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ARTICLE

The *Pseudoomphalina kalchbrenneri* complex in North America

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Abstract: *Pseudoomphalina kalchbrenneri* is a Eurasian species. In North America the *Pso. kalchbrenneri complex* is represented by ***Pseudoomphalina anticostica*** sp. nov. and *Pso. compressipes* in the east and *Pso. intermedia* in the west. *Pseudoomphalina farinacea* and *Pso. felleoides* are later synonyms for *Pso. compressipes*. The somewhat similar *Pseudolaccaria pachyphylla* occupies a temperate band through Eurasia, confirmed by sequencing in both eastern and western North America. It differs from species of the *Pso. kalchbrenneri* complex by smaller size, finely granular pileus, non-decurrent gills, and lack of hymenial cystidia. All species of the *Pso. kalchbrenneri* complex are uncommon, and macroscopically similar. *Pseudoomphalina kalchbrenneri* and *Pso. intermedia* can be identified by their distribution (Europe and western North America, respectively) and lack of cystidia. The cystidiate eastern North American *Pso. anticostica* and *Pso. compressipes* can be differentiated by the smaller spores of the latter. *Pseudoomphalina cokeri* is the most ancestral species on the *Pseudoomphalina* lineage, while *Clitocybe thujana* and *Agaricus apertus* (*Clitocybe*/*Clitocybula aperta*) fall outside *Pseudoomphalina* and *Pseudolaccaria*. We add 21 new sequences to GenBank, including six types (*Agaricus compressipes*, *Clitocybe felleoides*, *C. farinacea*, *C. intermedia*, *C. thujana*, *Agaricus apertus*), and one new species (*Pso. anticostica*).

Key words: ITS sequences, holotype barcoding, molecular phylogeny, *Tricholoma*.

Résumé : *Pseudoomphalina kalchbrenneri* est une espèce eurasienne. En Amérique du Nord, le complexe *Pso. kalchbrenneri* est représenté par ***Pseudoomphalina anticostica*** sp. nov. et *Pso. compressipes* dans l'est et *Pso. intermedia* dans l'ouest. *Pseudoomphalina farinacea* et *Pso. felleoides* sont des synonymes postérieurs de *Pso. compressipes*. *Pseudolaccaria pachyphylla*, assez similaire, occupe une bande tempérée à travers l'Eurasie, ce que confirme le séquençage réalisé dans l'est et l'ouest de l'Amérique du Nord. Il diffère des espèces du complexe *Pso. kalchbrenneri* par sa taille plus petite, un chapeau finement granuleux, des lames non décurrentes et l'absence de cystides dans l'hyménium. Toutes les espèces du complexe *Pso. kalchbrenneri* sont rares et similaires à l'échelle macroscopique. *Pseudoomphalina kalchbrenneri* et *Pso. intermedia* peuvent être identifiés par leur distribution (Europe et ouest de l'Amérique du Nord, respectivement) et l'absence de cystides. *Pseudoomphalina anticostica* et *Pso. compressipes*, espèces cystidiées de l'est de l'Amérique du Nord, peuvent être différenciés par les spores plus petites du dernier. *Pseudoomphalina cokeri* est l'espèce la plus ancestrale de la lignée des *Pseudoomphalina*, alors que *Clitocybe thujana* et *Agaricus apertus* (*Clitocybe*/*Clitocybula aperta*) se situent à l'extérieur des *Pseudoomphalina* et *Pseudolaccaria*. Les auteurs ajoutent 21 nouvelles séquences à GenBank, dont six types (*Agaricus compressipes*, *Clitocybe felleoides*, *C. farinacea*, *C. intermedia*, *C. thujana*, *Agaricus apertus*) et une nouvelle espèce (*Pso. anticostica*). [Traduit par la Rédaction]

Mots-clés : séquences de l'ITS, codage à barré d'holotypes, phylogénie moléculaire, *Tricholoma*.

Introduction

Traditionally, the genus *Tricholoma* Fr. was the repository for a wide variety of fungi that could not be placed elsewhere, which eventually necessitated dissection of diverse unrelated groups. Singer (1936) erected the genus *Cantharellula* Singer for former species of *Tricholoma* with spores having an amyloid reaction. *Cantharellula* grew to encompass several subgenera, including the subgenus *Pseudoomphalina* Singer (Singer 1948). In addition to the amyloid reaction of its spores, this subgenus differs from the morphologically similar genus *Omphalina* Quél. by its presumed saprotrophic lifestyle, in contrast to the latter's mutualism with bryophilous photobionts (Redhead et al. 2002). Over time, *Pseudoomphalina* was elevated to genus (Singer 1956), with *Omphalia kalchbrenneri* Bres., first described and illustrated by Giacomo Bresadola (1883), being the type species for the new genus. A sequenced epitype for the species was provided by Lavorato et al. (2015). In

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the same study, they reported that *Pseudoomphalina pachyphylla* was phylogenetically distant from other species in the genus, and created the new genus *Pseudolaccaria* Vizzini, Contu & Z.W. Ge to accommodate it.

While some species of *Pseudoomphalina* have some amount of dark purplish colour [*Pso. umbrinopurpurascens* (Maire) Contu, limited to the Mediterranean region, and in North America *Pso. angelesiana* (A.H. Sm. & Hesler) Vizzini, Contu & Z.W. Ge, and *Pso. cokeri* (Hesler) Vizzini, Contu & Z.W. Ge], the *Pso. kalchbrenneri* complex produces sporocarps that are tan to brown. The only known species of the complex in Eurasia is *Pso. kalchbrenneri*, with matching sequences confirmed to date from Estonia, Switzerland, and Scandinavia. A similar species, *Omphalia graveolens* S. Petersen (1907), which was transferred to *Pseudoomphalina* by Singer (1986), is currently treated as a synonym of *Pso. kalchbrenneri* (Knudsen 2012). In North America, *Pso. kalchbrenneri* has been reported on internet sites and foray lists, but so far no sequences of the species are available from this continent. Four other brown species have been described in North America: *Pso. compressipes* (Peck) Singer, *Pso. farinacea* (Murrill) Singer, *Pso. felleoides* (Kauffman) Singer, and *Pso. intermedia* (Kauffman) Singer (nom. inval.). Interestingly, the spore length range for all these four, as described in their respective protologues, reached below the shortest reported for the European *Pso. kalchbrenneri*. In addition to these four, Lavorato et al. (2015) identified *Clitocybe aperta* (Peck) Sacc. and *Clitocybe thujana* H.E. Bigelow as morphologically similar species, worthy of further study.

Finding a specimen in 2015, eventually identified as *Pso. kalchbrenneri* (Bres.) Singer in the Canadian province of Newfoundland and Labrador (NL), triggered our interest in this genus. We found only one other record of a species of *Pseudoomphalina* Singer in NL, *Pso. pachyphylla* (Fr.) Knudsen [since then combined as *Pseudolaccaria pachyphylla* (Fr.) Vizzini & Contu], collected at the 2012 annual foray of Foray Newfoundland & Labrador, the mushroom club of the province. Whereas our *Psl. pachyphylla* fits its description well, the specimen identified as *Pso. kalchbrenneri*, while matching macroscopically, had smaller spores than reported for the species from Europe. Spore length range for *Pso. kalchbrenneri* was 6.5–11.5 μm in a large study from the former Czechoslovakia (Kotlaba and Pouzar 1995), 7–10 μm from Bresadola's type specimen of *Omphalia kalchbrenneri* Bres. (Kotlaba and Pouzar 1995), and 6.5–9.5 μm from Scandinavia (Knudsen 2012). By contrast, 40 random spores from our specimen measured 5.5–8.2 μm in length, which is shorter than ranges previously reported from Europe. This intercontinental discrepancy in spore size prompted us to investigate the identity of the species found in NL; suggestions made during the review process led us to extend the regional study to an overview of the *Pso. kalchbrenneri* complex in North America.

Materials and methods

Collecting and morphological methods

Specimen collection, preparation, and microscopy was done as described in Voitk et al. (2017). To eliminate inter-observer error, a single-observer (I. Saar) spore study was carried out to compare the species, but the descriptions are based on all observations by the authors. Twenty-one new collections were studied and sequenced for this study (Table 1), including the holotypes of *Agaricus apertus*, *Agaricus* (*Clitocybe*) *compressipes*, *Clitocybe felleoides*, *C. farinacea*, *C. intermedia*, and *C. thuyana*. The abbreviations of fungaria are used according to Index Herbariorum (Thiers 2019). Because these are not common species, an attempt was made to study as many as could be located through web-based databases (primarily MyCoPortal, www.mycoportal.org; and MushroomObserver, www.mushroomobserver.org) and searches of private and public herbaria. Suitable collections were not included if the owner/custodian could not be contacted, collections were ensconced in other research projects, or they were over 75 years old, provided we already had sampled the taxon they likely represented. To construct the phylogeny, additional sequences deposited in GenBank and UNITE were added to the analysis.

Molecular methods

DNA of recent collections was extracted with lysis procedure in 10× Reaction Buffer B (0.8 mol/L Tris–HCl, 0.2 mol/L $(NH_4)_2SO_4$, 0.2% *w*/*v* Tween-20; Solis Biodyne, Tartu, Estonia), including Proteinase K (0.5 mg/mL; ThermoFisher Scientific Inc., Waltham, Massachusetts, USA) and incubated at 56 °C overnight. A High Pure PCR template preparation kit (Roche Diagnostics GmbH, Mannheim, Germany) was used for the older specimens, following the protocol from the manufacturer. The PCR amplification was performed with the primers ITSOF (5′-ACTTGGTCATTTAGAGGAAGT-3′) – LB-W (5′-CTTTTC-ATCTTTCCCTCACGG-3′), or ITSOF – ITS4B (5′-CAGGAG-ACTTGTACACGGTCCAG-3′) for the ITS region, using 5× HOT FIREPol® Blend Master Mix Ready to Load (with 10 mmol/L $MgCl_2$; Solis BioDyne) with 0.5 μmol/L of each primer and 1–3 μL of DNA solution. In the case of ancient samples, the amplifications were done in two shorter parts using primer pairs ITSOF – ITS2 (5′-GCTGCGTTCTTC-ATCGATGC-3′) and 58SF (5′-ATGCATCGATGAAGAACGC-3′) – ITS4B. The PCR amplification program was as follows: an initial denaturation at 95 °C for 15 min, followed by 35 cycles at 95 °C for 30 s, at 55 °C for 30 s, at 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR products were purified enzymatically (10 U Exonuclease I – 1 U FastAP™ Thermosensitive Alkaline Phosphatase; ThermoFisher Scientific), according to the manufacturer's instructions. The sequences were performed by Macrogen Europe (Amsterdam, the Netherlands) using primers ITS5 (5′-GGAAGTAAAAGTCGTAACAAGG-3′) and

Table 1. Collections from which new sequences have been generated for this study.

GenBank/UNITE No.	Herbarium No. (duplicate No.)	Species	Year	Location	Collector (collection No.)
MK400237/UDB035648	NYSf289, holotype	*Agaricus* (*Clitocybe*) *apertus*	1876	USA, New York	Charles Horton Peck
MK400236/UDB035024	NYSf827, holotype	*Agaricus* (*Clitocybe*) *compressipes*	1879	USA, New York	Charles Horton Peck
MK400235/UDB035009	NY657635, holotype	*Clitocybe farinacea*	1911	USA, New York	William Alphonso Murrill
MK400234/UDB035007	MICH10141, holotype	*Clitocybe felleoides*	1925	USA, Michigan	Calvin Henry Kauffman (C.H.K 2359)
MN326458/UDB0778024	MICH10152, holotype	*Clitocybe intermedia*	1925	USA, Washington	Calvin Henry Kauffman
MK400238/UDB039571	MICH10215, holotype	*Clitocybe thujana*	1941	USA, Washington	Alexander Hanchett Smith (AHS17618)
MK400231/UDB034959	DAOM950273 (TU117630)	*Pseudolaccaria pachyphylla* (as *Pso. pachyphylla*)	2012	CANADA, NL	Renée Lebeuf (TN1-227)
MK982247/UDB0754146	MIN956134	*Pseudoomphalina anticostica* (as *Pso. kalchbrenneri*)	2013	USA, Minnesota	Peter Kennedy (IDENT16)
MK982243/UDB0754097	MIN956467	*Pseudoomphalina anticostica* (as *Pso. kalchbrenneri*)	2013	USA, Minnesota	Peter Kennedy (IDENT24)
MK982242/UDB0754094	DAOM970939, holotype (TU117691, isotype)	*Pseudoomphalina anticostica* (as *Pso. kalchbrenneri*)	2015	CANADA, Quebec	Renée Lebeuf (HRL2133)
MK400233/UDB035004	ACAD2571	*Pseudoomphalina compressipes* (as *Pso. felleoides*)	1953	CANADA, Nova Scotia	Kenneth Archibald Harrison
MK400232/UDB034981	CMMF002076	*Pseudoomphalina compressipes* (as *Pso. kalchbrenneri*)	1993	CANADA, Quebec	Yves Lamoureux
MK982246/UDB0746162	DAOM11115	*Pseudoomphalina compressipes* (as *Clitocybe pinophila*)	1942	CANADA, Ontario	J.W. Groves
MK400230/UDB032729	DAOM950274 (TU117476)	*Pseudoomphalina compressipes* (as *Omphalina* sp.)	2014	CANADA, NL	Andrus Voitk (14.10.11.av03)
MN326459/UDB0778025	MICH53940	*Pseudoomphalina compressipes* (as *Clitocybe intermedia*)	1961	USA, Michigan	Alexander Hanchett Smith (AHS64466)
MN326460/UDB0778026	MICH55730	*Pseudoomphalina intermedia* (as *Clitocybe intermedia*)	1947	USA, Oregon	Alexander Hanchett Smith (AHS28172)
MK982245/UDB0754100	MICH55774	*Pseudoomphalina intermedia* (as *Clitocybe kalchbrenneri*)	1966	USA, Idaho	Alexander Hanchett Smith (AHS73912)
MK982244/UDB0754098	MICH55778	*Pseudoomphalina intermedia* (as *Clitocybe kalchbrenneri*)	1972	USA, Idaho	Alexander Hanchett Smith (AHS82876)
MK400229/UDB031100	TU109855	*Pseudoomphalina kalchbrenneri*	2015	ESTONIA	Jarkko Korhonen, Lasse Kosonen
MK982240/UDB0746161	TU114962	*Pseudoomphalina kalchbrenneri* (as. *Pso. compressipes*)	2017	SWITZERLAND	Ivan Cucchi
MK982241/UDB0746162	TU114963	*Pseudoomphalina kalchbrenneri* (as. *Pso. compressipes*)	2017	SWITZERLAND	Ivan Cucchi

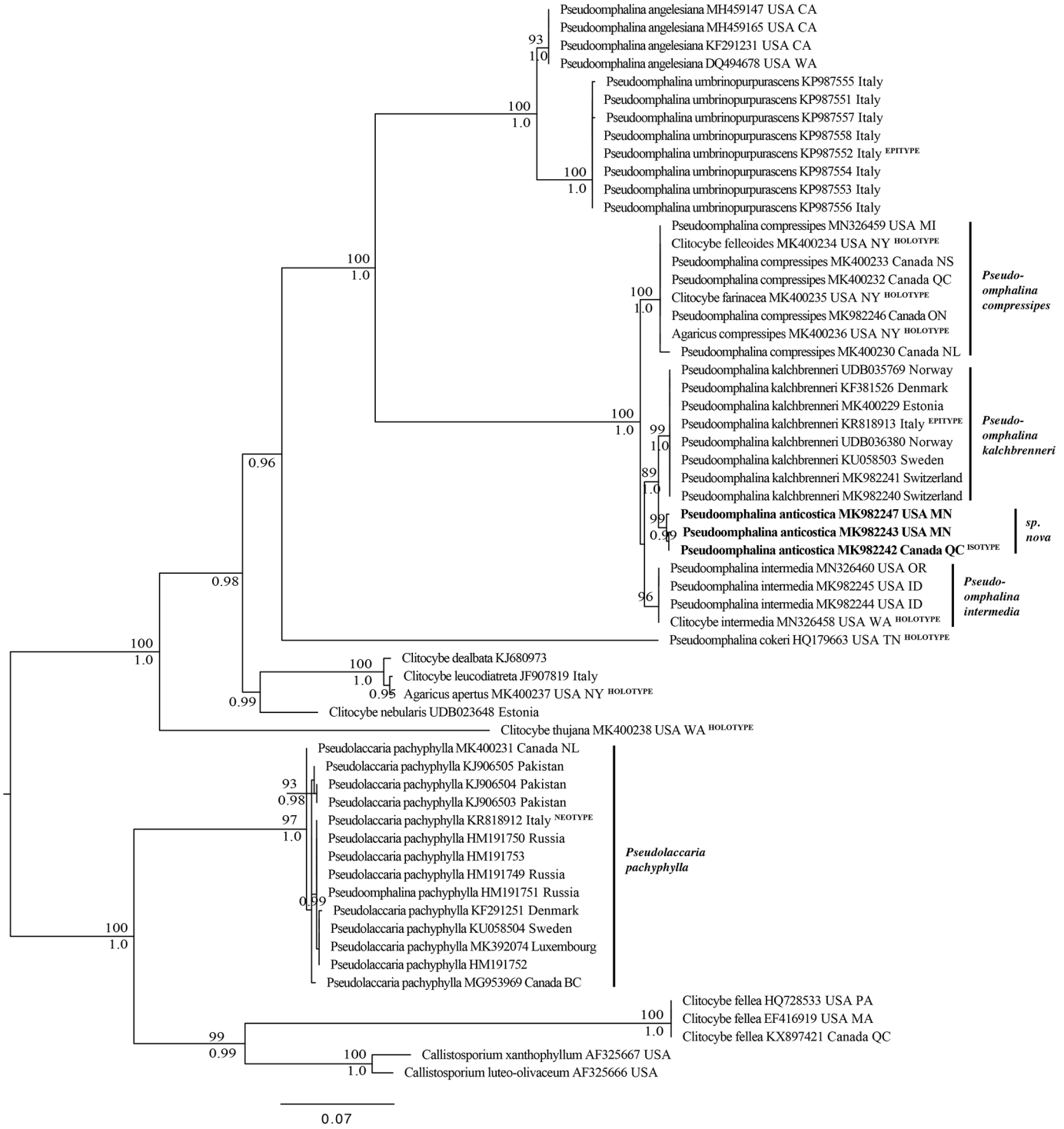
Note: *Pso.*, *Pseudoomphalina*; NL, Newfoundland and Labrador.

ITS4 (5′-TCCTCCGCTTATTGATATGC-3′). In the case of two partial PCR products, we additionally used ITS2 and ITS3 (5′-GCATCGATGAAGAACGCAGC-3′). The sequences were inspected and assembled using Sequencher 5.4.6 software (Gene Codes, Ann Arbor, Michigan, USA). The DNA sequences (Table 1) were uploaded into the PlutoF cloud database (Abarenkov et al. 2010), including the collection data, and are reachable through public web output (UNITE; https://unite.ut.ee; Kõljalg et al. 2013; Nilsson et al. 2019).

Phylogenetic analyses

Alignments were performed using L-INS-i strategy as implemented in MAFFT v7.427 (Katoh and Standley 2013). Minor manual adjustments and preliminary analyses were performed with SeaView 4.7 (Gouy et al. 2010). Bayesian inference of phylogeny was performed with MrBayes 3.2.6 (Ronquist et al. 2012) with default values, and the first 100K generations without reaching a stable likelihood score were discarded. Maximum likelihood (ML) analysis was performed with RAxML-HPC Black-

Fig. 1. The best maximal likelihood (ML) tree of ITS data. Bootstrap values of maximum likelihood analyses (≥80%) and Bayesian Posterior Probabilities (≥0.95) are presented above and below the branches, respectively.



Box v.8.2.12 (Stamatakis 2014), at the Cipres Science Gateway (Miller et al 2010; http://www.phylo.org/).

Results

Phylogeny

Pseudoomphalina and *Pseudolaccaria* arise from separate lineages, confirming the need for a separate genus for *Psl. pachyphylla* (Fig. 1). Sequences of *Psl. pachyphylla* from eastern and western North America fall in the clade containing the European neotype for that species, providing the first sequence-confirmed evidence of that species on the North American continent. The lineage leading to *Pso. kalchbrenneri* forms four separate and well-supported clades. The most ancestral pathway leads to a clade with collections from eastern North America [NL, Nova Scotia (NS), New York (NY), Quebec (QC), Ontario (ON), Michigan

(MI)], including the type specimens for *Ag. compressipes*, *C. farinacea*, and *C. felleoides*. This species is identified as *Pso. compressipes*, after the earliest valid name. The sister lineage from *Pso. compressipes* leads to a pathway with a clade from western North America [Idaho (ID), Oregon (OR), Washington (WA)] containing the holotype for *C. intermedia* Kauffman, so we herein transfer that epithet to *Pseudoomphalina*. The sister lineage from that pathway leads to two sister clades. One is the European *Pso. kalchbrenneri*, and the other is a clade with collections from eastern North America [QC, Minnesota (MN)], which we name as a new species of *Pseudoomphalina* below.

Agaricus apertus arose in a lineage with strong support that was sister to that leading to the *Pseudoomphalina* clade (Fig. 1). A BLAST search on the UNITE homepage (Kõljalg et al. 2013; https://unite.ut.ee) revealed the closest phylogenetic relative (98% matching base pair sequences) to *A. apertus* to be sequence JF907819, identified as *Clitocybe leucodiatreta* Bon. The ITS sequence (JF907819) belongs in the same species hypothesis (SH482221.07FU, https://plutof.ut.ee/#/doi/10.15156/BIO/SH482221.07FU) with three other sequences identified as *C. dealbata* (KJ680973, KJ680974) and *Clitocybe rivulosa* (KJ680978). A BLAST search in UNITE found the closest phylogenetic relatives of *C. thujana*, with 85% matching base pair sequences, to be one specimen identified as a species of *Tephrocybe* (Fr.) Donk (KP192565) and two as *Lyophyllum turcicum* Sesli, Vizzini & Contu (KJ158159, KU183491). The generic placement of these and related species (*Agaricus apertus* and *Clitocybe thujana*) awaits further studies.

Morphology

North American collections of *Pseudolaccaria pachyphylla* fit the description for that species both macro- and microscopically (Fig. 2H). The three North American species in the *Pso. kalchbrenneri* complex all resemble Bresadola's illustration of *Omphalia kalchbrenneri* (Fig. 2F) and the photo of the Italian epitype (Fig. 2G); no obvious macroscopic differentiating characters are evident. Microscopically, the presence of rare to numerous filamentous cheilocystidia (Figs. 3C and 3D) differentiates the two eastern North American species from the western *Pso. intermedia* and the European *Pso. kalchbrenneri*.

Spore sizes overlap, but single-observer ranges and averages (Fig. 4) revealed some difference between the species, even if the small sample size may not permit firm conclusions. Our measurements agree with previous reports and confirm the intercontinental differences we had noted in our initial studies of the NL specimen, but also reveal that the spores of these species are closer in size than initially suspected. The spore length of three sequence-identified European specimens of *Pso. kalchbrenneri* range from 5.5 to 10.0 μm, a full 1.0 μm shorter than the reported 6.5 μm low, thus bringing the longer spores of the European species closer to the shorter North American species. *Pseudoomphalina compressipes* has the shortest spores, and is the only species with mature spores under 5 μm long (10%). The relatively good clustering of the average sizes per specimen, as well as the greater number of collections and spores measured, suggests this is a reliable conclusion. *Pseudoomphalina anticostica*, the other eastern North American species, has the greatest range and longest spores, almost matching *Pso. kalchbrenneri*.

Taxonomy

Pseudoomphalina anticostica Lebeuf, Kennedy & I. Saar, sp. nov. (Figs. 2A, 2B, and 3A–3D)

MYCOBANK: MB832367.

TYPIFICATION: CANADA, Quebec, Anticosti Island, Lac Plantain, 49.8607°N, 64.3972°W, 27 m a.s.l., in *Picea* forest, in litter, 10 September 2015, *Renée Lebeuf*, *HRL2133* (holotype, DAOM970939; isotype, TU117691). GenBank: ITS = MK982242; MycoBank: MBT388480.

ETYMOLOGY: The epithet refers to Anticosti Island, where the holotype was collected.

DIAGNOSIS: Species in the *Pso. kalchbrenneri* complex, macroscopically similar to others. Distinguished by the presence of hymenial cystidia and its eastern North American distribution from the western North American *Pso. intermedia* and the European *Pso. kalchbrenneri*. ITS sequence data and larger spores differentiate it from the sympatric *Pso. compressipes*.

Description

MACROMORPHOLOGY: Pileus 1.5–4.5 cm in diameter, convex at first, depressed in the centre, becoming infundibuliform with age, with a margin incurved becoming strongly crenulate-lobate in old age; surface glabrous, hygrophanous, shiny; colour brownish orange to greyish orange (Methuen: 5B4, 6C-D6-7). Lamellae adnate then decurrent, distant, becoming strongly forked and intervenose with age, thick, waxy, moderately broad; colour off-white becoming pale brownish orange in old age. Stipe 2.8–5.0 cm × 0.4–1.6 cm, central, first cylindrical becoming flattened and flexuous with age, hollow; surface glabrous, concolorous with the cap, covered by white tomentum at base and bearing white rhizomorphs. Context thin; colour whitish. Smell farinaceous; taste farinaceous, bitter. Spore deposit not obtained.

MICROMORPHOLOGY: Spores (Fig. 3A; three collections, four basidiomata, 101 spores, two observers) 5.0–11.5 μm × 3.1–4.9 μm, average = 7.2 μm × 4.0 μm, Q = 1.2–2.6, $Q_{average}$ = 1.8, smooth, ellipsoid, amyloid. Basidia (Fig. 3B) 29–50 μm × 6–7 μm, four-spored. Cheilocystidia (Fig. 3C) 20–50 μm high, protruding up to 25 μm above the hymenium, 3–5 μm wide, 2–5 μm at the apex, abundant, filamentous, sometimes knobby, rarely branched, rarely capitate. Pleurocystidia rare, present close to the gill edge, similar to cheilocystidia. Pileipellis (Fig. 3D) is a cutis made up of repent hyphae 4–9 μm wide, mostly smooth, rarely finely incrusted. Clamps abundant in all tissues.

Fig. 2. Species of *Pseudoomphalina* (A–G) and *Pseudolaccaria pachyphylla* (H). (A–B) ***Pseudoomphalina anticostica***, MIN956467 & HRL2133 (holotype). (C) *Pseudoomphalina compressipes*, CMMF002076. Reproduced by permission of Yves Lamoureux and the Cercle des mycologues de Montréal Fungarium (CMMF). (D–E) *Pseudoomphalina intermedia*, MICH55730 & MICH10152 (holotype; both reproduced by permission of the Regents of the University of Michigan). (F–G) *Pseudoomphalina kalchbrenneri* lectotype, illustration by Giacomo Bresadola from his 1928 Iconographica Mycologia (Bresadola 1928, reproduced by permission of Museo delle Scienze di Trento, Italy), and epitype from Sardinia (reproduced with permission from Fabio Padovan). (H) *Pseudolaccaria pachyphylla*, TN1-227.

ECOLOGY, HABITAT, AND DISTRIBUTION: Putative saprobe. So far known from three collections, one made in mid-September in *Picea* needle litter in Quebec, Canada, and two made in early October on soil under young conifers in northern Minnesota, USA.

ADDITIONAL SPECIMENS EXAMINED: USA, MINN, Carlton, UMN Cloquet Forestry Center, 46.679°N, 92.518°W, 365 m a.s.l., on soil, under monoculture plots of *Picea glauca* and *Larix decidua*, 5 October, 2013, *Nhu Nguyen & Peter Kennedy*, *IDENT16* (MIN956134); idem, *IDENT24* (MIN956467).

COMMENT: Given the small number of collections available, the sympatric *Pso. compressipes* and *Pso. anticostica* are difficult to distinguish macroscopically. See the *Discussion* section for a consideration of spore size. In the phylogenetically confirmed collections, the pileus of the former showed a paler colour, mid-brown to tan to light straw, whereas the pileus of the three confirmed collections of the latter was rather brownish orange to greyish orange. The basidiomata on Fig. 2B show marked crenulation of the cap edge, with larger ones approaching lobulation; the two other collections look like Fig. 2A, resembling the other species. We suspect that Fig. 2A is more representative of the species, and the size and florid crenulation-lobulation are the result of post-maturity hyperplasia, rather than distinguishing characters for the species. More collections will be necessary to confirm noted differences. See under *Pseudolaccaria pachyphylla*, below, for differences from that taxon.

Pseudoomphalina compressipes (Peck) Singer, the Agaricales in modern taxonomy, p. 287. 1962 (Fig. 2C)

≡ *Agaricus compressipes* Peck (basionym), Annual Report on the New York State Museum of Natural History, 33, p. 18. 1883.
≡ *Clitocybe compressipes* (Peck) Sacc., Sylloge Fungorum, 5, p. 184. 1887.
≡ *Clitocybula compressipes* (Peck) Raithelh., Metrodiana, 9(2), p. 47. 1980.
= *Clitocybe farinacea* Murrill, North American Flora, 9(6), p. 401. 1916.
≡ *Pseudoomphalina farinacea* (Murrill) Singer, the Agaricales in modern taxonomy, 4, p. 291. 1986.
= *Clitocybe felleoides* Kauffman, Papers of the Michigan Academy of Science, Arts and Letters, 8, p. 194. 1928.
≡ *Cantharellula felleoides* (Kauffman) Singer, Lilloa, 22, p. 38. 1951 [1949].
≡ *Pseudoomphalina felleoides* (Kauffman) Singer, Sydowia, 15(1–6), p. 52. 1962.

TYPIFICATION: USA, New York, Albany Co., Albany, 1879, *Charles Horton Peck* (holotype, NYSf827).

Description

MACROMORPHOLOGY: Pileus 2–4 cm in diameter, arching downwards from a depressed to umbonate centre, edges lifting to become infundibuliform with crenate margin in age; surface glabrous, at times with concentric or reticulate watery cracks, hygrophanous, opaque ± mildly translucent at edge; mid-brown to tan to light straw colour. Lamellae decurrent, narrow to moderately broad, close to subdistant, forked and interveined; colour off-white to straw. Stipe 2–6 cm × 0.2–0.9 cm, central, ± equal, occasionally flattened ± longitudinally sulcate, pithy to hollow; surface glabrous; concolorous with to darker than cap, covered by a white tomentum at the base and forming white rhizomorphs. Context thin; colour whitish straw. Smell farinaceous. Spore deposit white.

MICROMORPHOLOGY: Spores (Fig. 3E; 8 collections, 10 basidiomata, 197 spores, three observers; see Fig. 4 for single-observer measurements) 4.4–10.0 μm × 2.6–6.0 μm, average = 6.4 μm × 3.8 μm, Q = 1.3–2.5, $Q_{average}$ = 1.7; smooth, ellipsoid; weakly to moderately amyloid. Basidia (Fig. 3F) four-spored, 32–35 μm × 7–8 μm, clavate. Cheilocystidia (Fig. 3D) 50–65 μm high, protruding up to 35 μm above the hymenium, 4–5 μm wide, 2–3 μm at the tips, very uncommon to abundant, filamentous, thin-walled, protruding up to 35 μm; pleurocystidia similar, rare to abundant, mostly present near gill edge. Pileipellis is a cutis made up of repent hyphae 3–6 μm wide, mostly smooth, rarely finely incrusted; abundant cylindrical digitate projections 5–27 μm × 2–3 μm observed in one collection (Fig. 3H). These projections were not noted in a second basidiome from the same collection. Clamps abundant in all tissues.

ECOLOGY, HABITAT, AND DISTRIBUTION: Putative saprobe. Terricolous on woody debris in open areas of or near leafy or mixed forests. Uncommon, occurs in scattered to moderate groups in the autumn; recorded across northeastern North America, as far west as Michigan.

ADDITIONAL SPECIMENS EXAMINED: CANADA, Quebec, Longueuil, 45.544154°N, 73.477185°W, 44 m a.s.l., in soil in a deciduous forest of *Quercus rubra* and *Acer* sp., 27 September 1993, *Yves Lamoureux* (CMMF002076); Newfoundland and Labrador, Newfoundland, Pynn's Brook, Deer Lake beach, under *Alnus* sp., *Salix* sp., 11 October 2014, *Andrus*

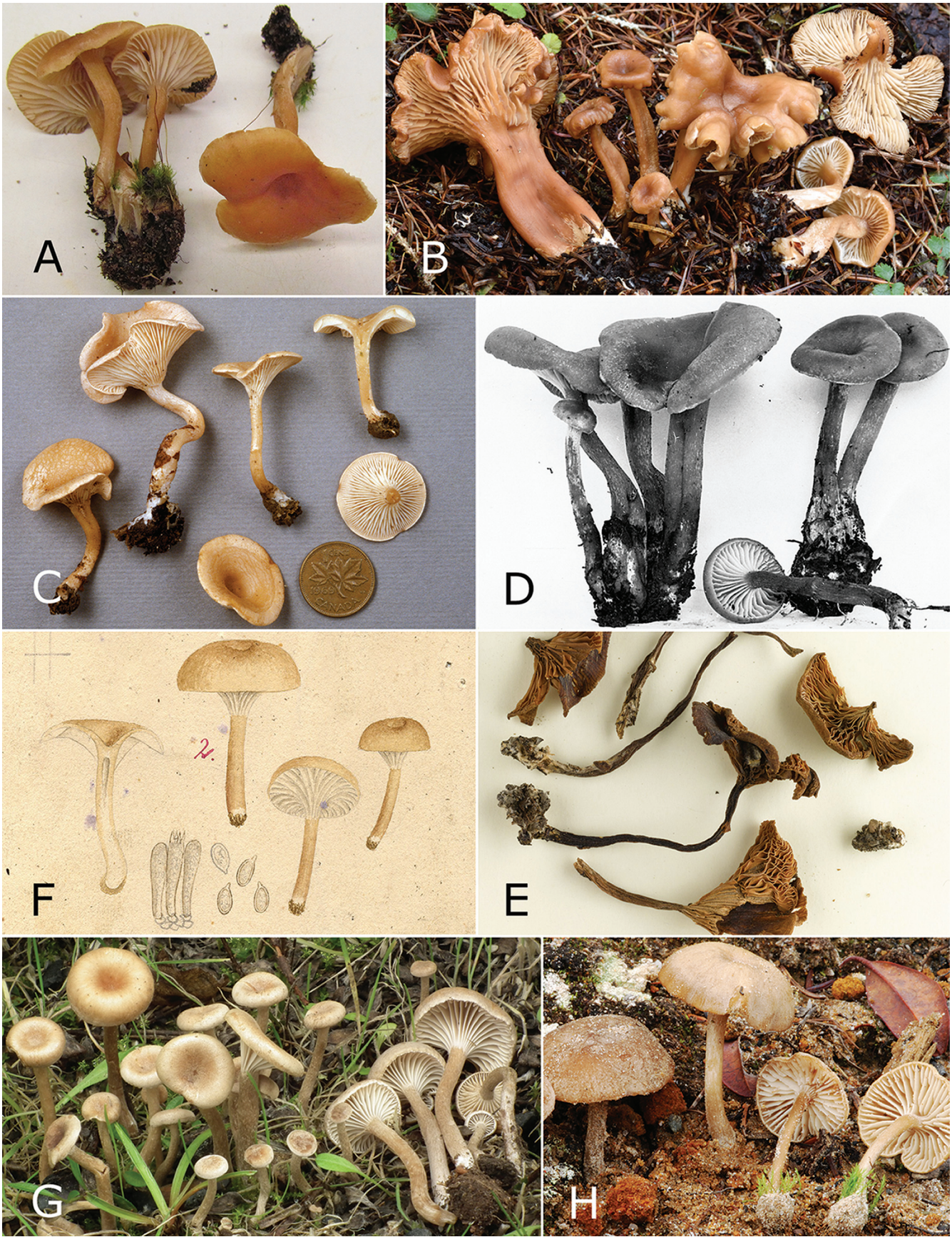
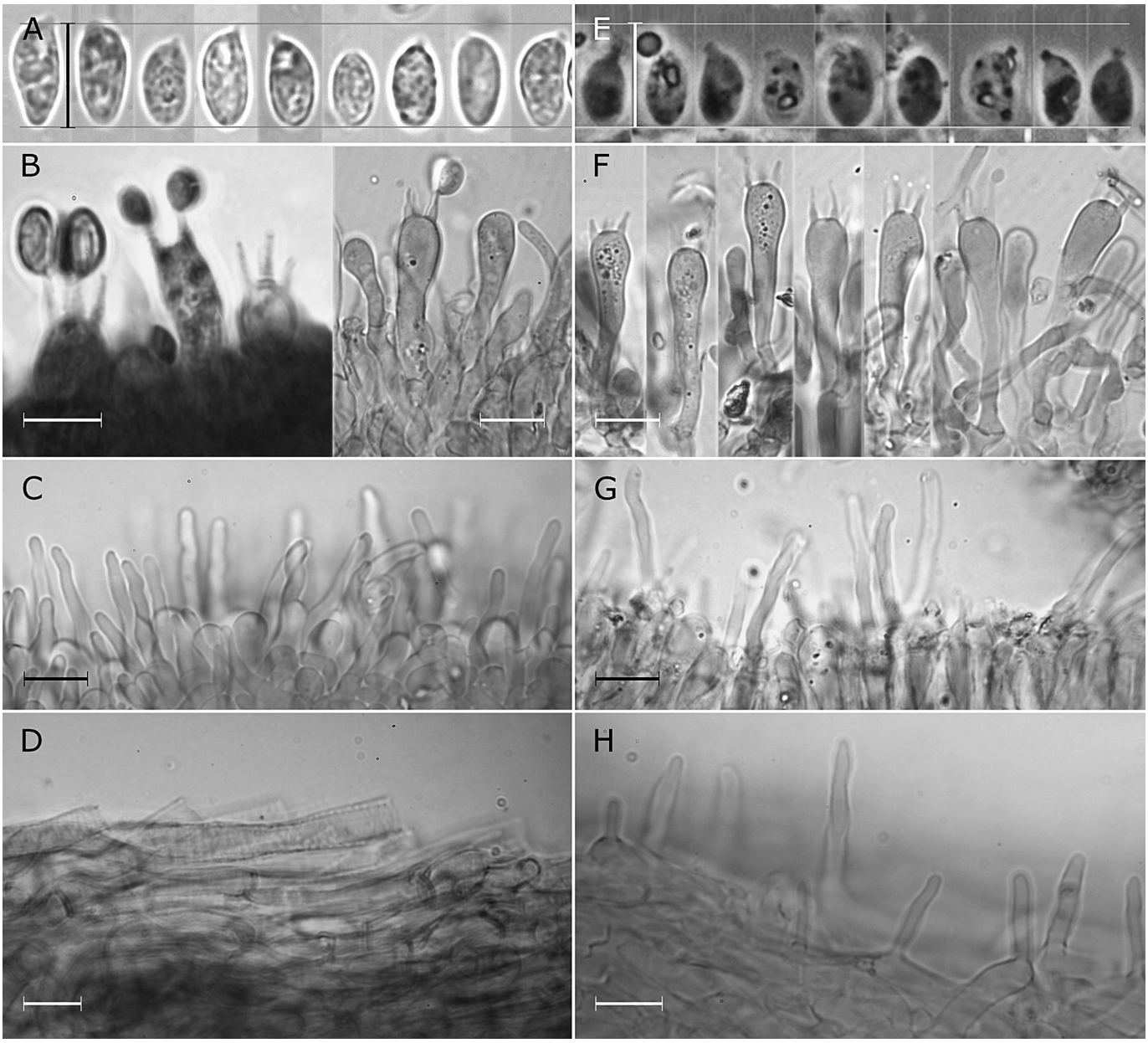


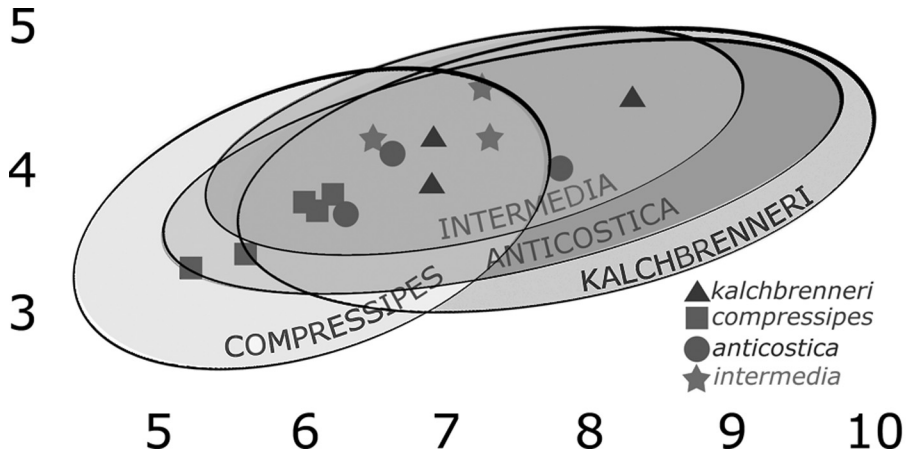
Fig. 3. Micromorphology of ***Pseudoomphalina anticostica*** (A–D; all from holotype, HRL2133) and *Pso. compressipes* (E–H; spores from the holotype, other photos from CMMF2076). (A and E) Basidiospores. (B and F) Basidia. (C and D) Cheilocystidia. (D and H) Pileipellis; cutis for all species, with a few lightly encrusted hyphae. Digitate projections of pileipellis hyphae noted in one basidiome of *Pso. compressipes*. All scale bars = 10 μm; A and E: distance between grey lines = 10 μm.



Voitk, *14.10.11.av03* (DAOM950274, TU117476); Nova Scotia, Kings, Kentville, A.E.S.K., 45.07662°N, 64.49592°W, in ravine, 22 September 1953, *K.A. Harrison*, *2571* (ACAD2574); Ontario, Ottawa, Woods south of Rideau River Ground, 15 September 1942, *J.W. Groves* (DAOM11115). USA, Michigan, Washtenaw, Ann Arbor, Saginaw Forestry Farm, north of Lake, 23 August 1925, *Calvin Henry Kauffman*, *2359* (MICH10141, holotype of *Clitocybe felleoides*); Washtenaw, Island Lake, 26 September 1961, *Alexander Hanchett Smith*, *64466* (MICH53940).

COMMENT: Digitate projections of pileipellis hyphae have not been noted before in this group, including the notes of Bigelow on the pileipellis of Peck's type specimen. Our examination of the type was of a small piece of gill, and did not include the pileipellis. We documented these projections in one basidiome of one collection (CMMF002076, Fig. 3H). Re-examination of two additional collections and of a different basidiome from the same collection did not uncover additional examples of these structures. More observations are needed to know whether this is a differentiating character or an uncommon event in this and possibly other species of the complex. Distribution in eastern North America separates this species from the western *Pso. intermedia* and the European *Pso. kalchbrenneri*; it

Fig. 4. Spore size graphs for *Pseudoomphalina kalchbrenneri* and the three North American species of the complex treated here, based on single-observer (IS) measurements. Length in micrometres plotted on the X axis and width on the Y. Large ovals show spore size ranges and smaller symbols represent average spore sizes of respective sequence-confirmed basidiomata.



also differs from both by the presence of cheilo- and pleurocystidia. It differs from the sympatric *Pso. anticostica* by smaller spores (see *Discussion*) and its ITS sequences. See the description of *Pseudolaccaria pachyphylla* for differences from that taxon.

Pseudoomphalina intermedia (Kauffman) Voitk, I. Saar, Lebeuf & Kennedy, comb. nov. (Figs. 2D and 2E)

≡ *Clitocybe intermedia* Kauffman (basionym), Papers of the Michigan Academy of Science, Arts and Letters, 8, p. 195. (1927) 1928.
≡ *Cantharellula intermedia* (Kauffman) Singer, Lilloa, 22, p. 238. 1951.
≡ *Pseudoomphalina intermedia* (Kauffman) Singer, Sydowia, 15(1–6), p. 53. 1962. Nom. inval., Art. 41.5 (Melbourne).
≡ *Clitocybula intermedia* (Kauffman) Raithelh., Metrodiana, 8(2–3), 29. 1979. Nom. inval., Art. 41.5 (Melbourne).

MYCOBANK: MB832368.

TYPIFICATION: USA, Washington, Grays Harbour, Lake Quinault, Olympic National Park, 47.4742°N, 123.8667°W, on soil, 17 October 1925, *Calvin Henry Kauffman* (holotype, MICH10152).

DIAGNOSIS: Species in the *Pso. kalchbrenneri* complex, morphologically similar to others. Distinguished by the lack of hymenial cystidia and its western North American distribution from the eastern North American *Pso. compressipes* and *Pso. anticostica*, and by distribution from the similarly acystidiate European *Pso. kalchbrenneri*. Differs from all by its ITS sequence data.

MACROMORPHOLOGY: Pileus 1.5–4 cm in diameter, soon planoumbilicate, at length umbilicate-subinfundibuliform, even, glabrous, very hygrophanous, dark tan to reddish-brown when moist, pinkish pale tan when dry; margin at first incurved, soon spreading and thin, paler than disc. Lamellae ascending-decurrent, close to crowded, narrow, thin, edge entire, pale grayish buff or pallid. Stipe 5–7 cm × 0.2–0.5 cm, slender, slightly incrassate downwards, stuffed, then hollow, subterete to compressed-furrowed, glabrous, innately subsilky upwards, dull tawny below, paler above, with white downy base and white rhizomorphs. Context thin. Odour and taste slightly to markedly farinaceous. Spore deposit white.

MICROMORPHOLOGY: Spores (three collections, three basidiomata, 55 spores, one observer) 5.9–8.8 μm × 3.5–5.0 μm, average = 7.1 μm × 4.3 μm, Q = 1.6–1.7, $Q_{average}$ = 1.6; smooth, ellipsoid, weakly amyloid. Basidia four-spored, approx. 34–38 μm × 5–7 μm. Cystidia not seen; said to be absent by Kauffman (1928). Clamps in all tissues.

ECOLOGY, HABITAT, AND DISTRIBUTION: Putative saprobe. Gregarious; terricolous, under pine in the late autumn. Recorded from northwestern North America (ID, OR, WA).

ADDITIONAL SPECIMENS EXAMINED: USA, Idaho, Bonner County, Upper Priest Lake, 48.78107°N, 116.90091°W, 3 October 1966, *Alexander Hanchett Smith, AHS73912* (MICH55774); idem, Priest River Experimental Forest, Priest Lake, 48.3621314°N, 116.76629°W, under cedar, October 1972, *Alexander Hanchett Smith*, *AHS82876* (MICH55778); Oregon, Wasco, Beaver Creek, Mt Hood National Forest, in cleared land, 24 October 1947, *Alexander Hanchett Smith*, *AHS28172* (MICH55730).

COMMENT: The species was combined to *Pseudoomphalina* by Singer (1962) without citing the basionym directly, making the name invalid. Kauffman's epithet remains valid, and we recombine it here, citing the basionym.

We have not seen the species in vivo, and were unable to find mycologists familiar with it, who could provide a current macroscopic description. The provided macroscopic description is adapted from Kaufmann's protologue, augmented by Smith's photos and field notes accompanying two sequenced specimens. Microscopic description based on our examination of sequence-identified exsiccatae, tempered by Kauffman and Smith. From the descriptions and Smith's black and white photo (Fig. 2D), the species seems macroscopically virtually indistinguishable from others in the complex. Absence of hymenial cystidia distinguishes it from the other North American species, and the distribution in

the Pacific northwest of North America sets it apart from all species in the complex, as do its ITS sequences. See the description of *Pseudolaccaria pachyphylla* for differences from that taxon.

Pseudolaccaria pachyphylla (Fr.) Vizzini & Contu, Phytotaxa, 291(1), p. 53. 2015 (Fig. 2H)

≡ *Agaricus pachyphyllus* Fr. (basionym), Observationes mycologicae, 1, p. 76. 1815.
≡ *Clitocybe pachyphylla* (Fr.) Gillet, Les Hyménomycètes ou description de tous les champignons qui croissent en France, 1, p. 169. 1874.
≡ *Camarophyllus pachyphyllus* (Fr.) P. Karst., Bidrag till kännedom av Finlands natur och folk, 32, p. 230. 1879.
≡ *Omphalia pachyphylla* (Fr.) Quél. Enchiridion fungorum in Europa media et praesertim in Gallia vigentium, p. 26. 1886.
≡ *Pseudoomphalina pachyphylla* (Fr.) Knudsen, Nordic Journal of Botany, 12(1), p. 76. 1992.

Description

MACROMORPHOLOGY: Pileus 1–3.5 cm in diameter, convex, usually with a depressed to umbilicate centre, becoming nearly plane; surface finely scaly, non-hygrophanous, tan to light straw colour. Lamellae sinuous, adnate, usually with small decurrent tooth, broad, thick, subdistant; colour off-white to light straw. Stipe 2–5 cm × 0.15–0.25 cm, ± equal with slightly swollen base; surface glabrous to finely tomentose; pithy; concolorous with cap or slightly darker; white tomentum at base. Context firm; colour whitish. Smell farinaceous to near-rancid. Spore deposit white.

MICROMORPHOLOGY: Spores (one collection, two basidiomata, 115 spores, two observers) 6.0–8.5 μm × 4.5–5.5 μm, average = 7.1 μm × 4.9 μm, Q = 1.3–1.7, $Q_{average}$ = 1.4, ellipsoid, smooth, weakly amyloid. Basidia four-spored, about 30 μm × 9 μm. Hymenial and pileal cystidia none. Clamps in all tissues.

ECOLOGY, HABITAT, AND DISTRIBUTION: Putative saprobe. Terricolous in sandy, poor soil and moss of open areas in or near mixed forests, autumn, in scattered to moderate groups; uncommon; recorded in a boreal band across the Northern Hemisphere.

SPECIMENS EXAMINED: CANADA, Newfoundland and Labrador, Newfoundland, Terra Nova Road, in coniferous forest, 27 September 2012, *Renée Lebeuf*, *TN1-227* (DAOM950273, TU117630).

COMMENT: Among differences from species in the *Pso. kalchbrenneri* complex are its smaller size, finely granular cap, non-decurrent to sub-decurrent gills, larger spores, lack of hymenial cystidia, preference for poor, sandy soil, circumpolar distribution, and phylogenetic placement. The ability to thrive in poor soil with little evident source of nutrition suggests that it may be worthwhile to question the lifestyle of this putative saprobe.

Discussion

This census is relatively limited compared with most continental-scale reviews, but because these species are uncommon, our 18 new North American sequences represent the majority of currently available collections, and provide as comprehensive overview of the group as possible. These findings show *Psl. pachyphylla* to be a cosmopolitan circumpolar species, so far unique in its genus, known from Eurasia and now also confirmed from both eastern and western North America. In contrast, species of the *Pso. kalchbrenneri* complex seem more parochial, with one species in Europe and three in North America. Although we suspected that our initial find may differ from the European *Pso. kalchbrenneri*, we did not expect to find that North America harboured three cryptic species, or that the three taxa were conspecific. To date there is no evidence of the existence of a second member in the *P. kalchbrenneri* complex in Europe.

Species of the *Pso. kalchbrenneri* complex resemble each other macroscopically; microscopically, filamentous hymenial cystidia are absent in *Pso. intermedia*, as well as *Pso. kalchbrenneri* (Knudsen 2012). Distribution will distinguish *Pso. kalchbrenneri*, the only species in Europe, and *Pso. intermedia*, the only North American species west of the Great Prairies. Distinguishing between the sympatric *Pso. compressipes* and *Pso. anticostica* is much more difficult, and may require molecular studies for certainty. However, despite significant overlap, spore size may help to separate these two species. Of the North American species, *Pso. compressipes* has the shortest spores and *Pso. anticostica* the longest. Our single-observer spore study found no spores of *Pso. anticostica* shorter than 5 μm, whereas 10% of the mature spores of *Pso. compressipes* were shorter than 5 μm. On the other end, the longest spore of *Pso. compressipes* measured 7.7 μm, whereas 7% of the spores of *Pso. anticostica* were over 8 μm in length. Measuring 20 spores from each of two separate specimens seemed to capture more than one example in both extremes, and may differentiate between the two.

In addition to spore size we noted two differences between these species. We found digitate projections of repent pileal hyphae on *Pso. compressipes*, and none on *Pso. anticostica*. The single observation in a small sample does not permit us to conclude whether this is a rare finding in one, some or all species of the complex. We also noted that *Pso. anticostica* seems to be more reddish than *Pso. compressipes*, but with experience limited to three collections it is also difficult to ascertain its significance. We hope that this study may promote greater awareness of these species, resulting in the discovery of more characters useful in their separation.

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