

Psathyloma sp. nov.

Psathyloma, a new genus in Hymenogastraceae described from New Zealand

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Abstract: A new genus *Psathyroma* is described based on collections of agarics from New Zealand. We describe two new species in the genus, *Ps. leucocarpum* and *Ps. catervatim*, both of which have been known and tentatively named for a long time awaiting a formal description. Morphological traits and phylogenetic analyses reveal that *Psathyroma* forms a strongly supported sister clade to *Hebeloma*, *Naucoria* and *Hymenogaster*. Morphologically *Psathyroma* resembles *Hebeloma* from which it differs mainly by producing smooth basidiospores with a germ pore. The geographical range of the genus has been demonstrated to include several regions in the southern hemisphere. A survey of published environmental sequences reveals that *Psathyroma* spp. were isolated from ectomycorrhizal root tips from Tasmania and Argentina, indicating an ectomycorrhizal association with southern beech.

Key words: Agaricales, mycorrhiza, Nothofagaceae, systematics, taxonomy

INTRODUCTION

Many brown-spored, lamellate agarics are found in the native forests of New Zealand where they constitute a dominant element during much of the fruiting season. Several have been studied extensively; for example the genera *Cortinarius* (Pers.) Gray sensu lato (Horak 1973a, b, 1981, 1987, 1999; Moser 1986; Horak and Wood 1990; Soop 1998, 2001, 2002, 2005, 2010, 2013, 2014; Gasparini and Soop 2008), *Descolea* Singer (Horak 1971), *Inocybe* (Fr.) Fr. and *Astrosporina* J. Schröt (Horak 1977), *Simocybe* P. Karst (Horak 1980a), *Phaeomarasmium* Scherff. (Horak 1980b) and *Psilocybe* (Fr.) P. Kumm. (Johnston and Buchanan 1995). On the other hand the genus *Hebeloma* (Fr.) P. Kumm. has been mentioned only sporadically in the taxonomic literature on New Zealand agarics (Horak 1983, Soop 2001, cf. Rees et al. 2013).

Psathyroma has been used informally as a generic name among mycologists in New Zealand since at least 1997. The name was proposed by E. Horak to designate a common agaric in southern beech forests and is a combination of the names *Psathyrella* and

Hebeloma, genera that are similar in macromorphology. The informal name has appeared in a number of publications. For example *Psathyroma* was established as a distinct lineage of ectomycorrhizal fungi in Hymenogastraceae Vittad. (Tedersoo and Smith 2013) and noted as present in Tasmania (Gates and Ratkowsky 2014). Matheny et al. (2015) demonstrated strong support for *Psathyroma* as nested in Hymenogastraceae.

Species of *Psathyroma* in New Zealand are small, brown-spored, often grow in large troops on the forest floor associated with southern beech (*Lophozonia* and *Fuscospora*) and are never found fruiting on wood. They have a cream or brown pileus, a white stipe, smooth basidiospores with a germ pore and a thin or lacking veil. Their strong resemblance to *Hebeloma* subg. *Denudata* often results in misidentifications based on macromorphological characters.

In this study the identity of a distinct genus *Psathyroma* based on its position in the phylogeny and its separation from *Hebeloma* and other members of the Hymenogastraceae is discussed. Our analysis is based on collections from New Zealand, using phylogenetic evidence supported by nuclear ribosomal internal transcribed spacers (ITS1-5.8S-ITS2 = ITS) and 28S nuc rDNA sequences (= 28S) and morphological features.

MATERIALS AND METHODS

Taxon sampling.—Representatives of all genera in the Hymenogastraceae were included (*Hebeloma*, *Naucoria* [Fr.] P. Kumm, *Hymenogaster* Vittad., *Wakefieldia* Corner & Hawker, *Anamika* K.A. Thomas, Peintner, M.M. Moser & Manim. and *Psathyroma*). Twelve specimens of *Psathyroma* were sequenced and two GenBank sequences identified as “Hymenogastraceae sp.” but with affinities to *Psathyroma* sequences (Matheny et al. 2015) were included. Species of *Galerina* Earle were used as outgroups (Gulden et al. 2005, Matheny et al. 2006, Boyle et al. 2006).

DNA extraction and sequencing.—Genomic DNA were extracted with the DNeasy Plant Mini Kit (QIAGEN, Redwood City, California) or the Nucleospin Plant II Mini Kit (Macherey-Nagel, Düren, Germany) following the manufacturer's protocols with minor modifications. The 28S and ITS loci were amplified with the LR0R and LR7 primers for the 28S gene (Vilgalys and Hester 1990) and the primers ITS1 and ITS4 for the ITS (from

White et al. 1990). For PCR amplification standard cycling protocols were performed under the following conditions for the 28S and the ITS on a Bio-Rad thermal-cycler (Bio-Rad Laboratories Inc., Hercules, California): 94 C for 2 min followed by 35 cycles of 94 C, 51 C and 48 C for the 28S and ITS locus, respectively, for 30 s and 72 C for 1 min, with a final extension of 72 C for 5 min. PCR amplifications used DreamTaq (Thermo Scientific, Waltham, Massachusetts) and 5Prime Taq (5Prime Inc, Gaithersburg, Maryland) polymerases.

Amplicons were sequenced commercially by LGC Genomics Ltd. (Berlin, Germany) from both directions, and reads were assembled into contigs with the CodonCode Aligner package (CodonCode Corp., Centerville, Massachusetts) (SUPPLEMENTARY TABLE I). Contigs were evaluated by BLAST against the NCBI nucleotide database (Altschul et al. 1990). Additional 28S and ITS sequences with significant similarity retrieved from GenBank (<http://www.ncbi.nlm.nih.gov/nucleotide>) were included (SUPPLEMENTARY TABLE II).

Alignments and phylogenetic reconstruction.—Sequences of the 28S and ITS were aligned independently by the PRANK algorithm (Löytynoja and Goldman 2005) using default settings (+F option off) and corrected manually after a visual inspection in Jalview (Waterhouse et al. 2009). Sequences that were too short were discarded (e.g. in case of 28S, sequences < 850 bp and < 350 bp for the ITS). Indels in the ITS region were recoded as presence/absence characters with gapcode.py script (2.1, <http://www.bioinformatics.org/~rick/software.html>) using an implementation of the simple indel coding algorithm (Simmons and Ochoterena 2000). After alignment of each gene region sequences of the 28S and ITS were concatenated into a supermatrix that is available at TreeBASE under S18479 (<http://www.treebase.org/treebase-web/home.html>).

We inferred phylogenies with Bayesian and maximum-likelihood (ML) methods. For Bayesian inference we used MrBayes 3.2.1 (Ronquist et al. 2012). Bayesian analysis was performed with the GTR+I model and the following settings: chain length of 10 million generations, a sampling frequency every 100 generations, two independent replicates, three heated and one cold chain per replicate. The concatenated alignment was partitioned into ITS, 28S and indel matrices and the parameters of the evolutionary model were estimated separately for the individual partitions. Indels were modeled with a two-state Markov model implemented in MrBayes for restriction sites. Burn-in was established by inspecting the convergence of likelihood values in Tracer and post burn-in trees were used to compute a 50% majority rule consensus tree. Maximum likelihood (ML) analyses were run in RAxML 7.0.4 (Stamatakis 2006) under the GTR+G model and specifying separate partitions for the ITS and 28S. Branch supports were estimated by 500 nonparametric

bootstrap replicates. Bootstrap percentages were summarized with the SUMTREES script of the Dendropy package (Sukumaran and Holder 2010). Individual nodes were considered strongly supported when bootstrap values (BS) were at least 70% and posterior probability values (PP) were at least 0.95.

A second dataset was assembled consisting of *Psathylooma* ITS sequences complemented with similar environmental sequences from GenBank based on BLAST. These sequences were aligned and analyzed with ML bootstrapping as described above.

Morphology.—Dried material was revived and mounted in 10% KOH. Revived material was washed in distilled water and transferred to Melzer's reagent for observation of the dextrinoid reaction in the wall of the basidiospore. Micrographs were obtained with Nikon Eclipse Ni microscope under DIC illumination. Spore ranges are recorded as mean \pm 1.5 SD covering 86% of measurements for a normal distribution. Observed maximum and minimum are in brackets. The number of measurements is recorded as N. Colors are recorded with reference to Korerup and Wanscher (1978). The alkaline reaction resulting in color changes to the basidiomata was tested by applying a 30% NaOH solution.

The majority of our *Psathylooma* specimens are deposited in the public herbaria of PDD and S. Some specimens are deposited in the personal herbaria of K. Soop (KS) and/or of J.A. Cooper (JAC). Our sequenced collections of *Hebeloma*, *Galerina* and *Naucoria* used for comparison in the phylogenetic analysis (SUPPLEMENTARY TABLE I) were deposited in BP or the personal herbaria of B. Dima (DB) and L.G. Nagy (NL).

RESULTS

We generated 23 28S and 22 ITS sequences for this study. After manual refinement alignments of the 28S and ITS loci were 1347 and 981 characters long, respectively. In total 217 gap characters were coded from indels of the ITS alignment and used as a separate partition in Bayesian analyses. In the concatenated dataset the two loci contained 2545 characters including indels.

Phylogenetic trees from the Bayesian and ML analyses have largely congruent topologies. The Bayesian consensus tree is illustrated (FIG. 1). Both the Bayesian and ML analyses recovered *Psathylooma* as a well-supported clade (PP = 1.0, BS = 86%). In Bayesian analyses *Psathylooma* appeared as a sister group to the other members of the Hymenogastraceae included in this study, whereas in the ML trees it was inferred as the sister

group to *Hebeloma*, although support for this was lacking (< 50%). The clade formed by *Psathyroma* specimens further split into two species-level groups, described here as *Ps. leucocarpum* and *Ps. catervatim*. Specimens of both species form strongly supported clades (PP = 1.0, BS = 99% for *Ps. catervatim* and PP = 1.0, BS = 100% for *Ps. leucocarpum*, FIG. 1). Notably *Ps. catervatim* seems to have more variation in the studied loci than *Ps. leucocarpum*. In addition, sequences of two specimens previously by Matheny et al. (2015) were grouped within *Psathyroma* (PBM3420, PBM3116). Further we identified four previous environmental sequences belonging to *Psathyroma* (FIG. 2), three of which have been isolated from *Nothofagus* forests in Argentina (as uncultured *Hebeloma* clones) forming a species-level clade nested within *Psathyroma* (Fernández et al. 2013, Nouhra et al. 2013). In addition, an environmental sequence from Tasmanian *Eucalyptus* forests (Horton 2011) is nested within *Ps. catervatim* (BS = 100%; FIG. 2).

TAXONOMY

Psathyroma E. Horak ex Soop, J.A. Cooper & Dima, gen. nov.

MycoBank MB 812051.

Typification: Type species: *Psathyroma leucocarpum* Soop, J.A. Cooper & Dima.

Etymology: Derived from the generic names *Psathyrella* and *Hebeloma* (gender neuter).

Basidiomata agaricoid, terrestrial, pileus viscid, universal veil absent or fugacious, cortina absent. Basidiospores pale brown, ± ellipsoid, smooth, dextrinoid, with a germ pore. Cheilocystidia abundant, variable shape, thin-walled, hyaline. Pleurocystidia absent. Clamp connections present. Pileipellis an ixocutis.

Known distribution: South Pacific (Australia, New Zealand, South America).

Species: *Psathyroma leucocarpum*, *Psathyroma catervatim*.

Comments: *Psathyroma* forms a distinct clade separate from other genera of Hymenogastraceae (FIG. 1). The genus is ectomycorrhizal and basidiomata are always found in Nothofagaceae forests fruiting on the forest floor. *Psathyroma* can be differentiated morphologically from *Hebeloma* by its smooth basidiospores with a large germ pore. *Psathyroma* and *Hebeloma* share similar macromorphology of the basidiomata; however, *Psathyroma* is typically smaller and more brittle than *Hebeloma*. The pileipellis composition is similar to that of *Hebeloma*. *Psathyroma* can be differentiated from *Naucoria* by their smooth basidiospores with a large germ pore as well as by the shape of the cheilocystidia. Moreover, *Naucoria* was not recorded with certainty from the native forests of New Zealand (Segedin and Pennycook 2001), presumably because of absence of their mycorrhizal hosts, mainly *Alnus* and *Salix*, in this region.

Psathyroma leucocarpum Soop, J.A. Cooper & Dima, sp. nov. FIGS. 3, 4.

MycoBank MB812052.

Typification: New Zealand. Canterbury, Glentui, Mount Richardson Track, 23 Apr 2014, J.A. Cooper JAC13340 (**holotype** PDD 105593). GenBank KT591549 (ITS), KT591571 (28S).

Etymology: from leukos (Greek) “white” and “karpós” (Greek) referring to the general appearance of the basidiomata.

Pileus 20–70 mm diam, rounded-conical, later expanded to almost plane, viscid, hygrophanous, white to gray-white (2B1) with a grayish yellow (2B3, 2B2) disk, glabrous; margin without veil remnants, not striate. Lamellae pale gray when young, later brownish (6C3, 7C3), fairly crowded, adnate to narrowly emarginate; edge slightly fimbriate. Stipe 35–65(–110) × 4–10 mm, cylindrical, dry; silvery white to gray-white, slightly zoned without visible veil remnants. Veil absent or fugacious; cortina absent. Context white. Odor insignificant; flavor faintly agaricoid or sweetish. Macrochemical reactions: NaOH negative or weakly yellow in context. Spore deposit cinnamon (6D5).

Basidiospores (6.5–)6.6–7.6(–7.7) × (3.9–)4.0–4.4 μm. Q = 1.6–1.9; mean 7.1 × 4.2 μm, Q = 1.7; N = 20, ellipsoid in face view, amygdaliform in side view, with lateral apiculus, smooth, pale brown, thick-walled, dextrinoid, often with refractive content in Melzer's, with a broad germ pore to 1.0 μm diam. Basidia 20–30 × 5–7 μm (excluding sterigma), clavate to subcylindrical, with basal clamp, four-spored, sterigma to 6 μm long × 2 μm wide at base. Pleurocystidia not observed. Cheilocystidia abundant (lamellar edge sterile), variable shape (clavate, lageniform, sphaeropedunculate), thin-walled, hyaline, with basal clamp, 25–40 × 3–10 μm. Pileipellis an ixocutis up to 70 μm thick composed of cylindrical, smooth, thin-thick-walled, hyaline hyphae to 5 μm diam embedded in a gelatinized matrix. Hypocutis of broadly globose, hyaline cells up to 20 μm diam over a dense layer of parallel hyaline hyphae. Pilea and lamella tissue inamyloid not dextrinoid. Stipitipellis a closely packed cutis of glassy-walled hyphae 5–10 μm diam. Caulocystidia not observed. Clamp connections present in all tissues.

Icones: Soop 2008, Pl. 106 sub *Pholiota* sp.

Habitat: Gregarious, common, associated with Nothofagaceae spp.

Other specimens examined: New Zealand. Taupo, Kiko Track, 27 Apr 2001, K. Soop BR141; Taupo, Te Iringa Track, 03 May 2001, K. Soop BR143; idem, 13 May 2011, J. Cooper JAC12071 (PDD 96311); Lake Taupo District, P.B. Matheny PBM3116 (PDD97878, TENN063883); Otago Lakes, Milford Rd. at Totara Rest Area, 22 Apr 2004, K. Soop BR182; idem 26 Apr 2008, K. Soop BR185 (PDD 94002, S F93258); Otago, Dunedin, Waipori Gorge Picnic Site, 13 May 2008, J. Cooper, JAC10801 (PDD 87646); idem, 13 May 2008, J. Cooper JAC10713 (PDD 87565); Otago Lakes. Milford Rd. at Deer Flat, 27 Apr 2006, K. Soop BR179 (PDD 88286); Otago, Dunedin, Government Track, 15 May 2008, J. Cooper JAC10802 (PDD 87647).

Comments: *Psathyroma leucocarpum* is somewhat larger than *Ps. catervatim* (see *Comments* below); this species differs from the latter mainly by being considerably paler, sometimes entirely white. Microscopically the two species are nearly identical.

Ps. leucocarpum resembles the common species *Psathyrella candolleana* (Fr.) Maire, except that the remnants of the veil at the margin of the pileus are missing and the pileus is moist to

viscid. *Psathyroma leucocarpum* forms a separate clade, well distinguished from the *Ps. catervatim* clade.

Psathyroma catervatim Soop, J.A. Cooper & Dima, sp. nov. FIGS. 3, 4.

MycoBank MB812053

Typification: New Zealand. Taupo, Te Iringa Track, 28 Apr 2001, K. Soop no. BR138

(**holotype** PDD 107742). GenBank KT591545 (ITS), KT591567 (28S).

Etymology: *catervatim* (Latin) referring to frequent fruiting “en masse” or “in troops.”

Pileus 15–45 mm diam, ± conical, then expanded to campanulate with a shallow umbo or a small nipple, viscid, hygrophanous; warmly yellow-brown (6E7) to hazel-brown (6E8) or gray-brown (6E4), center sometimes darker; glabrous to finely innate fibrillose; margin without veil remnants, not striate. Lamellae pale gray when young, later brownish, fairly crowded (L = 44, l = 3), narrowly emarginate, not lacrymate. Stipe 35–70 × 3–6 mm, cylindrical, slender, dry; white with a white sheen from fine fibrils or thin zones, apex ± pruinose. Veil absent or fugacious, white, cortina absent. Context white, marbled grayish tan in pileus, brittle. Odor faintly raphanoid or like paint; flavor insignificant to slightly fetid.

Macrochemical reactions: NaOH negative. Spore deposit color not noted.

Basidiospores (6.8–)6.7–7.7(–7.9) × 4.0–4.6(4.7) μm, Q=1.5–1.9; mean 7.2 × 4.3 μm, Q = 1.7; N = 20, ellipsoid in face view, amygdaliform in side view, with lateral apiculus, smooth, pale brown, thick-walled, dextrinoid, with broad germ pore to 1 μm diam. Basidia 20–30 × 5–7 μm (excluding sterigma), clavate to subcylindrical, with basal clamp, four-spored, sterigma to 3 μm long × 1 μm wide at base. Pleurocystidia not observed.

Cheilocystidia abundant (lamellar edge sterile), variable shape (clavate, lageniform, sphaeropedunculate), thin-walled, hyaline, with basal clamp, occasionally branching, 25–40 × 5–10 μm. Pileipellis an ixocutis to 100 μm thick composed of cylindrical, smooth, thin to thick-walled, hyaline hyphae to 5 μm diam embedded in a gelatinized matrix. Hypocutis of

broadly globose, hyaline cells up to 20 µm diam over a dense layer of parallel pale brown hyphae. Pilea and lamella tissue inamyloid not dextrinoid. Stipitipellis a closely packed cutis of glassy-walled hyphae 5–10 µm diam. Caulocystidia present at stem apex as tufts of erect cylindrical hyphae to 20 × 5 µm. Clamp connections present in all tissues.

Icones: Soop 2008, Pl. 105 sub *Pholiota psathyrelloides*.

Habitat: Gregarious, common, associated with Nothofagaceae spp.

Other specimens examined: New Zealand. Taupo, Te Iringa Track, 29 Apr 2001, K. Soop BR140; idem, 13 May 2011, J. Cooper JAC12072 (PDD 96312); Otago Lakes, Milford Rd. at Knobbs Flat, 24 Apr 2003, K. Soop BR151; Otago, Haast Pass, 19 Apr 1999, K. Soop BR122 (PDD 70515). Australia. Tasmania: P.B. Matheny PBM3420 (TENN065471), GenBank: HQ840663 (ITS), HQ840664 (28S).

Comments: This common fungus may be encountered in large troops on the floor of Nothofagaceae forests. With a brown pileus and a white stipe it reminiscent of a small *Hebeloma* but is brittle with the pileus easily falling off. If there is a veil, it is thin and hardly discernible. The pileus is remarkably variable from pale gray-brown to dark, saturated date brown. *Psathyroma catervatim* is similar in appearance to *Pholiota psathyrelloides* Singer, a South American species (cf. Horak 1979, p 252). However, we have been unable to obtain the holotype of Singer's type on loan for comparison, and thus the synonymy between the two species remains speculative. GenBank sequence HQ840663 deposited as Hymenogastraceae from Tasmania (Matheny et al. 2015) represents a *Psathyroma* and is similar to sequences of *P. catervatim*.

DISCUSSION

A group of common agarics in the native forests of New Zealand has long been known and identified among local mycologists under the tentative name of *Psathyroma*. Here we confirm the status of *Psathyroma* as a new genus using phylogenetic analyses and morphology. The genus forms a strongly supported clade in Hymenogastraceae where it is a weakly supported sister clade to *Hebeloma*, *Hymenogaster* and *Naucoria* as also noted in Matheny et al. (2015).

At present two species are recognized, the type *Ps. leucocarpum* and *Ps. catervatim*, differing macroscopically by color and size of the basidiomata. Currently there are no records of additional species in New Zealand, but our analyses confirm the evidence of a third species in South America, first indicated by Tedersoo and Smith (2013). To investigate whether it is a question of Singer's Patagonian species, mentioned above, is a topic for future research. Moreover, *Ps. catervatim* exhibits an intraspecific genetic variation that might be translated into additional species or infraspecific taxa, although the morphology of the taxon appears to be fairly uniform.

Psathyroma appears to be restricted to Nothofagaceae forests of the southern hemisphere, and nearly all records of basidiomata are confined to New Zealand. However, environmental sequences indicate its presence in South America (Tedersoo and Smith 2013) and a separate species in Australia (Nouhra 2013). Gates and Ratkowsky (2014) and Matheny et al. (2015) report findings of a species similar if not identical to *Ps. catervatim* in Australia, where environmental sequences also were detected (Horton, 2013). We suspect that *Psathyroma* is ectomycorrhizal, and this is supported by the isolation of sequences belonging to *Psathyroma* present on ectomycorrhizal root tips (FIG. 2; Tedersoo et al. 2009, Horton 2011, Nouhra et al. 2013, Fernández et al. 2013). This is the first example known to us of ectomycorrhizal fungi with basidiospores having an apical germ pore.

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LEGENDS

FIG. 1. Majority-rule consensus phylogram of the Hymenogastraceae inferred with MrBayes from the concatenated alignment of ITS and 28S sequences. Numbers above or below branches represent nodal supports (posterior probability/ML bootstrap percentage); values above 0.5 and 50% are shown. Voucher numbers are indicated only at newly generated sequences except those of two Hymenogastraceae sequences retrieved from GenBank. New *Psathyloma* sequences marked in boldface. Bar indicates 0.01 expected change per site per branch.

FIG. 2. Maximum-likelihood phylogram of *Psathyloma* and related environmental ITS sequences. Numbers above or below the branches represent nodal support (bootstrap percentage), values above 70% only are shown.

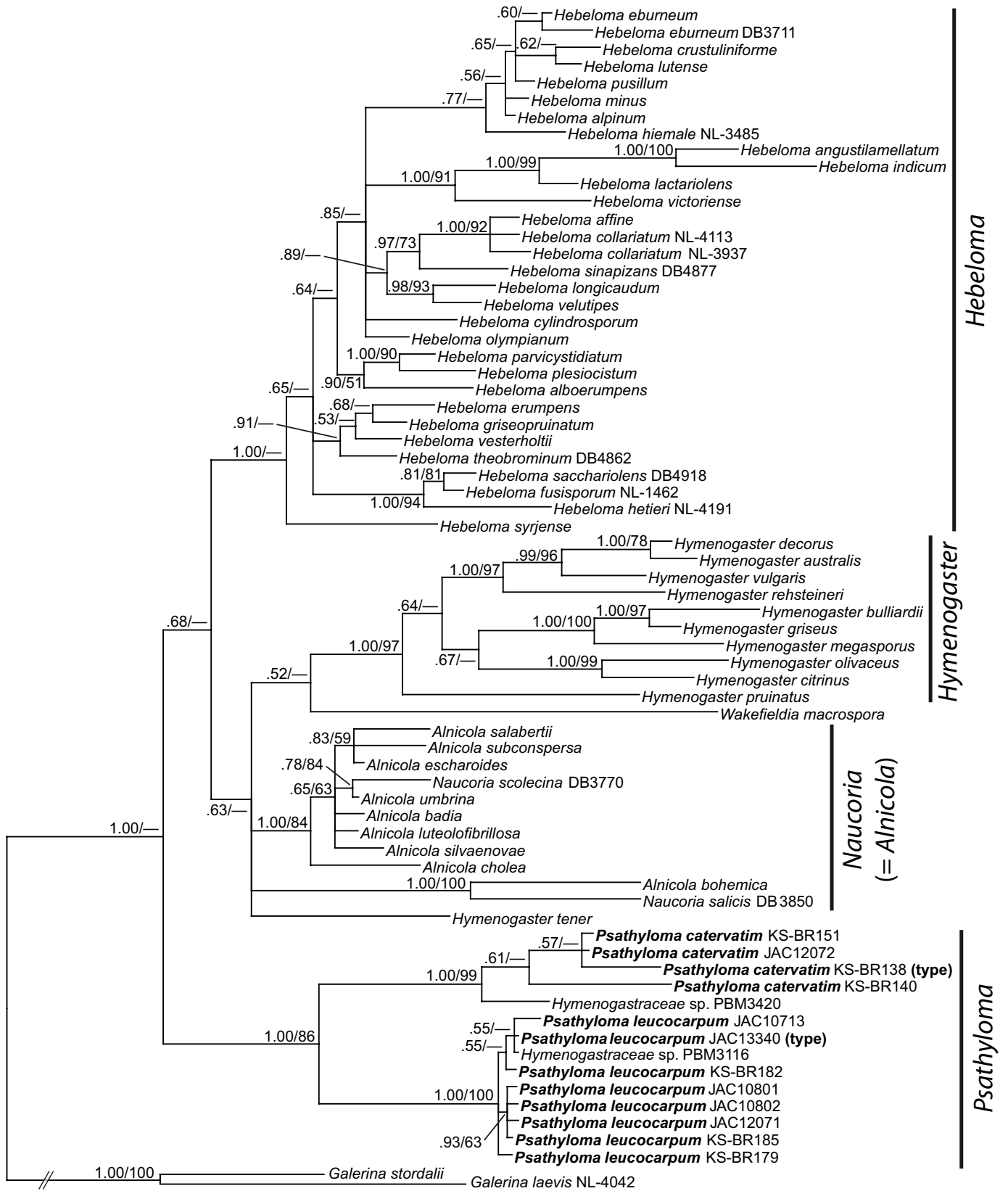
FIG. 3. Basidiomata. *Psathyloma leucocarpum*. A. KS-BR141. B. JAC13340 holotype. *Psathyloma catervatim*. C. KS-BR138 holotype. D. KS-BR140.

FIG. 4. Micromorphological characters. *Psathyloma leucocarpum*, JAC13340 holotype. A. Basidiospores. B. Cheilocystidia. C. Basidia. *Psathyloma catervatim*, KS-BR138 holotype. D. Basidiospores. E. Cheilocystidia. F. Basidia. Bar = 10 μm .

FOOTNOTES

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