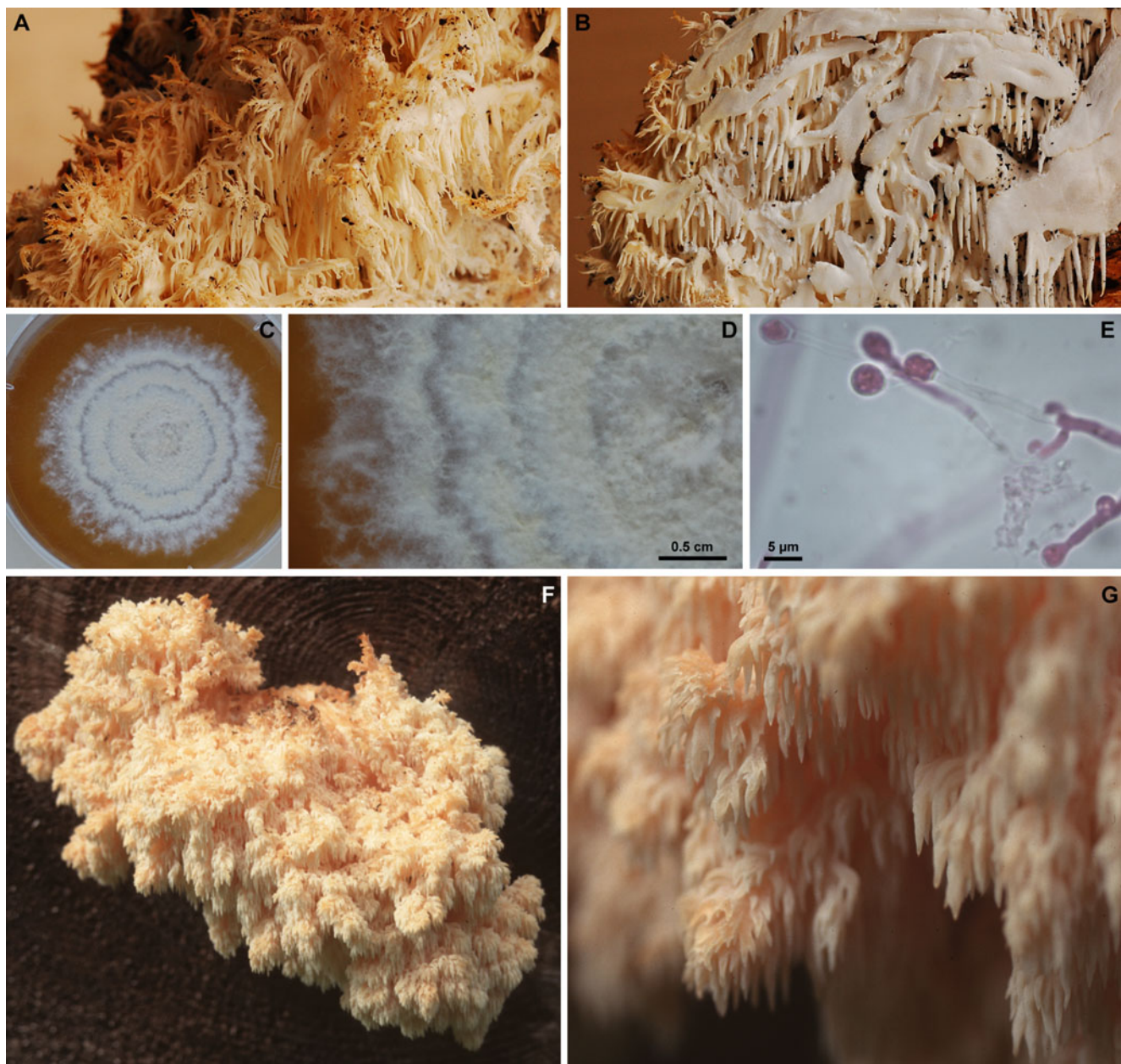


Fig. 2 a–e *Hericium rajchenbergii*. a) detail of basidiome. b) section through basidiome showing arrangements of spines. c–d) Culture in malt agar after 6 weeks. e) terminal chlamydospores produced in

culture. f–g *Hericium alpestre* NH 13240. f) basidiome emerging from a cut surface of an *Abies* tree. g) detail of basidiome showing arrangements of spines

configuration; the other two collections (*D. fragilis*) were likewise juvenile but resupinate with just bundles of spines emerging directly from the wood. These two specimens were the origin for the two cultures used in the crossing tests by Ginns (1985). By that time, *D. fragilis* had only been recorded from hardwood.

Consequently, no crossing tests have so far demonstrated that *H. americanum* and *H. alpestre* are incompatible. The highly similar morphology and ITS sequences could indicate that the two species in fact are conspecific. At present, however, we prefer to keep them distinguished from each

other because of the differences in their geographical distribution and substrate preferences.

Hericium alpestre Fig. 2f and g

Hericium alpestre seems to constitute a paraphyletic taxon in the ITS phylogeny. The samples originate from Central to Eastern Europe, including the Russian part of the Caucasus, and all were collected on *Abies*. A specimen reported from a Korean study is of uncertain origin. It is noteworthy that a sample annotated as *H.*

americanum (DQ206987) and collected on hardwood in USA is included in this paraphyletic clade. The genetic divergence among the samples here referred to as *H. alpestre* is quite small.

Because of the unfortunate determination mistake mentioned above it is important to establish a clear interpretation of what *H. alpestre* really stands for, and typification is therefore proposed here. In his description of the new species, Persoon (1825) wrote, “Ad truncos abietinos, in vallesiatis subalpinis detectum a L. Thomas”, but no specimen was mentioned. A seemingly original material of the species is present in herb. Persoon, Leiden (L 910256–1300) but there are no further indications than the taxon name. The material is meagre, consisting of some tufted spines, but spore size is in full accordance with earlier descriptions of the species (Bernicchia and Gorjón 2010). Because of the bad condition of the material and uncertainties about its origin, we therefore propose a neotype from central Europe, but we choose to retain the species name from Persoon (*H. alpestre*).

Proposed neotype: *Hericium alpestre* Pers., Romania, Suceava region, Codrul Secular Slatioara. On a dead standing tree of *Abies*, 1985-10-16, coll. Nils Hallenberg, NH 9161 (GB), GenBank accession JQ716936 (ITS).

Hericium erinaceus

H. erinaceus appears as three subclades with weak support values (Fig. 1). The specimens within a subclade generally belong to the same or adjacent geographical regions. One well-supported subclade features all of the representatives from the USA that grow on *Quercus*. Another subclade is mainly composed of representatives from East Asia. Within the latter subclade the recently described *H. bharengense* is included (Das et al. 2011). Whether this species can be distinguished as a good taxon, or if it is an example of intraspecific variation within the East Asian populations cannot be certified from this study. It is also a possibility that the two subclades reported here represent different species.

A summary of diagnostic characteristics is given in Table 2 for the species of *Hericium* dealt with here. Spore measurements were taken from MycoBank (Crous et al. 2004).

Discussion

The phylogenetic analysis based on ITS sequences did not fully resolve the *Hericium* species relationships. However, we could obtain molecular clades which together with morphological and ecological data, as well as earlier performed

crossing tests, led us to a better understanding of diversity in the genus and the species boundaries.

The *Hericium coralloides* clade is well supported and seems to be composed of at least three species. Two of them, *H. rajchenbergii* and *H. coralloides*, share the basidiome morphology, with single spines in a comblike arrangement. We did not study material of the third taxon, *Hericium sp.*, but this is likely to share a similar macro morphology.

The *Hericium abietis* clade is another well-supported clade and even in the absence of herbarium vouchers it is obvious that this species has a transberingian distribution (Lomolino et al. 2006), although it was earlier believed to be restricted to the NW Pacific in North America. This kind of distribution pattern has earlier been found in *Flammulina velutipes* (Curtis) Singer and *Panellus stipticus* (Bull.) P. Karst. (Petersen and Hughes 2007).

To distinguish the species in the complex of *H. alpestre* - *H. americanum* - *H. erinaceus* is more difficult because of the great variation exposed by different developmental stages and the limited resolution in ITS phylogeny. The crossing test study by Ginns (1985) shows convincingly that *H. americanum* and *H. erinaceus* are two distinct species. The differences in geographical distribution and substrate preferences between *H. americanum* and *H. alpestre* also seem to be distinct enough to allow for acceptance of these two species. However, for many of the accessions to GenBank from East Asia detailed information is lacking on morphology and substrate preferences. It seems that crossing tests could be a valuable tool to further reveal species delimitations in this region.

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