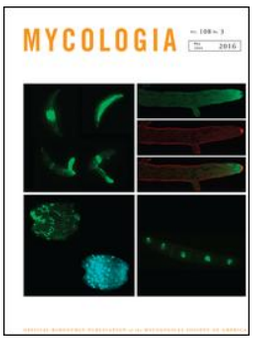

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Adventurous cuisine in Laos: *Hebeloma parvisporum*, a new species in *Hebeloma* section *Porphyrospora*

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ABSTRACT

Hebeloma parvisporum is described as new and placed within *H.* sect. *Porphyrospora*. This mushroom is sold as an edible in markets of Laos under the local name "wai khom." *Hebeloma* sect. *Porphyrospora* is discussed and expanded to include the species formerly included in the genus *Anamika* and recently transferred to *Hebeloma*. *Hebeloma* sect. *Porphyrospora* currently comprises 16 species, 14 of which are known only from the western Pacific and Indian subcontinent. All species in this section share the character of having red-brown spores when fresh, atypical for other sections of *Hebeloma*, which causes the lamellae to be red-brown. However, this red-brown color fades when the material is dried. The close links, morphologically and molecularly, between *H. parvisporum* and other members of *H.* sect. *Porphyrospora*, particularly *H. victoriense*, are shown.

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INTRODUCTION

Hebeloma species are generally regarded as poisonous after consumption by humans in Europe and much of North America (Arora 1986; Bresinsky and Besl 1990; Benjamin 1995). Indeed, the common English name for mushrooms of this genus is "Poison Pie" (Holden 2008–2016; Buczacki et al. 2012; Marren 2012; Siegel and Schwarz 2016). Carrasco-Hernández et al. (2015) reviewed the existing literature and found that cytotoxic triterpenes, lanostane-type triterpene esters, neurotoxic cucurbitane-type glycosides and 6,7-seco-caryophyllenes, and related sesquiterpenoids may be implicated in *Hebeloma* toxicity. *Hebeloma* poisonings typically cause gastrointestinal symptoms in humans that pass after several days. It is not known whether all European and North American *Hebeloma* species are poisonous, but foraging for *Hebeloma* is strongly discouraged (Besl and Bresinsky 1990), particularly given the difficulty of species identification within the genus. Moreover, it cannot be taken for granted that all reports of toxic compounds refer to the correct species or even species group (Beker et al. 2016).

By contrast, there are reports of edible *Hebeloma* species from Mexico and Nigeria (Montoya et al. 2002, 2004, 2008; Pérez-Moreno et al. 2008, 2009; Aremu et al. 2009; Carrasco-Hernández et al. 2015), where, for example, Montoya and colleagues (2002) noted that people considered the *Hebeloma* species they were eating to be of "excellent quality." In Laos, too, a species of *Hebeloma* is sold in markets and on roadsides (FIG. 1A) as edible. It is called "wai khom," referring to a bitter taste, which remains, to some degree, after cooking (O. S. Pedersen, personal observation). This species is macroscopically reminiscent of *H. victoriense* (*H.* sect. *Porphyrospora*) described from Victoria, Australia. After careful examination and comparison with existing species, we concluded that it is a species new to science. It is here described as *Hebeloma parvisporum*.

Yang et al. (2005) were the first to discuss a possible link between *Hebeloma* sect. *Porphyrospora* and the genus *Anamika* originally based on *A. indica* (Thomas et al. 2002). The internal transcribed spacer (ITS)-based phylogenetic hypothesis presented in Yang et al. (2005) shows *H. porphyrosporum* (as *H. sarcophyllum*; see Beker et al. 2016) to be sister species of the then known three members of the genus *Anamika*. The authors, however, concluded that the molecular evidence they had was inadequate to resolve the

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Supplemental data for this article can be accessed on the publisher's Web site.

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Figure 1. A. *Hebeloma parvisporum* as sold in a market in Xieng Khouang. B–D. *Hebeloma parvisporum* holotype (HNL 500968). E. *Hebeloma parvisporum* (HNL 500884). F–G. *Hebeloma porphysporum* (HJB14262) spore deposit. F. Fresh. G. After 1 y. Photographs: A–E. T. Læssøe; F–G. H. J. Beker, reproduced from Beker et al. (2016) with permission.

relationship between *Hebeloma* and *Anamika*. It was Rees et al. (2013) who, based on ITS, showed that members of the genus *Anamika* are closely related to some Australian *Hebeloma* species not sampled in Yang et al. (2005), and that the genus *Anamika* could not be maintained without rendering *Hebeloma* paraphyletic. The phylogenetic hypothesis of Rees et al. (2013) suggested a monophyletic relationship between *H. porphyrosporum* (as *H. sarcophyllum*), *H. victoriense*, both members of *H.* sect.

Porphyrospora (Konrad and Maublanc 1948; Holland and Pegler 1983; Singer 1986), *H. aminophilum* and relatives, as well as *Anamika* species, referred to as the /Porphyrospora clade. Rees et al. (2013) were the first to demonstrate a well-supported monophyletic relationship between species from Asia (China, India, northern Thailand, Japan) and Oceania (Australia, Melanesia, Polynesia, and New Zealand), further referred to as the western Pacific Rim clade. The ITS phylogeny later presented by Kropp (2015) did not support this clade, but the western Pacific Rim clade, including *Anamika*, the then new species *H. ifeleletorum* from American Samoa, and the species groups around *H. victoriense* and *H. aminophilum*, was well supported and consistent with the results of Rees et al. (2013).

Characters originally employed to support the genus *Anamika* were the possession of pleurocystidia, only rarely found in other *Hebeloma* species, the formation of so-called cavernae between the loosening perispore and the spore ornaments, the rather strong spore ornamentation, and the ectomycorrhizal association with Dipterocarpaceae (Thomas et al. 2002). Yang et al. (2005) mentioned taxa in the Fagaceae as additional potential hosts and noted the dry pileipellis and the purplish to reddish-brown spore color. These characters would support joining *Anamika* and *H.* sect. *Porphyrospora*, but Yang et al. (2005) argued that the presence of pleurocystidia was of high taxonomic value in *Anamika* and, given their absence in *H.* sect. *Porphyrospora* and inability to reject statistically the monophyly of *Hebeloma* with respect to *Anamika*, decided to keep the two taxa separate. At that time, only a single European sequence of the section existed.

Our ongoing analyses support Yang et al. (2005), Rees et al. (2013), and Kropp (2015), and we consider *Anamika* as part of *Hebeloma*. In this paper, we discuss *Hebeloma* sect. *Porphyrospora* and some of the characters the species within this section share. In particular, we discuss the red-brown spores, when fresh, that characterize this section and are atypical for other sections within *Hebeloma*. The spore color causes the lamellae and the spore deposit to be red-brown, but this red-brown color fades when the material is dried and eventually disappears altogether. It is demonstrated that *H. parvisporum* collected from Laos fits both morphologically and molecularly within *H.* sect. *Porphyrospora*. ITS data are augmented by analysis of partial DNA sequences of *MCM7* (minichromosome maintenance complex component 7), a gene that encodes a DNA replication licensing factor.

To date, little has been written about the biogeographic distribution of *Hebeloma* as a consequence of the difficulty of species determination. Only recently has it become possible to understand the biogeography of this genus. *Hebeloma* sect. *Porphyrospora* is biogeographically of particular interest given the distribution of its 16 currently recognized species, 14 of which are known only from the western Pacific and Indian subcontinent, whereas for the other two, one is known only from Europe and the other only from North America.

MATERIALS AND METHODS

Basidiomes were collected in Fagaceae-rich woodlands devoid of Dipterocarpaceae in Laos (Lao People's Democratic Republic) in the upland areas of Xieng Khouang Province, dried, and accessioned at the National Herbarium of Laos (HNL) with duplicates at the Copenhagen Fungarium (C).

Sequence data were obtained from dried specimen by direct sequencing following methods detailed in Eberhardt (2012), Vesterholt et al. (2014), Eberhardt et al. (2016), and Cripps et al. (2019). *Flammula alnicola* was used for rooting, and two species of *Alnicola* (*Naucoria* fide Species Fungorum [Index Fungorum Partnership 2019]) (*A. amarescens* and *A. salicis*) were used as additional outgroups. Northern Hemispheric *Hebeloma* sections were represented by material used in earlier publications (TABLE 1) and by Beker et al. (2016). Eight Australian and Asian taxa were represented by their types. Newly generated sequences were accessioned to GenBank (MK957190, MK961944–MK961971, and MK961990–MK962019). For several collections, the ITS was sequenced a second time to verify the DNA extracts prior to attempting to access other loci. In all cases save *H. subvictoriense* (see below), our results supported earlier published data. Material of all sequenced collections (apart from HMAS 280191 and MEL 2382694) was available for examination.

Sequence alignments were done online in MAFFT using the E-INS-i option (Katoh et al. 2017). Alignments were viewed and reformatted using AliView 1.24 (Larsson 2014). Maximum likelihood (ML) analyses were calculated in RAxML 8.2.10 (Stamatakis 2014) locally or on CIPRES (Miller et al. 2010) with the GTRGAMMA or GTRGAMMA+I option, 10 (single locus) or 20 searches for the best ML tree, using the MRE option to limit the number of bootstrap replicates or with at least 1000 replicates.

The compatibility of the two loci was accessed following the principle of Kauff and Lutzoni (2002),

Table 1. Sequences used in the analysis.

Species	Country	HJB database record no.	Voucher	GenBank accession nos.	
				ITS	*MCM7*
Alnicola amarescens	Switzerland	HJB11116	HJB11116	MK961996	MK961952
A. salicis	UK: Isle of Man	HJB14745	HJB14745	MK962001	MK961960
Flammula alnicola	Germany	—	GLM-F045994	MK957190	MK961971
Hebeloma aestivale	UK	HJB9291	HJB9291	KT218221	MK961944
H. alboerumpens	Spain	HJB13021	JVG1090114-15	JQ751220	JQ751104
H. alpinum	Switzerland	HJB11132	HJB11132	KM390590	KM390046
H. aminophilum	New Zealand	HJB10682	PDD 102982	MK961993	MK961949
H. aminophilum	Australia	HJB16823	HO 586929	MK962007	MK961966
H. aminophilum f. hygrosarx	Australia	HJB1000297	PERTH 06659152	MK962016	MK961969
H. angustilamellatum	Thailand	HJB12251	GENT RW07-470	MK961997	MK961953
H. angustilamellatum	Laos	HJB14851	HNL 501000	MK962003	MK961962
H. angustilamellatum	Laos	HJB17006	HNL 501053	MK962010	—
H. angustilamellatum	China	HJB1000408	HKAS 42927	AY575919	—
H. bulbiferum	Croatia	HJB13083	TUR-A 177060	KT218422	MK961956
H. cavipes	Spain	HJB9433	HJB9433	KT217362	KT216685
H. celatum	Germany	HJB13621	BR 5020184119676	KT218446	MK961957
H. crustuliniforme	Spain	HJB11237	HJB11237	JN943870	KF309440
H. cylindrosporum	France	HJB12763	HJB12763	JQ751210	JQ751106
H. dunense	Belgium	HJB14141	AdH11031	KY271835	MK961959
H. ifeleletorum	American Samoa	HJB1000386	UTC 00235643	MK962019	MK961970
H. indicum	India	HJB12902	IB 19991200	MK961999	MK961955
H. indicum	India	HJB1000384	IB 19971307	AF407163	—
H. khogianum	New Caledonia	HJB1000408	M-0124631	GU591635	—
H. lactariolens	Japan	HJB1000560	LAU HC88/95	AY818352	—
H. lactariolens	China	—	HMAS 280191	KX513590	—
H. laterinum	France	HJB13703	HJB13703	MK962000	MK961958
H. mediorufum	New Zealand	HJB10688	PDD 102995	KM390572	KM390042
H. mediorufum	New Zealand	HJB10689	PDD 102983	KM390552	KM390037
H. mesophaeum	Iceland	HJB11050	HJB11050	MK961995	MK961951
H. parvisporum	Laos	HJB14850	HNL 501009	MK962002	MK961961
H. parvisporum	Laos	HJB14852	HNL 500968	MK962004	MK961963
H. parvisporum	Laos	HJB17004	HNL 500914	MK962008	—
H. parvisporum	Laos	HJB17005	HNL 500984	MK962009	—
H. parvisporum	Laos	HJB17007	HNL 500884	MK962011	—
H. plesiocistum	Spain	HJB11514	JVG1021214-5	EU570170	JQ751115
H. porphyrosporum	Italy	HJB10344	HJB10344	MK961992	MK961947
H. porphyrosporum	Spain	HJB10767	HJB10767	MK961994	MK961950
H. radicosum	Belgium	HJB10262	HJB10262	MK961990	MK961945
H. radicosum	Italy	HJB10314	HJB10314	MK961991	MK961946
H. sarcophyllum	USA	HJB15696	DPL10569	MK962005	MK961964
H. sarcophyllum	USA	HJB17783	MO301904	MK962014	—
H. sinapizans	England	HJB10628	HJB10628	JQ751191	JQ751119
H. subvictoriense	Australia	HJB1000299	MEL 2331640	MK962017	—
H. syrjense	France	HJB12064	HJB12064	JQ751206	JQ751122
H. syrjense	Finland	HJB12396	C 26197F	JQ751218	JQ751123
H. theobrominum	Belgium	HJB10063	HJB10063	FJ816623	JQ751125
H. vaccinum	Belgium	HJB9965	HJB9965	KT217371	KT216689
H. velutipes	France	HJB10547	HJB10547	EU570174	MK961948
H. vesterholtii	Italy	HJB11869	HJB11869	FJ943239, FJ943240	JQ751135
H. victoriense	New Zealand	HJB12401	PDD 93802	MK961998	MK961954
H. victoriense	Australia	HJB16704	HO 586713	MK962006	MK961965
H. vinosophyllum	Japan	HJB17411	MO287712	MK962012	MK961967
H. vinosophyllum	Japan	HJB17413	MO299315	MK962013	MK961968
H. westraliense	Australia	HJB1000134	PERTH 01012665	MK962015	—
H. youngii	Australia	HJB1000343	BRI AQ669300	MK962018	—
H. youngii	Australia	—	MEL 2382694	KP012873	—

Note. Herbarium abbreviations follow Index Herbariorum and are given in capital letters followed by a space or hyphen and the herbarium number. Private collections are indicated by the lack of a space between the letters and numbers. MO refers to https://mushroomobserver.org/.

assuming a conflict to be significant if two different relationships for the same set of taxa, one being monophyletic and the other nonmonophyletic, are supported by bootstrap of more than 70% in ML analyses.

The data sets were then concatenated. PartitionFinder 1.1.1 (Lanfear et al. 2012) was used to determine the best-fitting partitioning scheme under the Bayesian information criterion (BIC). ML analyses were run unpartitioned and partitioned using the suggested three partitions under the GAMMAINV model, with or without accounting specifically for invariable positions. The results did not show relevant differences in topology or branch lengths.

A Bayesian inference (BI) analysis was run with MrBayes 3.2.6 (Ronquist et al. 2012) on CIPRES. The BI analysis was done unpartioned in two runs with four chains including one heated chain each, using the GTRINVGAMMA model and a uniform prior and sampling one tree of each run every 10 000 generations. The analysis was stopped automatically after 5.67 million generations. The first 25% of trees were discarded as burn-in.

The acceptance rates of chain swaps, the PRSF (potential scale reduction factor) for model parameters, and taxon bipartitions indicated that convergence was reached (Ronquist et al. 2011). Trees were visualized using FigTree 1.4.4 (Rambaut 2006–2018) and submitted to TreeBASE (accession no. TB2:S24468). Relationships between species are termed fully supported if bootstrap support is 100% or posterior probability is 1, respectively.

Details of morphological analyses were provided in Beker et al. (2016). For each collection, at least 50 spores were measured in Melzer's reagent, excluding the apiculus. The maximum length and width of each spore were measured, and its Q value (ratio of length to width) calculated. Average length, width, and Q value were calculated and recorded alongside the median, standard deviation, and 5th and 95th percentiles. The assessment and coding of spore characters followed Beker et al. (2016) and Vesterholt (2005). The average width of the widest part of the cheilocystidium in the vicinity of the apex appears to be an important character in the separation of species within *Hebeloma* (Vesterholt 2005). It is also important, when determining this average width near the apex, not to be selective with regard to the cystidia chosen for measurement. To determine the average width at the apex, about 100 cheilocystidia were measured on the lamellae edge. For other measurements, at least 20 cheilocystidia, separated from the lamella edge, were measured from each collection. Because of the complex shapes of the cheilocystidia, four measurements were made: length, width at apex (A), width at narrowest point in central region (M), and maximum width in lower half (B). The measurements were given in this order, and an average value was calculated for each of these measurements. For each cheilocystidium, the ratios A/M, A/B, and B/M were calculated and averaged across all cheilocystidia measured. Measurements were made in 5% KOH and Melzer's reagent. For all other details with regard to our methodology, see Beker et al. (2016). Each collection studied has a database record number associated with that collection; we give these numbers because we intend to make the database publicly available.

RESULTS

The data sets included 56 ITS and 42 *MCM7* sequences (TABLE 1). Bootstrap support was based on 350 or 500 replicates, respectively. The single-locus ML results obtained under the GTRGAMMA model (SUPPLEMENTARY FIGS. 1–2) were compatible, with the exception of subclades in *Hebeloma* sect. *Denudata*. These differences were considered irrelevant for the question at hand.

The ML result was calculated under the GTRGAMMA model of the concatenated unpartitioned data set (1436 sites). Bootstrap support was based on 1000 replicates. The topology of the ML tree is shown in FIG. 2. The consensus tree resulting from the BI analysis differed from the depicted ML tree only at few supported parts of the backbone (see TreeBASE submission). Posterior probabilities were based on 852 trees and included in FIG. 2.

The five collections that we refer to as *H. parvisporum*, and on which our description is based, were morphologically and molecularly congruous. We obtained ITS data for all collections of *H. parvisporum* and *MCM7* data for two of them. The species *H. parvisporum* received full bootstrap and posterior probability support. All molecular results supported the monophyly of the *H. victoriense* group within *H.* sect. *Porphyrospora* and a sister clade relationship of *H. parvisporum* and the *H. victoriense* clade (FIG. 2). The latter included *H. khogianum, H. subvictoriense*, and *H. victoriense*.

The clade including species from the western Pacific Rim (*H. aminophilum* and forma *hygrosarx, H. angustilamellatum, H. ifeleletorum, H. indicum, H. khogianum, H. lactariolens, H. parvisporum, H. subvictoriense, H. victoriense, H. westraliense*, and *H. youngii*) was highly supported by bootstrap and Bayesian support values in all results (95–99%). Further, the clade was consistently split in the same two subclades receiving high or very high support (93–100%). The sister clade of the western Pacific Rim taxa consisted of the Northern Hemispheric *H. porphyrosporum, H. sarcophyllum*, and *H. vinosophyllum* from Europe, North America, and Asia, respectively. It was supported with 99% bootstrap and full Bayesian support. The clade including all sequenced taxa of *H.* sect. *Porphyrospora* as circumscribed below received 95% bootstrap support and full Bayesian support. These results supported the inclusion of *Anamika* species in *H.* sect. *Porphyrospora* and in the genus *Hebeloma*.

TAXONOMY

Hebeloma sect. *Porphyrospora* Konrad & Maubl. ex Vesterh. Fungi N Eur 3:25. 2005.

Type: Hebeloma porphyrosporum Maire.

≡ *Hebeloma* sect. *Porphyrospora* Konrad & Maubl., Encycl Mycol 14:183. 1948. [1949], nom. inval. (ICN Art. 39.1, 40.1).

Included species: Hebeloma aminophilum including *H. aminophilum* f. *hygrosarx, H. angustilamellatum, H. ifeleletorum, H. indicum, H. kammala, H. khogianum, H. lactariolens, H. parvisporum, H. porphyrosporum, H. sarcophyllum, H. subvictoriense, H. victoriense, H. vinosophyllum, H. westraliense, H. youngii*.

Figure 2. ML topology of concatenated ITS and *MCM7* sequences of *Hebeloma* and *Alnicola*. *Flammula alnicola* is used for rooting purposes. Bootstrap support based on 1000 replicates and posterior probabilities based on a BI analysis are indicated at the branches. Assignment of species to sections follows Beker et al. (2016). **T** indicates type collections. Thick branches indicate full support. AS = Asia; EU = Europe; NA = North America; O = Oceania; gr. = group.

Description [emended]: Basidiomes with or without distinct veil remnants on the stipe and pileus. Pileus more or less uniformly colored or distinctly two-colored or even three-colored, giving a rosette appearance, the color in the center ranging from very pale and creamy or yellowish to dark brick or fuscous, occasionally with pileus cuticle showing signs of cracking and sometimes with remains of the universal veil distinct on the pileus margin. Lamellae adnexed, emarginate, to adnate, becoming pink to reddish brown, then

vinaceous to purple-brown as the spores mature. Stipe often browning from the base upward, occasionally distinctly rooting, but not with a long "root," often with a distinct ring or with cortina remnants, usually pruinose at apex and more fibrillose or velutinous below. Smell variously described as indistinct, fruity, soapy, reminiscent of *Cortinarius purpurascens*, aromatic, reminiscent of *Lactarius porninsis*; taste mild to bitter. Spore deposit reddish brown but losing the reddish/purplish tinge with time.

Basidiospores av. spore dimensions 6.6–12.1 × 5.1–7 µm, av. spore Q range 1.21–1.90; amygdaloid or citriform, occasionally fusiform, dextrinoid or indextrinoid, ornamentation ranging from punctate to warty, perispore loosening ranging from never to almost always. Basidia av. dimensions 20.7–32.5 × 5.8–8.8 µm, av. Q 2.70–4.90; usually 4-spored. Cheilocystidia av. length between 23 and 70 µm; av. width dimensions: widest part in the vicinity of apex A: 2.2 < A< 8.3, median M: 2.7 < M < 7.8, base B: 2.9 < B < 10; ratios: 0.41 < A/M < 2.48, 0.3 < A/B < 3.27, 0.74 < B/M < 2.93; cylindrical to ventricose or lageniform and lanceolate, occasionally clavate-stipitate or even capitate-stipitate, less often clavate-lageniform, often mucronate to rostrate, sometimes with septa, thin-walled without pigmentation. Pleurocystidia often present, usually similar to cheilocystidia but can be smaller or larger.

Remarks: Hebeloma porphyrosporum, H. sarcophyllum, and *H. vinosophyllum* are three clearly distinct taxa but molecularly closely related (FIG. 2). The inclusion of *H. vinosophyllum* in the clade of *H.* sect. *Porphyrospora* in FIG. 2 is in line with expectations based on morphology (Hongo 1965) but was not supported by the analyses of Rees et al. (2013), who already suspected that the sequence they used for that species had been misidentified.

The ITS sequence we obtained from a single fragment of the type of *H. subvictoriense* was not identical to GU591634 published earlier. We did not consider the earlier sequence, suspecting that it was chimeric. It differed from our sequence by 18 sites (more than 7%) in the ITS1 but was identical in the ITS2. BLAST searches against UNITE (Nilsson et al. 2019) and National Center for Biotechnology Information (NCBI) databases suggest that the ITS1 belongs to an unknown species of *Hebeloma*. Our sequence supports the morphological similarity between *H. victoriense* and *H. subvictoriense* (Holland and Pegler 1983; Rees et al. 2013), and they may well be conspecific. *Hebeloma khogianum* (Bresinsky 2000) is also very similar morphologically and molecularly, and we suspect this too may be conspecific.

Hebeloma aminophilum, H. aminophilum f. *hygrosarx*, and *H. westraliense* (Miller and Hilton 1987; Bougher et al. 1991; Rees et al. 2013) all have similar morphology and are molecularly very similar to each other. Further research will be required to determine whether these taxa are also conspecific. Although we were not able to obtain molecular data from *H. kammala* (Grgurinovic 1997), we suspect from the morphology that it may also be very closely related, if not conspecific, with *H. aminophilum.*

To date within Europe, we know of only one species within *H.* sect. *Porphyrospora, H. porphyrosporum* (Beker et al. 2016). Similarly, we are only aware of a single taxon from this section that occurs in North America, *H. sarcophyllum* (Peck 1873). Josserand and Smith (1941) argued that *H. porphyrosporum* and *H. sarcophyllum* should be considered synonyms, but this synonymy was rejected by Beker et al. (2016). The molecular results shown here support these two species as distinct. A third species, molecularly and morphologically similar to these two species, is *H. vinosophyllum*, originally described from east Asia (Hongo 1965) but also recorded in Indo-China (Ho et al. 2014). Although molecularly close, *H. porphyrosporum, H. sarcophyllum*, and *H. vinosophyllum* do not overlap in their distribution according to current knowledge.

Within the western Pacific Rim, there are a number of species, in addition to *H. vinosophyllum*, that may be ascribed to this section. When describing *H. vinosophyllum*, Hongo (1965) noted what he called the remarkable color of the lamellae and spore deposit and their similarity to features in *H. sarcophyllum*. It does appear that the most important morphological feature that characterizes members of this section is the spore color as the spores mature. This has been described variously as red-brown, vinaceous, purple-brown, porphyry, etc. Although this color seems distinct in fresh material, it does disappear over time. FIG. 1F–G illustrates the color of a fresh spore deposit from *H. porphyrosporum* and the same spore deposit 1 y later. Although this reddish color of the mature spores has been regularly recorded for almost all species we include within this section, there are two species, namely, *H. angustilamellatum* and *H. indicum*, within the section for which the color has never been explicitly stated. However, the original descriptions for these two species do mention the spore deposit color, and although in both cases it is stated as brown, the color is given as 7D5 to 7E5 for *H. angustilamellatum* (Yang et al. 2005) and 7E5 to 7E6 for *H. indicum* (Thomas et al. 2002). These color codes are from Kornerup and Wanscher (1961) and can be interpreted as fawn to dark brick (see Beker et al. 2016 and Vesterholt 2005). By contrast, *Hebeloma* spore deposits, for species from all other sections, are usually recorded in the ranges 5D4–6, 5E4–7, 5F8, 6D5, 6E4–6, and 6F4–8 (clay buff to isabella to

brownish olive, grayish brown to umber or sepia), as described in Beker et al. (2016). From Europe, according to Beker et al. (2016), only *H. porphyrosporum* has a spore deposit described as dark brick (7F7, 8E5). But, as stated above, it must be emphasized that this color does disappear with time and the spore deposit eventually becomes umber. This could be one reason why Smith et al. (1983) did not treat spore color as a taxonomically important character in *Hebeloma*.

As a side note, Locquin (1977) split the genus *Hebeloma* into four genera, based on, among other characters, spore color. These genera are currently considered synonyms of *Hebeloma* (e.g., Beker et al. 2016). One of these genera was *Sarcoloma* defined by "Cap more or less viscid; Stem naked; Spore deposit reddish-Brown" (Locquin 1977), including *H. lignicola, H. porphyrosporum*, and *H. sarcophyllum. Hebeloma lignicola* was described by Rick (1938) from Brazil (as *H. lignicolum*). The inclusion of *H. lignicola* in *Sarcoloma* by Locquin is based on the cinnamon-colored dense lamellae; according to Rick (1938, 1961), the spores are argillaceous and thus not of remarkable color. It is reported as growing on wood (Rick 1938, 1961), with a striate transparent cap margin and the lamellae becoming watery; it is unlikely that this taxon belongs to the genus *Hebeloma*.

Hebeloma parvisporum Sparre Pedersen, Læssøe, Beker & U. Eberh., sp. nov. FIGS. 1B–D, 3
MycoBank MB832243

Typification: LAOS. XIENG KHOUANG: Laethong, Phoukhout (19.742408, 103.258102, approx. 1135 m above sea level [a.s.l.]), on soil under Fagaceae, 18 Aug 2015, *T. Læssøe, O.S. Pedersen* (**holotype** HNL 500968, **isotype** C-F-122153 (C), database record HJB14852). GenBank: ITS = MK962004; *MCM7* = MK961963.

Diagnosis: Differs from all phylogenetically confirmed species of the genus by the small size of the spores and the low spore Q value.

Etymology: *parvisporum* (Latin), in reference to the small spores.

Description: Basidiomes often gregarious in caespitose groups or scattered. Pileus (40–)70–120 mm wide, convex to broadly umbonate; surface dry or slightly viscid, with clear veil remnants often forming a band around the pileus; cuticle color predominantly orange-brown (5B6, 5C6), sometimes with distinct cracking and with paler margin, off-white to cream-colored; pileus margin involute in immature basidiomes, becoming wavy (undulate) when old. Lamellae adnate, sometimes with a small decurrent tooth, 4–6 mm deep at the widest point, moderately dense or crowded, thin, with 76–84 full length lamellae and 2–3 lamellules between the lamellae, off-white to grayish when young, later pinkish or grayish red (8C3) to purplish and eventually vinaceous to purple-brown following spore maturity; droplets on the lamellae distinct and visible to the naked eye; edges strongly fimbriate and white; the white edge remains when the basidiome is dried, but the reddish-brown color of the lamellae disappears with time. Stipe 75–155 mm long and with central width 9–30 mm (up to 40 mm at the base), cylindrical in the upper part but usually clavate toward the base, sometimes distinctly bulbous or tapering and even occasionally slightly but distinctly rooting, basal shape often described as turnip-shaped, i.e., widening toward a clavate base before beginning to taper toward a short "root," white or alutaceous, becoming hollow with age; surface dry, floccose, with floccules usually in bands around the stipe, giving the appearance of broad brown belts; pruinose in the area between the veil and the lamellae attachment. Veil clearly visible as a thin membrane completely covering the lamellae in immature and even mature basidiomes, often persisting, leaving a clear ring zone on the stipe as the pileus expands and the veil breaks away. Flesh white, almost never discoloring where bruised. Smell indistinct; taste bitter. Spore deposit purple-brown (10E4) when fresh, fading to fawn (7D5) after 1 y. Exsiccata with no particular characteristics.

Basidiospores 6.6–8.3 × 4.7–6.5 µm, based on n = 52 spores of the holotype, 5th to 95th percentile range 6.7–7.8 × 5.4–6.3 µm, with median 7.4 × 5.9 µm and av. 7.3 × 5.9 µm with SD length 0.34 µm and width 0.33 µm; Q value 5th to 95th percentile range 1.20–1.32, with median 1.24 and av. 1.25 with SD 0.05; spore size based on five collections, median 6.7–7.4 × 5.5–5.9 µm and av. 6.6–7.38 × 5.5–5.9 µm with SD length 0.34–0.53 µm and width 0.31–0.42 µm, av. Q 1.21–1.26, amygdaloid to nearly ellipsoid, with small apiculus and rounded apically, with a distinct thinning of the apical wall and never any sign of papilla, guttulate with one or occasionally more oily drops, usually very strongly ornamented, warty, with a strongly loosening perispore on almost every mature spore (almost making the spores appear spherical at low magnification) and weakly but distinctly dextrinoid (O3/4; P3; D2/3); spore color under the microscope yellow-brown to brown. Basidia 20–29 × 6–9 µm, av. 21.5–26.3 × 7.1–8.1 µm, cylindrical to clavate, without pigmentation, 4-spored. Cheilocystidia 41–51 × 6.5–8.3 × 3.0–4.7 × 2.9–4.3 µm avs. based on approx. 20 selected cheilocystidia of each of the five collections and 41 × 6.5 × 3.8 × 3.3 µm av. for holotype; width near apex holotype 5% to 95% percentile range 4.9–8.3 µm, with median 6.5 µm and av. 6.5 µm with SD 0.98 µm; across five collections, median 6.5–8.4 µm and av. 6.5–8.3 µm. Cheilocystidium av. ratios A/M: 1.8–2.48, A/B: 2.08–3.27,

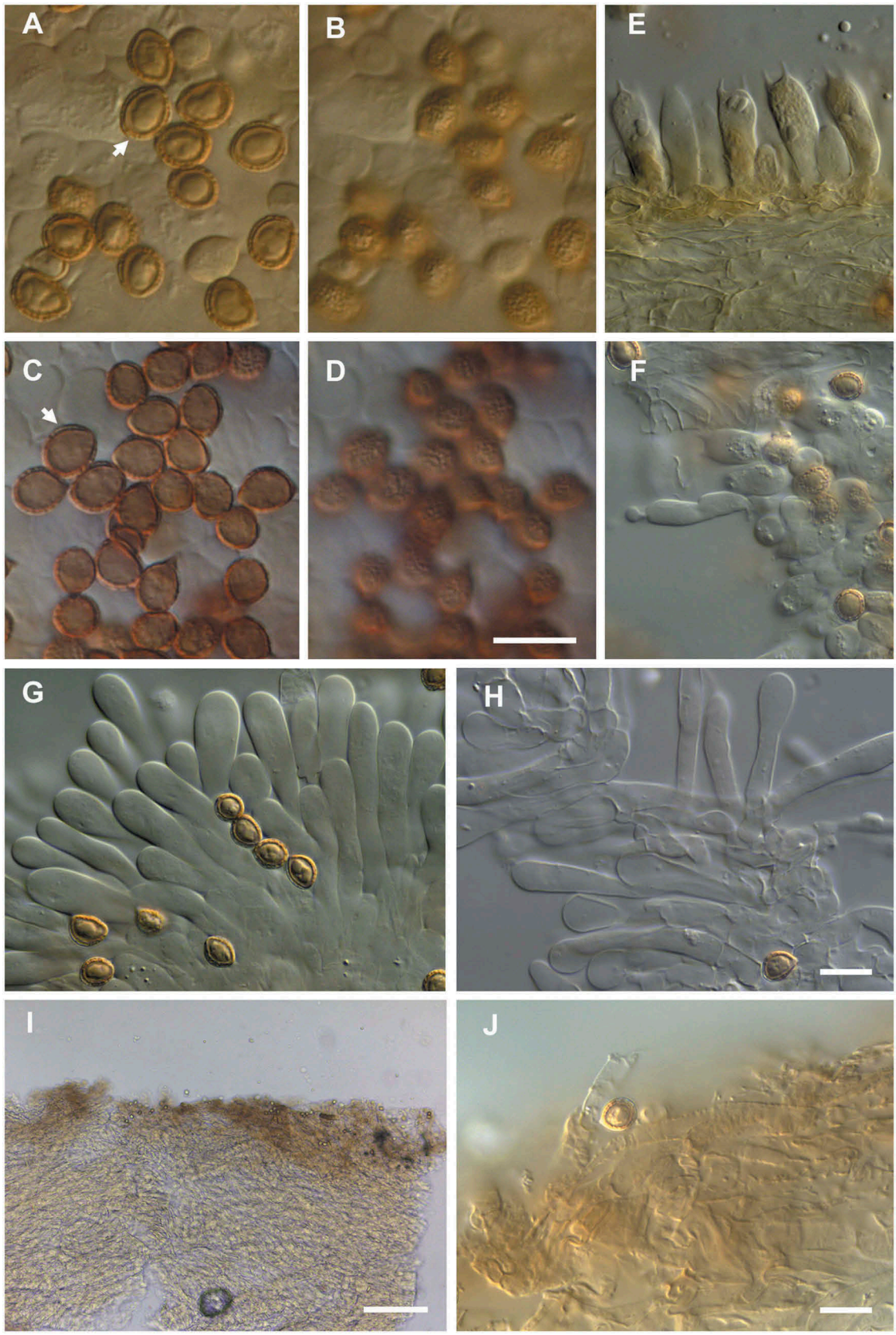

Figure 3. *Hebeloma parvisporum* holotype (HNL 500968). A, C. Spores in 5% KOH and Melzer's reagent, respectively. Arrows indicate loosening perispore. B, D. Spore ornamentation in 5% KOH and Melzer's reagent, respectively, at ×1600. E. Basidium. F. Pleurocystidium. G. Cheilocystidia. H. Caulocystidia in 5% KOH at ×1000. I. Cutis at ×125. J. Encrusted epicutis hyphae in KOH at ×1000. Bars: D = 10 µm; H = 10 µm; I = 10 µm; J = 100 µm. Photographs: H. J. Beker.

B/M: 0.74–1.16, mostly clavate-stipitate or capitate-stipitate, rarely swollen toward the base, occasionally with unclamped septa or some thickening of the apical wall. Pleurocystidia absent or rare, found in only one of the collections examined, sparse and only found close to the lamella edge, short, ventricose and/or mucronate. Caulocystidia resembling the cheilocystidia but tending to be larger, up to 80 µm long. Pileipellis an ixocutis with a very thin epicutis only about 10 µm thick, with gelatinized and encrusted hyphae up to 5 µm wide. Cutis orange-brown and the trama below the cutis made up of cylindrical and ellipsoid cells up to 12 µm wide. Clamp connections present throughout the basidiome.

Ecology and distribution: In Fagaceae (presumably *Quercus* and/or *Castanopsis*)-rich upland woodlands without Dipterocarpaceae but sometimes intermixed with Pinaceae, Laos, Aug. *Hebeloma angustilamellatum* was found in several sites in the same habitat.

Additional collections examined: LAOS. XIENG KHOUANG: Ban Bong, Phoukhout (19.672180, 103.135841, approx. 1150 m a.s.l.), under Fagaceae 15 Aug 2015, *T. Læssøe, O.S. Pedersen* (HNL 500884, database record HJB17007); Phonekham, Pek (19.494286, 103.269110, approx. 1125 m a.s.l.), under Fagaceae, 16 Aug 2015, *T. Læssøe, O.S. Pedersen* (HNL 500914, database record HJB17004); Sui, Phoukhout (19.530514, 102.8659, approx. 1150 m a.s.l.), under Fagaceae, 19 Aug 2015, *T. Læssøe, O.S. Pedersen* (HNL 500984, database record HJB17005); Thoum, Khoun (19.314945, 103.409749, approx. 1130 m a.s.l.), under Fagaceae, 20 Aug 2015, *T. Læssøe, O.S. Pedersen* (HNL 501009, database record HJB14850).

Remarks: Hebeloma parvisporum is currently only known from Laos. It was depicted and discussed under the name *H.* aff. *victoriense* in Læssøe et al. (2019). The small, strongly ornamented, warty spores with Q value less than 1.30 and with strongly loosening perispores are sufficient, microscopically, to distinguish this species from other species of *Hebeloma* that we have encountered. The capitate-, clavate-, or spathulate-stipitate cheilocystidia are reminiscent of *H.* subsect. *Crustuliniformia* of *H.* sect. *Denudata*. Macroscopically, this species is very distinctive and reminiscent of *H. victoriense* but is smaller, less robust, and more slender.

We are not aware that the species has been described before in *Hebeloma* or any other genus. Considering the spore color, it might be mistaken for an *Entoloma* species, but both macro- and microscopically the two genera are easily distinguished. *Hebeloma lactariolens* was first described in *Alnicola*, but although *Hebeloma* and *Alnicola* are in the same family, it is rare that they are mistaken for one another. The species might be mistaken for a *Pholiota*, if fresh material were not available.

In the diagnosis, the restriction to phylogenetically confirmed species of *Hebeloma* was made, because a number of species that have been described as *Hebeloma* have smaller spores than *H. parvisporum*. These taxa have since been shown not to belong to the genus (e.g., Beker et al. 2016), but not all of these species have been transferred to other genera yet. This also applies to *H. microsporum* (Eberhardt et al. 2018).

DISCUSSION

Hebeloma parvisporum is a distinctive species both macroscopically as well as microscopically and can easily be recognized and distinguished from similar taxa even in the field. Macroscopically, it most closely resembles *H. victoriense* with the dry appearance of the pileipellis, the membranous ring, and the reddish-brown lamellae, but it is smaller and more slender than *H. victoriense*. Further, as far as we are aware, *H. parvisporum* and members of the *H. victoriense* group do not overlap in their geographic distribution.

Microscopically, the species is easy to recognize. *Hebeloma parvisporum* has spores that are shorter, and have a lower Q value, than any *Hebeloma* we have so far encountered. This character alone is sufficient to differentiate this taxon from all other known *Hebeloma*. Molecularly, this species is also distinct, even based on ITS alone.

We include *H. parvisporum* within *H.* sect. *Porphyrospora*. With the red-brown spores, which are otherwise typical *Hebeloma* spores, and presence in the western Pacific Rim, this taxon fits well within the section morphologically, biogeographically, and phylogenetically (FIG. 2). To date, there is limited information available with regard to *Hebeloma* in this region of the world. In particular, the ectomycorrhizal relationships that exist in these regions are poorly understood and not well noted to genus level within Fagaceae. Surveys of the region where *H. parvisporum* were collected only revealed one additional species of *Hebeloma, H. angustilamellatum*.

Although the ML support of the monophyly of *Hebeloma* as a genus is somewhat wanting, the BI result supports the monophyly. Thus, our analyses agree with the taxonomic decision of Rees et al. (2013) to include *Anamika* in *Hebeloma. MCM7* data alone, as well as the concatenated ITS and MCM7 data, support the monophyly of *H.* sect. *Porphyrospora* as circumscribed above, at least for the species for which we had data available.

Although we did not receive full bootstrap support for *H.* sect. *Porphyrospora* in this wider sense, we consider the

character of the spore color, reddish-brown when fresh, becoming a more dullish brown later, as crucial, because this character only occurs within this group and nowhere else in *Hebeloma* (see discussion on *H.* sect. *Porphyrospora*).

The western Pacific Rim clade of *H.* sect. *Porphyrospora* with its two well-supported subclades is very similar across all analyses (Rees et al. 2013; Kropp 2015; FIG. 2), both in branching pattern and in the rather long branch lengths between species or species groups. This pattern, wherein the Northern Hemispheric species are more closely related and in the Southern Hemisphere there are fewer species with long internal and terminal branches within the clades, is the same as that described for *Laccaria* (Sheedy et al. 2013; Wilson et al. 2017). The same might be true for *H.* sect. *Denudata* with numerous and often difficult to distinguish Northern Hemispheric taxa (Eberhardt et al. 2015, 2016; Beker et al. 2016) and its Australasian sister clade comprising *H. mediorufum, H. nothofagetorum*, and *H. lacteocoffeatum* (Rees et al. 2013). However, branch lengths between species might change considerably if further species of *H.* sect. *Porphyrospora* are discovered. Also, the recognition of different numbers of species in the *H. aminophilum* and *H. victoriense* groups could challenge this view. Thus, at this time, it is difficult to assess how this pattern may change as more material becomes available.

To our knowledge, none of the Australasian species or other western Pacific Rim species in *H.* sect. *Porphyrospora* are considered edible. There are a number of studies showing that *Hebeloma* contains compounds toxic to humans (Carrasco-Hernández et al. 2015), but owing to the problems that existed to identify *Hebeloma* to species, in most cases it is impossible to know in retrospect which species of *Hebeloma* (and how many) were used in these studies. One exception exists, namely, the studies by Fujimoto and coworkers (Fujimoto et al. 1982, 1986, 1987) demonstrating toxic compounds in *H. vinosophyllum*, which, although not part of the western Pacific Rim clade of *H.* sect. *Porphyrospora*, is a member of the section. Some members of *H.* sect. *Porphyrospora* are famous for their own "cuisine"; they are known as ammonia fungi (Suzuki et al. 2003), occurring in the vicinity of bones from buried mammals.

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LITERATURE CITED

Aremu MO, Basu SK, Gyar SD, Goyal A, Bhowmik PK, Datta Banik S. 2009. Proximate composition and functional properties of mushroom flours from *Ganoderma* spp., *Omphalotus olearius* (DC.) Sing. and *Hebeloma mesophaeum* (Pers.) Quél. used in Nasarawa State, Nigeria. Malaysian Journal of Nutrition 15:233–241.

Arora D. 1986. Mushrooms demystified. Berkeley, California: Ten Speed Press. 1056 p.

Beker HJ, Eberhardt U, Vesterholt J. 2016. Hebeloma (Fr.) P. Kumm. Lomazzo, Italy: Edizioni Tecnografica. 1232 p.

Benjamin DR. 1995. Mushrooms: poisons and panaceas—a handbook for naturalists, mycologists, and physicians. New York: W.H. Freeman. 416 p.

Bougher NL, Tommerup IC, Malajczuk N. 1991. Nuclear behaviour in the basidiomes and ectomycorrhizas of *Hebeloma westraliense* sp. nov. Mycological Research 95:683–686.

Bresinsky A. 2000. *Hebeloma khogianum* sp. nov., *Hygrocybe fibula* sp. nov. et autres macromycètes de la Nouvelle-Calédonie. Bulletin trimestriel de la Société Mycologique de France 116:217–229.

Bresinsky A, Besl H. 1990. A colour atlas of poisonous fungi; a handbook for pharmacists, doctors, and biologists. London, UK: Wolfe. 251 p.

Buczacki S, Shields C, Ovenden D. 2012. Collins fungi guide. London, UK: Harper Collins Publishers. 604 p.

Carrasco-Hernández V, Pérez-Moreno J, Quintero-Lizaola R, Espinosa-Solares T, Lorenzana-Fernández A, Espinosa-Hernández V. 2015. Edible species of the fungal genus *Hebeloma* and two neotropical pines. Pakistan Journal of Botany 47:319–326.

Cripps C, Eberhardt U, Schütz N, Beker HJ, Evenson VS, Horak E. 2019. The genus *Hebeloma* in the Rocky Mountain alpine zone. MycoKeys 46:1–54.

Eberhardt U. 2012. Methods for DNA barcoding fungi. In: Kress JW, Erickson DL, eds. DNA barcodes: methods and protocols. New York: Humana Press Imprint. p. 183–205.

Eberhardt U, Beker HJ, Vesterholt J. 2015. Decrypting the *Hebeloma crustuliniforme* complex: European species of *Hebeloma* section *Denudata* subsection *Denudata*. Persoonia 35:101–147.

Eberhardt U, Beker HJ, Vesterholt J, Schütz N. 2016. The taxonomy of the European species of *Hebeloma* section *Denudata* subsections *Hiemalia, Echinospora* subsect. nov. and *Clepsydroida* subsect. nov. and five new species. Fungal Biology 120:72–103.

Eberhardt U, Schütz N, Krause C, Beker HJ. 2018. *Hebelomina* (Agaricales) revisited and abandoned. Plant Ecology and Evolution 151:96–109.

Fujimoto H, Suzuki K, Haginiwa H, Yamazaki M. 1986. New toxic metabolites from a mushroom, *Hebeloma vinosophyllum*. I. Structures of hebevinosides I, II, III, IV, and V. Chemical and Pharmaceutical Bulletin 34:88–99.

Fujimoto H, Haginiwa H, Suzuki K, Yamazaki M. 1987. New toxic metabolites from a mushroom, *Hebeloma vinosophyllum*. II Isolation and structures of hebevinosides VI, VII, VIII, IX, X, and XI. Chemical and Pharmaceutical Bulletin 35:2254–2260.

Fujimoto H, Yamazaki M, Suzuki A. 1982. Survey of the toxic *Hebeloma* and isolation of the toxic principle of *H. vinosophyllum*. Transactions of the Mycological Society of Japan 23:405–412.

Grgurinovic CA. 1997. Larger fungi of South Australia. Adelaide, Australia: The Botanic Gardens of Adelaide and State Herbarium and The Flora and Fauna of South Australia Handbooks Committee. 725 p.

Ho B-TQ, Pham N-DH, Shimizu K, Fukiharu T, Truong BN, Suzuki A. 2014. The first record of *Hebeloma vinosophyllum* (Strophariaceae) in Southeast Asia. Mycotaxon 128:25–36.

Holden L. 2008–2016. English names for fungi (Mar 2016). [cited 2019 Apr 20]. Available from: https://www.britmycolsoc.org.uk/application/files/3214/5925/9120/English_names_Mar_2016.pdf

Holland AA, Pegler DN. 1983. *Hebeloma victoriense* and the genus *Metraria*. Transactions of the British Mycological Society 80:157–186.

Hongo T. 1965. Notes on Japanese larger fungi (17). Journal of Japanese Botany 40:311–318.

Index Fungorum Partnership. 2019. Species Fungorum. [cited 2019 Apr 20]. Available from: http://www.speciesfungorum.org/Names/Names.asp

Josserand M, Smith AH. 1941. Notes on the synonymy of French and American agarics II. Mycologia 33:483–505.

Katoh K, Rozewicki J, Yamada KD. 2017. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics bbx108:1–7.

Kauff F, Lutzoni F. 2002. Phylogeny of the Gyalectales and Ostropales (Ascomycota, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. Molecular Phylogenetics and Evolution 25:138–156.

Konrad P, Maublanc A. 1948. Les Agaricales. Classification, revision des espèces, iconographie, comestibilité. Agaricaceae. Paris, France: Paul Lechevalier & Fils. 469 p.

Kornerup A, Wanscher JH. 1961. Reinhold color atlas. Guide to accurate color matching. New York: Reinhold Publishing Company. 224 p.

Kropp BR. 2015. A Samoan *Hebeloma* with phylogenetic ties to the western Pacific. Mycologia 107:149–156.

Læssøe T, Pedersen OS, Sysouphanthong P. 2019. An introduction to the edible, poisonous and medicinal fungi of northern Laos. Privately published, printed in Bangkok. 192 p.

Lanfear R, Calcott B, Ho SYW, Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29:1695–1701.

Larsson A. 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. Bioinformatics 30:3276–3278.

Locquin MV. 1977. Flore mycologique vol. 3—text. Cortinariales A. Paris, France: J.-F. Guyot. 159 p.

Marren P. 2012. Mushrooms. Oxford, UK: British Wildlife Publishing. 272 p.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. In: Xavier J, ed. Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, Louisiana, 14 November 2010. Piscataway, NJ: Institute of Electrical and Electronics Engineers (IEEE). p. 1–8.

Miller OK, Hilton RN. 1987. New and interesting agarics from Western Australia. Sydowia 39:126–137.

Montoya A, Estrada-Torres A, Caballero J. 2002. Comparative ethonomycological survey of three localities from LA Malinche volcano. Mexico J Ethnobiol 22:103–133.

Montoya A, Hernández N, Mapes C, Kong A, Estrada-Torres A. 2008. The collection and sale of wild mushrooms in a community of Tlaxcala, Mexico. Economic Botany 62:413–424.

Montoya A, Kong A, Estrada-Torres A, Cifuentes J, Caballero J. 2004. Useful wild fungi of La Malinche Nacional Park, Mexico. Fungal Diversity 17:115–143.

Nilsson RH, Larsson K-H, Taylor AFS, Bengtsson-Palme J, Jeppesen TS, Schigel D, Kennedy P, Picard K, Glöckner FO, Tedersoo L, Saar I, Kõljalg U, Abarenkov K. 2019. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Research 47: D259–D264.

Peck CH. 1873. Annual Report of the State Botanist (1869). Annual Report on the New York State Museum of Natural History 23:27–135.

Pérez-Moreno J, Lorenzana Fernández A, Carrasco Hernández V, Yescas-Pérez A. 2009. Los hongos comestibles silvestres del Parque Nacional Izta-Popo, Zoquiapan y Anexos. Montecillo, Texcoco, Estado de México: Colegio de Postgraduados, Fondo Sectorial de Investigación Ambiental (SEMARNAT), Consejo Nacional de Ciencia y Tenologia (CONACyT). 167 p.

Pérez-Moreno J, Martínez-Reyes M, Yescas-Pérez A, Delgado-Alvarado A, Xoconostle-Cázares B. 2008. Wild mushroom markets in central Mexico and a case study at Ozumba. Economic Botany 62:425–436.

Rambaut A. 2006–2018. FigTree. Tree figure drawing tool. Version 14.4.4. [cited 2019 Mar 20]. Available from: http://tree.bio.ed.ac.uk/

Rees B, Midgley D, Marchant A, Lerkins A, Orlovich D. 2013. Morphological and molecular data for Australian *Hebeloma* species do not support the generic status of *Anamika*. Mycologia 105:1043–1058.

Rick JE. 1938. Agarici Riograndenses. Lilloa 3:399–455.

Rick JE. 1961. Basidiomycetes Eubasidii no Rio Grande do Sul, Brasília. Iheringia 8:296–450.

Ronquist F, Huelsenbeck JP, Teslenko M. 2011. Draft MrBayes version 3.2 manual: tutorials and model summaries. [cited 2019 May 27]. Available from: http://mrbayes.sourceforge.net/mb3.2_manual.pdf

Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Sucharard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:539–542.

Sheedy EM, Van de Wouw AP, Howlett BJ, May TW. 2013. Multigene sequence data reveal morphologically cryptic phylogenetic species within the genus *Laccaria* in southern Australia. Mycologia 105:547–563.

Siegel N, Schwarz C. 2016. Mushrooms of the Redwood Coast. Berkeley, California: Ten Speed Press. 610 p.

Singer R. 1986. The Agaricales in modern taxonomy. Koenigstein, Germany: Sven Koeltz Scientific Books. 1069 p.

Smith AH, Evenson VS, Mitchel DH. 1983. The veiled species of *Hebeloma* in the western United States. Ann Arbor, Michigan: University of Michigan Press. 219 p.

Stamatakis A. 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313.

Suzuki A, Fukiharu T, Tanaka C, Ohono T, Buchanan PK. 2003. Saprobic and ectomycorrhizal ammonia fungi in the southern hemisphere. New Zealand Journal of Botany 41:391–406.

Thomas KA, Peintner U, Moser MM, Manimohan P. 2002. *Anamika*, a new mycorrhizal genus of Cortinariaceae from India and its phylogenetic position based on ITS and LSU sequences. Mycological Research 106:245–251.

Vesterholt J. 2005. The genus *Hebeloma*. Tilst, Denmark: Svampetryk. 146 p.

Vesterholt J, Eberhardt U, Beker HJ. 2014. Epitypification of *Hebeloma crustuliniforme*. Mycological Progress 13:553–562.

Wilson AW, May TW, Mueller GM. 2017. Biogeography of the ectomycorrhizal mushroom genus *Laccaria*. In: Tedersoo L, ed. Biogeography of mycorrhizal symbiosis. Heidelberg, Germany: Springer International Publishing. p. 273–296.

Yang ZL, Matheny PB, Ge Z-W, Slot JC, Hibbett DS. 2005. New Asian species of the genus *Anamika* (Euagarics, hebelomatoid clade) based on morphology and ribosomal DNA sequences. Mycological Research 109:1259–1267.