Revisiting *Hebeloma* (Hymenogastraceae, Agaricales) in Japan: four species recombined into other genera but three new species discovered

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Abstract

Here, we present the results of studies of Japanese *Hebeloma* collections. The four species described by Imai as *Hebeloma* (*H. fimicola*, *H. helvolescens*, *H. humosum*, and *H. tomoeae*) are not from the genus *Hebeloma*, but are members of *Agrocybe*, *Homophron*, or *Pholiota*. Recombinations are made. *Hebeloma crustuliniforme* f. *microspermum*, described by Hongo, is a synonym of *H. nanum*. Three species of *Hebeloma* are described as new to science, all currently known only from Japan. Two of these species, *H. asperosporum* and *H. cinnamomeum*, are members of *H.* sect. *Denudata* while the third species *H. citrisporum* belongs to *H.* sect. *Velutipes*. Japanese records of *H. cavipes*, *H. eburneum*, *H. hygrophilum*, *H. subtortum*, and *H. velutipes* are validated. In total, fifteen species of *Hebeloma* are confirmed from Japan; this is compared with previous checklists.

Keywords Basidiomycota · Ectomycorrhizal fungi · Type studies

Introduction

A number of species of the genus *Hebeloma* appear to be indigenous, or possibly even endemic, to Japan. The latter include species such as *Hebeloma luchuense* and *H. radicosoides* (*H.* sect. *Scabrispora*), *H. sagarae* (*H.* sect. *Myxocybe*), for which neither observations nor sequence data were

found from other countries (status 16 June 2021). *Hebeloma lactariolens* and *H. vinosophyllum* (*H.* sect. *Porphyrospora*) have been described from Japan, but have also been reported from other countries (e.g., Ho et al. 2014; Cho et al. 2016; Wu et al. 2019; Eberhardt et al. 2021a).

Katamoto (2010) produced a checklist where he listed 15 distinct species of *Hebeloma* recorded for Japan. The 15 species listed are *H. crustuliniforme*, *H. crustuliniforme* f. *microspermum*, *H. fimicola*, *H. helvolescens*, *H. humosum*, *H. longicaudum*, *H. luchuense*, *H. mesophaeum*, *H. radicosoides*, *H. radicosum*, *H. sacchariolens*, *H. sinuosum*, *H. spoliatum*, *H. tomoeae*, and *H. vinosophyllum*. Katamoto did not include in his list *Hebeloma lactariolens*; this was only recombined into *Hebeloma* in 2013 (Rees et al. 2013). Accessing the Global Biodiversity Information Facility (www.gbif.org accessed 10 June 2021) gives 202 occurrences of *Hebeloma* in Japan. Of these 202 occurrences, 166 reference a preserved specimen and 131 give a species name. Additional to the names given by Katamoto and *Hebeloma lactariolens* are also *Hebeloma leucosarx* (one record, no preserved specimen), *Hebeloma microsporum* (one record, but not this taxon, see below under *H. cinnamomeum*), *Hebeloma pusillum* (one record, no preserved specimen), and *H. sordescens* (one specimen recorded as *H. testaceum* from 1935). iNaturalist (www.iNaturalist.org accessed 10

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June 2021) gives a single record of *Hebeloma* for Japan, *H. crustuliniforme*.

One reason for this rather small number of taxa and records is that while it is normally straightforward for a competent field mycologist to identify a mushroom as being a *Hebeloma*, determining the species has in the past been notoriously difficult. This has been partly because of the macroscopic similarity of species, but also because of the confused interpretation of species concepts by many authors (e.g., Moser 1983; Smith et al. 1983; Arora 1986; Hansen and Knudsen 1992; Breitenbach and Kränzlin 2000; Bon 2002; Vesterholt 2005). As a result of this confusion, many mycologists ignore *Hebeloma* in the field, which results in few records; within herbaria, many collections determined as *Hebeloma* remain undetermined at species level. For example, the TNS herbarium currently holds a total of 223 collections of *Hebeloma*, out of which a total of 210 were collected in Japan, but more than 70 collections remain unidentified to species.

In 2016, Beker et al. produced a monograph on *Hebeloma* in Europe, which was intended to provide a foundation for species names and concepts. Since that publication, several papers have appeared describing new species in Southeast Asia and Japan, as well as clarifying the infrageneric classification of species from these areas (for example: Eberhardt et al. 2020a, 2020b, 2021a).

We examined 106 collections of *Hebeloma*, including the holotypes of all species described, from Japan: *H. fimicola*, *H. helvolescens*, *H. humosum*, *H. tomoeae* (Imai 1938); *H. vinosophyllum* (Hongo 1965); *H. crustuliniforme* f. *microsporum* (Hongo 1966); *H. lactariolens* (Cléménçon and Hongo 1994); *H. luchuense* (Fukiharu and Hongo 1995); *H. radicosoides* (Sagara et al. 2000); and *H. sagarae* (Eberhardt et al. 2020a).

With regard to the types studied, *H. luchuense* and *H. radicosoides* were confirmed within *H. sect. Scabrispora*, *H. sagarae* was confirmed within *H. sect. Myxocybe*, and both *H. lactariolens* and *H. vinosophyllum* were confirmed within *H. sect. Porphyrospora* (Eberhardt et al. 2020b). The Japanese collections of *H. spoliatum*, referred to by Eberhardt et al. (2020b), were similar to or conspecific with *H. danicum*, and it was noted that further research was required to decide on conspecificity. This is addressed here.

Within this paper, we also present and discuss our findings with regard to additional type studies of species of *Hebeloma*, described from Japan, and provide a list of *Hebeloma* species we have found during analysis of collections sent to us by citizen scientists published on Mushroom Observer (<https://mushroomobserver.org/>) and herbarium collections, particularly those from the National Museum of Nature and Science (TNS). Included are three species new to science: *Hebeloma asperosporum* is only known from the remote island of Amami Ōshima, while *H. cinnamomeum* and *H. citrisporum* are described from the island of Honshu.

Materials and methods

All material studied was dried material from, primarily, the National Museum of Nature and Science (TNS) and the Hokkaido University Museum (SAPA), but also included a few collections sent to us directly by U. Kawasaki. This was compared with material, sequenced and discussed in Beker et al. (2016), Cripps et al. (2019), and Eberhardt et al. (2020a, 2020b, 2021a).

Sequences were obtained from the dried basidiomes by direct sequencing. Internal transcribed spacer sequences were generated following methods detailed in Eberhardt (2012), and Cripps et al. (2019); *RPB2* and *TEF1a* sequences following Eberhardt et al. (2021b); and sequences of a variable region (V6) of the mitochondrial SSU followed Gonzalez and Labarère (1998). Sequencing was carried out at LGC Genomics (Berlin). Sequences were edited using Sequencher vs. 4.9 (Gene Codes Corp., Ann Arbor, Michigan). Newly generated sequences were accessioned to GenBank (MT157290, MZ725546–MZ725550, MZ724681, MZ782100–MZ782148, MZ782867–MZ782889, and MZ782921–MZ782985). Tables 1 and 2 summarize all sequences used in the analyses.

Alignments were viewed and reformatted using ALIVIEW 1.27 (Larsson 2014). Sequence alignments were done online in MAFFT using the E-INS-i option (Katoh et al. 2005, 2019) or locally with the “MAFFT-globalpair” setting of MAFFT 7.471 (Katoh and Standley 2013). Maximum likelihood (ML) phylogenetic analyses were run in IQ-TREE (Nguyen et al. 2015) either locally (version 2.1.3) or online (Trifinopoulos et al. 2016). Branch support was obtained through 1000 replicates of ultrafast bootstrap (Minh et al. 2013; Hoang et al. 2018) and Shimodaira–Hasegawa (SH)-like approximate likelihood ratio tests (Guindon et al. 2010). Support values are given as SH-like approximate likelihood ratio test support [%] / ultrafast bootstrap support [%], for SH-like approximate likelihood ratio test support $\geq 80\%$ and ultrafast bootstrap support $\geq 95\%$. These values were selected following the recommendations of Minh et al. (2021), who also recommend using SH-like approximate likelihood ratio test support alongside with (ultrafast) bootstrap. Model selection (Kalyaanamoorthy et al. 2017) was done using the BIC criterion, including FreeRate models and merging partitions if possible (protein coding loci were originally partitioned according to position (coding) and non-coding). The study was submitted to TREEBASE (acc. no. TB2:S28657). Trees were visualized using FIGTREE 1.4.4 (Rambaut 2006–2018). Results of Beker et al. (2016), Grilli et al. (2016), Frings et al. (2020), and Tian and Matheny (2021) guided the selection of the roots for the topologies. The compatibility of different loci was assessed following the principle of Kauff and Lutzoni

Table 1 Sequences used in the analyses of taxa outside *Hebeloma*. Herbarium abbreviations (if known) follow Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>) and are separated from the specimen numbers by a space or by a hyphen

Species	Collection no	Country	ITS Genbank/ UNITE acc. no	Citation
<i>Agrocybe firma</i>	TENN RMA17	USA	MG663239	Matheny, P.B. and Swenie, R.A., unpubl., subm. 10-Dec-2017
<i>Agrocybe firma</i>	CBS 390.79	unknown	MN306192	Frings et al. 2020
<i>Agrocybe firma</i>	GLM-F045867	Germany	MZ019447	Eberhardt et al., Mycologia, in press
<i>Agrocybe flexuosipes</i> holotype	NYS-F-001221	USA	MN017805	Eberhardt et al., Mycologia, in press
<i>Agrocybe humosa</i>	SAPA 10000033	Japan	MZ725546	Here
<i>Agrocybe imaii</i>	SAPA 10000036	Japan	MZ725547	Here
<i>Agrocybe pediades</i>	LE 262811	Russia	JN684798	Malysheva and Kiyashko 2011
<i>Agrocybe pediades</i>		India	KT272410	Chaudhary and Tripathi, unpubl., subm. 09-Jul-2015
<i>Agrocybe pediades</i>	MO270391	Mexico	KY646479	Rockefeller, A., unpubl., subm. 23-Feb-2017
<i>Agrocybe pediades</i>		Iraq	LC458686	Suliaman et al., unpubl., subm. 19-Jan-2019
<i>Agrocybe pediades</i>	HFJAU 0368	China	MN258622	Huo, unpubl., subm. 01-Aug-2019
<i>Agrocybe pediades</i>	TUF 106288	Estonia	UDB011682	Liiv, 06-Jul-2018
<i>Agrocybe pediades</i>	O-F-21680	Norway	UDB036650	NORBOL (Norwegian Barcode of Life)
<i>Agrocybe praecox</i>	MSC 378486	UK	AY194531	Hallen et al. 2003
<i>Agrocybe praecox</i>	GLM-F045869	Germany	MZ019448	Eberhardt et al., Mycologia, in press
<i>Agrocybe praecox</i>	TROM-F-17213	Norway	UDB037131	NORBOL
<i>Agrocybe praecox</i>	O-F-302315	Norway	UDB037255	NORBOL
<i>Agrocybe praecox</i>	SMNS-STU-F-0900850	Germany	MZ019432	Eberhardt et al., Mycologia, in press
<i>Agrocybe putaminum</i>	PDD 96108	New Zealand	KM975434	Cooper and Park, unpubl., subm. 15-Oct-2014
<i>Agrocybe putaminum</i>	MO116752	USA	MH285875	Rockefeller unpubl., subm. 03-May-2018
<i>Agrocybe smithii</i>	UWO T-792, Z-45	USA	KC176295	Thorn et al. 1996
<i>Agrocybe smithii</i>	UWO T-792, Z-45	USA	KC176296	Thorn et al. 1996
<i>Agrocybe smithii</i>	TENN 066942 (PBM3793)	USA	MG663269	Matheny et al., unpubl., subm. 11-Dec-2017
<i>Agrocybe smithii</i>	MO310653	Canada	MH558289	Matheny and Hobbs, unpubl., subm. 28-Jun-2018
Environmental sequence		Estonia	UDB0575407	Tedersoo et al. 2020
Fungal isolate	2013071701	Japan	LC100010	Fukasawa, unpubl., subm. 20-Nov-2015
<i>Homophron camptopodum</i>	TUF 118215	Estonia	UDB015582	Liiv, 06-Jul-2018
<i>Homophron cernuum</i>	BRNM 705614	Czech Republic	AM712287	Vašutová et al. 2008
<i>Homophron cernuum</i> epitype	GB DB2013652266	Denmark	KJ939632	Örstadius et al. 2015
<i>Homophron helvolens</i> holotype	SAPA 10000035	Japan	MZ725549	Here
<i>Homophron</i> sp.	WTU-F-023854	USA	MZ725550	Here
<i>Homophron spadiceum</i>	TAKK08.11.12.1-2	Japan	AB594840	Kobayashi and Hoshino, unpubl., subm. 18-Oct-2010
<i>Homophron spadiceum</i>	BRNM 705613	Czech Republic	AM712288	Vašutová et al. 2008
<i>Homophron spadiceum</i>	GB 981111 Epitype	Germany	DQ389729	Larsson and Örstadius 2008

Table 1 (continued)

Species	Collection no	Country	ITS Genbank/ UNITE acc. no	Citation
<i>Homophron spadiceum</i>	JCS100905B	USA	FJ168610	Slot et al. 2010
<i>Homophron spadiceum</i>	TRTC156998	Canada	JN021090	Dentinger et al. 2011
<i>Homophron spadiceum</i>	HC-PNNT-106	Mexico	KT875089	Garibay-Orijel et al., unpubl., subm. 05-Oct-2015
<i>Homophron spadiceum</i>	HC-PNNT-300	Mexico	KT875090	Garibay-Orijel et al., unpubl., subm. 05-Oct-2016
<i>Homophron spadiceum</i>	CUH AM031	India	KU928134	Yangdol et al. 2016
<i>Homophron spadiceum</i>	TENN 071834 (PBM4137)	USA	MG773815	Matheny et al., unpubl., subm. 07-Dec-2017
<i>Homophron spadiceum</i>	MO111084	Mexico	MG993188	Rockefeller, unpubl., subm. 24-Feb-2018
<i>Homophron spadiceum</i>	MycoMap7004	USA	MK564559	Russell, unpubl., subm. 22-Feb-2019
<i>Homophron spadiceum</i>	MO224603	USA	MN906125	Russell, unpubl., subm. 04-Jan-2020
<i>Homophron spadiceum</i>	MO110531	USA	MN906126	Russell, unpubl., subm. 04-Jan-2020
<i>Homophron spadiceum</i>	TUF 118222	Estonia	UDB015406	Liiv, 06-Jul-2018
<i>Homophron spadiceum</i>	TUF 106436	Estonia	UDB015694	Liiv, 06-Jul-2018
<i>Homophron spadiceum</i>	TUF 118801	Estonia	UDB019586	Liiv, 06-Jul-2018
<i>Homophron spadiceum</i>	O-F-251569	Norway	UDB036170	Fonneland, 27-Oct-2018
<i>Homophron spadiceum</i>	O-F-301571	Norway	UDB036893	Fonneland, 27-Oct-2018
<i>Homophron spadiceum</i>	GLM-F046017	Germany	MZ724623	Here
<i>Homophron</i> cf. <i>spadiceum</i>	MO377580	USA	MT271783	Clements, unpubl., subm. 30-Mar-2020
<i>Lacrymaria hypertropicalis</i>	XAL Guzman29585	Mexico	KC992958	Örstadius et al. 2015
<i>Lacrymaria hypertropicalis</i>	MO353205	USA	MK346140	Rockefeller, unpubl., subm. 29-Dec-2018
<i>Lacrymaria lacrymabunda</i>	GB EL7-03	Sweden	DQ389724	Larsson and Örstadius 2008
<i>Lacrymaria lacrymabunda</i>	K(M) 234056	UK	MZ159649	Gaya et al., unpubl., subm. 30-Apr-2021
<i>Pholiota brunnescens</i>	TENN 052897 (TFB5897)	Mexico	KF871789	Matheny and Bougher 2017
<i>Pholiota brunnescens</i>	WTU 10337	USA	MG735270	Matheny et al. 2018
<i>Pholiota brunnescens</i>	GAL137545, WTU 21130	USA	MG735298	Matheny et al. 2018
<i>Pholiota brunnescens</i>	PBM527, WTU 10342	USA	MG735299	Matheny et al. 2018
<i>Pholiota brunnescens</i>	Stz9021, WTU 10354	USA	MG735303	Matheny et al. 2018
<i>Pholiota brunnescens</i>	MTS4953b, WTU 10343	USA	MG735305	Matheny et al. 2018
<i>Pholiota brunnescens</i>	ET32, TENN 074791, HMJAU 37361	China	MN209732	Tian and Matheny 2021
<i>Pholiota brunnescens</i>	ET22, TENN 074782, HMJAU 37363	China	MN209733	Tian and Matheny 2021
<i>Pholiota brunnescens</i>	TUF 133578	Pakistan	UDB0780780	Gohar, 01-Dec-2020
<i>Pholiota brunnescens</i> holotype	AHS3525, MICH 11657	USA	MG735292	Matheny et al. 2018
<i>Pholiota castanea</i>	TENN 071878	USA	MH016952	Matheny et al. 2018
<i>Pholiota castanea</i>	PBM4254, TENN 074736	USA	MN337888	Tian and Matheny 2021
<i>Pholiota castanea</i> holotype	TENN 020269	USA	HQ222025	Matheny et al. 2018
<i>Pholiota chocenensis</i> holotype	PRM 895066	Czech Republic	NR_155622	Holec et al. 2014
<i>Pholiota foedata</i>	MIN 47532	USA	MZ019457	Eberhardt et al., Mycologia, in press
<i>Pholiota foedata</i> holotype	NYS-F-001228	USA	MN017804	Eberhardt et al., Mycologia, in press
<i>Pholiota gallica</i>	PRM 933232	France	LN889967	Holec et al. 2016

Table 1 (continued)

Species	Collection no	Country	ITS Genbank/ UNITE acc. no	Citation
<i>Pholiota gallica</i> holotype	MPU Herb. Chevassut 3478	France	HG007988	Holec and Kolařík 2014
<i>Pholiota luteobadia</i> holotype	AHS43222, MICH 11688	USA	MG735289	Matheny et al. 2018
<i>Pholiota polychroa</i>	PBM2866, TENN 062649	USA	MG735317	Matheny et al. 2018
<i>Pholiota polychroa</i>	CBS 349.34	Canada	MH855561	Vu et al. 2019
<i>Pholiota</i> sp.	PBM3057, TENN 063855	USA	MG735314	Matheny et al. 2018
<i>Pholiota tomoeae</i> lectotype	SAPA 10000032	Japan	MZ724681	Here
<i>Pholiota tomoeae</i> syntype	SAPA 10000031	Japan	MZ725548	Here
<i>Psathyrella camptopus</i>	IB 1997-956	Russia	KC992956	Örstadius et al. 2015
<i>Psathyrella crenulata</i> type	MICH WK8/10/64-5	USA	KC992957	Örstadius et al. 2015
<i>Psathyrella</i> sp.	TAKK08.9.6.5-2	Japan	AB594839	Kobayashi and Hoshino, unpubl., subm. 18-Oct-2010
<i>Psathyrella</i> sp.	GB LÖ134-98	Sweden	DQ389726	Larsson and Örstadius 2008
<i>Psathyrella variata</i>	BRNM 705636	Austria	AM712289	Vašutová et al. 2008
<i>Psathyrella</i> cf. <i>variata</i>	WU 13716	Czech Republic	AM712290	Vašutová et al. 2008

(2002), assuming a conflict to be significant if two different relationships for the same set of taxa, one being monophyletic and the other non-monophyletic, are supported by $\geq 85\%$ SH-like approximate likelihood ratio test support or $\geq 95\%$ ultrafast bootstrap support. Alignments of different loci were concatenated and analyzed, indicating branches with conflicting results from single locus analyses by dashed lines. Country codes in Figs. 2, 3, 4, 5 and 6 follow ISO 3166–1 alpha-2 (<https://www.iso.org/iso-3166-country-codes.html>, accessed 22 Jun 2021).

Details of morphological analyses were provided in Beker et al. (2016). The amount of macroscopic detail available to us varied hugely from collection to collection as it was dependent on the detail provided by the collector. Where one of the authors was the collector, each specimen was photographed and observed both in the field when characters were still fresh, and later in the laboratory. Fresh basidiomes of each specimen were dried using a food dehydrator (Snackmaster Express FD-60; Nesco/American Harvest, Milwaukee, WI, USA).

All microscopic analysis was carried out on dried material, using a Leica DMRZA2 microscope with a Leica DFC495 camera connected to a computer running Leica Application Suite (LAS) V4 software. A number of photographs were taken of the spores at $\times 500$ and $\times 1600$, which were then measured using the LAS software. Photographs were also taken of the cheilocystidia on the lamella edge at $\times 500$ and of individual cystidia and basidia at $\times 1000$. The material was then examined in 5% KOH. Again, photographs were taken of the spores at $\times 500$ and $\times 1600$ and of the cheilocystidia (and pleurocystidia if any were present) and basidia at $\times 500$ and $\times 1000$.

For each *Hebeloma* collection, wherever possible, at least 50 spores were measured in Melzer's reagent, excluding the

apiculus. The maximum length and width of each spore was 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 5% and 95% percentiles. The degree of dextrinoidity, ornamentation, and the degree of loosening of the perispore was observed and classified. For the assessment of the degrees of ornamentation (O0, O1, O2, O3, O4), of the loosening perispore (P0, P1, P2, P3), and for the dextrinoidity (D0, D1, D2, D3, D4), we used 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 lamella edge. For other measurements, some 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), see Fig. 1. 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 as we intend to make the database publicly available.

Table 2 Sequences used in the analyses of *Hebeloma* spp. Herbarium abbreviations (if known) follow Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>). Private collections are EG (Edmondo Grilli), EL (Erhard Ludwig†), HJB (Henry J. Beker), NS (Noah Siegel), and SP (Serge Poumarat); MO refers to mushroom observer (<https://mushroomobserver.org/>)

Species	Database ref	Collection no	Country	GenBank acc. no. ITS	GenBank acc. no. <i>TEF1a</i>	GenBank acc. no. <i>RPB2</i>	GenBank acc. no. mitSSU V6	Published by
<i>H. aestivale</i>	HJB13626	HJB13626	Germany	KT218447	KT217675	KT217767		Grilli et al. 2016
<i>H. aestivale</i>	HJB13801	SP-10.11.03	Spain	KT218454	KT217678	KT217769		Grilli et al. 2016
<i>H. aestivale</i>	HJB10439	HJB10439	UK	KT218282	KT217631	KT217716		Grilli et al. 2016
<i>H. albidulum</i>	HJB18372	HJB18372	USA	MZ782147	MZ782953	MZ782921		Here
<i>H. albidulum</i>	HJB16965	HJB16965	USA	MZ782142	MZ782954	MZ782922		Here
<i>H. albidulum</i>	HJB14702	HJB14702	USA	MZ782105	MZ782955	MZ782923		Here
<i>H. ammophilum</i>	HJB12374	GB EL-281-08	Hungary	KT217509	KT216849	KT216980	KT217297	Eberhardt et al. 2016
<i>H. ammophilum</i>	HJB14471	EL-1886I	Hungary	MZ782104	MZ782956	MZ782924	MZ782867	Here
<i>H. ammophilum</i>	HJB15417	HJB15417	Italy	MZ782106	MZ782957	MZ782925	MZ782868	Here
<i>H. ammophilum</i>	HJB16438	EG-101029.01	Italy	MZ782140	MZ782958	MZ782926	MZ782869	Here
<i>H. ammophilum</i>	HJB16439	EG-121019.01	Italy	MZ782141	MZ782959	MZ782927	MZ782870	Here
<i>H. asperosporum</i>	HJB16250	TNS TNS-F-75704	Japan	MZ782138	MZ782960	MZ782928	MZ782871	Here
<i>H. asperosporum</i>	HJB16251	TNS TNS-F-75705 (holotype)	Japan	MZ782139	MZ782961	MZ782929	MZ782872	Here
<i>H. bulbiferum</i>	HJB13083	HJB EC177060	Croatia	KT218422	KT217667	KT217754		Grilli et al. 2016
<i>H. bulbiferum</i>	HJB10300	HJB10300	Italy	KT218261	KT217615	KT217704		Grilli et al. 2016
<i>H. bulbiferum</i>	HJB10812	C JV-03-587	Italy	KT218318	KT217645	KT217730		Grilli et al. 2016
<i>H. cavipes</i>	HJB10537	HJB10537	France	KT217402	KT216799	KT216916	KT217198	Eberhardt et al. 2016
<i>H. cavipes</i>	HJB13227	HJB13227	Poland	MZ782102	MZ782962	MZ782930	MZ782873	Here
<i>H. cavipes</i>	HJB9433	HJB9433	Spain	KT217362	KT216780	KT216877	KT217158	Eberhardt et al. 2016
<i>H. cavipes</i>	HJBNS3537	NS3537	USA	MZ782148	MZ782963	MZ782932	MZ782874	Here
<i>H. cavipes</i>	HJB14374	HJB14374	USA	MZ782103	MZ782964	MZ782931	MZ782875	Here
<i>H. celatum</i>	HJB13621	BR 5020184119676	Germany	KT218446	KT217674	KT217766		Grilli et al. 2016
<i>H. celatum</i>	HJB12857	MK-MAK 08-10021	North Macedonia	KT218413	KT217664	KT217752		Grilli et al. 2016
<i>H. celatum</i>	HJB13799	SP-10.11.02	Spain	KT218453	KT217677	KT217768		Grilli et al. 2016
<i>H. cinnamomeum</i>	HJB16236	TNS TNS-F-59098	Japan	MZ782128	MZ782965	MZ782933	MZ782876	Here
<i>H. cinnamomeum</i>	HJB16245	TNS TNS-F-73984	Japan	MZ782134	MZ782966	MZ782934	MZ782877	Here
<i>H. cinnamomeum</i>	HJB16246	TNS TNS-F-74039	Japan	MZ782135	MZ782967	MZ782935	MZ782878	Here
<i>H. cinnamomeum</i>	HJB15837	TNS TNS-F-82067 (holotype)	Japan	MZ782111	MZ782968	MZ782936	MZ782879	Here
<i>H. cinnamomeum</i>	HJB15838	HJB15838	Japan	MZ782112	MZ782969	MZ782937	MZ782880	Here
<i>H. cinnamomeum</i>	HJB16173	TNS TNS-F-1387	Japan	MZ782113				Here
<i>H. cinnamomeum</i>	HJB16213	TNS TNS-F-42284	Japan	MZ782114				Here
<i>H. cinnamomeum</i>	HJB16214	TNS TNS-F-43723	Japan	MZ782115				Here
<i>H. cinnamomeum</i>	HJB16216	TNS TNS-F-44535	Japan	MZ782116				Here
<i>H. cinnamomeum</i>	HJB16220	TNS TNS-F-44863	Japan	MZ782118				Here
<i>H. cinnamomeum</i>	HJB16221	TNS TNS-F-44864	Japan	MZ782119				Here

Table 2 (continued)

Species	Database ref	Collection no	Country	GenBank acc. no. ITS	GenBank acc. no. <i>TEF1a</i>	GenBank acc. no. <i>RPB2</i>	GenBank acc. no. mitSSU V6	Published by
<i>H. cinnamomeum</i>	HJB16226	TNS TNS-F-46098	Japan	MZ782121				Here
<i>H. cinnamomeum</i>	HJB16228	TNS TNS-F-49380	Japan	MZ782122				Here
<i>H. cinnamomeum</i>	HJB16229	TNS TNS-F-49387	Japan	MZ782123				Here
<i>H. cinnamomeum</i>	HJB16230	TNS TNS-F-49389	Japan	MZ782124				Here
<i>H. cinnamomeum</i>	HJB16234	TNS TNS-F-58915	Japan	MZ782126				Here
<i>H. cinnamomeum</i>	HJB16235	TNS TNS-F-59097	Japan	MZ782127				Here
<i>H. cinnamomeum</i>	HJB16238	TNS TNS-F-60045	Japan	MZ782129				Here
<i>H. cinnamomeum</i>	HJB16243	TNS TNS-F-72963	Japan	MZ782132				Here
<i>H. cinnamomeum</i>	HJB16244	TNS TNS-F-73028	Japan	MZ782133				Here
<i>H. cinnamomeum</i>	HJB16247	TNS TNS-F-74060	Japan	MZ782136				Here
<i>H. cinnamomeum</i>	HJB16199	TNS TNS-F-38024	Japan	MZ782144				Here
<i>H. citrisporum</i>	HJB15832	MO255034	Japan	MZ782109	MZ782971	MZ782938		Here
<i>H. citrisporum</i>	HJB15833	BR 5020214140236 V (holotype)	Japan	MZ782110	MZ782972	MZ782939		Here
<i>H. citrisporum</i>	HJB16217	TNS TNS-F-44560	Japan	MZ782117	MZ782970	MZ782940		Here
<i>H. citrisporum</i>	HJB17412	MO295075	Japan	MZ782145	MZ782973	MZ782941		Here
<i>H. citrisporum</i>	HJB17414	MO299321	Japan	MZ782146	MZ782974	MZ782942		Here
<i>H. crustuliniforme</i>	HJB13713	BR BR-MYCO-1739 89-68 (epitype)	France	KF309424	KT216860	KF309495	KM390510	Eberhardt et al. 2015, 2016
<i>H. crustuliniforme</i>	HJB12807	L WAG-W9581	Netherlands	KF309415	KT216854	KF309492	KM390452	Eberhardt et al. 2015, 2016
<i>H. crustuliniforme</i>	HJB11237	HJB11237	Spain	JN943870	KT216824	KF309480	KM390380	Schoch et al. 2012; Eberhardt et al. 2015, 2016
<i>H. echinosporum</i>	HJB13524	BR BR-MYCO 174907-16 (holotype)	France	KT217548	KT216858	KT216993	KT217330	Eberhardt et al. 2016
<i>H. erebium</i>	HJB11857	C JV-06-690	Denmark	KT218373	KT217657	KT217745		Grilli et al. 2016
<i>H. erebium</i>	HJB13620	HJB13620	Germany	KT218445	KT217673	KT217765		Grilli et al. 2016
<i>H. erebium</i>	HJB14180	LOD IK-H0182	Poland	KT218463	KT217682	KT217773		Grilli et al. 2016
<i>H. hiemale</i>	HJB8890	HJB8890	Belgium	GQ869484	KT216772	KT216867	KT217148	Beker et al. 2010; Eberhardt et al. 2016
<i>H. hiemale</i>	HJB10758	HJB10758	Belgium	KT217433	KT216814	KT216941	KT217231	Eberhardt et al. 2016
<i>H. hiemale</i>	HJB11704	BR BR-MYCO 174905-14 (epitype)	France	GQ869505	KT216833	KT216964	KT217279	Eberhardt et al. 2016
<i>H. hiemale</i>	HJB17443	C C-F-106776	Greenland	MW445625	MZ782975	MZ782943	MZ782881	Eberhardt et al. 2021b; here
<i>H. hiemale</i>	HJB9384	HJB9384	UK	GQ869482	KT216778	KT216875	KT217156	Beker et al. 2010; Eberhardt et al. 2016
<i>H. incarnatum</i>	HJB10132	HJB10132	Finland	KT218239	KT217606	KT217695		Grilli et al. 2016

Table 2 (continued)

Species	Database ref	Collection no	Country	GenBank acc. no. ITS	GenBank acc. no. <i>TEF1a</i>	GenBank acc. no. <i>RPB2</i>	GenBank acc. no. mitSSU V6	Published by
<i>H. incarnatum</i>	HJB10139	HJB10139	Finland	KT218246	KT217607	KT217697		Grilli et al. 2016
<i>H. incarnatum</i>	HJB13589	HJB13589	Germany	KT218441	KT217672	KT217764		Grilli et al. 2016
<i>H. leucosarx</i>	HJB11694	HJB11694	Belgium	KT218361	KT217652	KT217740		Grilli et al. 2016
<i>H. leucosarx</i>	HJB10140	HJB10140	Finland	KT218247	KT217608	KT217698		Grilli et al. 2016
<i>H. leucosarx</i>	HJB9289	HJB9289	UK	KT218219	KT217599	KT217687		Grilli et al. 2016
<i>H. matritense</i>	HJB9485	BR BR-MYCO-174910-19 (holotype)	Spain	KT217364	KT216781	KT216879	KT217160	Eberhardt et al. 2016
<i>H. matritense</i>	HJB9486	HJB9486	Spain	KT217365	MZ782976	KT216880	KT217161	Eberhardt et al. 2016 ; here
<i>H. populinum</i>	HJB14114	HJB GK-5803	Greece	KT217563	KT216862	KT217002	KT217342	Eberhardt et al. 2016
<i>H. populinum</i>	HJB13758	HJB13758	UK	KT217560	KT216861	KT217000	KT217341	Eberhardt et al. 2016
<i>H. quercetorum</i>	HJB13497	HJB13497	Cyprus	KT218437	KT217670	KT217761		Grilli et al. 2016
<i>H. quercetorum</i>	HJB10327	HJB10327	Italy	KT218268	KT217620	KT217708		Grilli et al. 2016
<i>H. quercetorum</i>	HJB13418	HJB13418	Spain	KT218435	KT217669	KT217760		Grilli et al. 2016
<i>H. sacchariolen</i>	HJB10321	HJB10321	Italy	KT218266	KT217618	KT217706		Grilli et al. 2016
<i>H. sacchariolen</i>	HJB9020	HJB9020	UK	KT218216	KT217597	KT217684		Grilli et al. 2016
<i>H. sinapizans</i>	HJB10360	HJB10360	Belgium	JQ768359	KT217627	JQ751077		Eberhardt et al. 2013 ; Grilli et al. 2016
<i>H. sinapizans</i>	HJB13530	BR 5020184118648	France	KT218440	KT217671	KT217763		Grilli et al. 2016
<i>H. sinapizans</i>	HJB10628	HJB10628	UK	JQ751191	KT217637	KT217721		Eberhardt et al. 2013 ; Grilli et al. 2016
<i>H. sordidulum</i>	HJB15800	UWO	Canada	MZ782108	MZ782977	MZ782947	MZ782882	Here
<i>H. sordidulum</i>	HJB12269	HJB12269	USA	MZ782101	MZ782978	MZ782944	MZ782883	Here
<i>H. sordidulum</i>	HJB12287	HJB12287	USA	MZ782100	MZ782979	MZ782945	MZ782884	Here
<i>H. sordidulum</i>	HJB15700	HJB15700	USA	MZ782107	MZ782980	MZ782946	MZ782885	Here
<i>H. sordidulum</i>	HJB16978	HJB16978	USA	MZ782143	MZ782981	MZ782948	MZ782886	Here
<i>H. subconcolor</i>	HJB17065	C C-F-8242	Greenland	MW445847	MZ782982	MZ782949		Eberhardt et al. 2021b ; here
<i>H. subconcolor</i>	HJB11114	HJB11114	Switzerland	KT218330	KT217646	KT217732		Grilli et al. 2016
<i>H. subconcolor</i>	HJB11142	HJB11142	Switzerland	KT218332	KT217647	KT217734		Grilli et al. 2016
<i>H. vaccinum</i>	HJB9965	HJB9965	Belgium	KT217371	KT216784	KT216883	KT217167	Eberhardt et al. 2016
<i>H. vaccinum</i>	HJB10067	HJB10067	Belgium	KT217373	KT216785	KT216885	KT217169	Eberhardt et al. 2016
<i>H. vaccinum</i>	HJB17492	C C-F-106767	Greenland	MW445830	MZ782983	MZ782952	MZ782887	Eberhardt et al. 2021b ; here

Table 2 (continued)

Species	Database ref	Collection no	Country	GenBank acc. no. ITS	GenBank acc. no. <i>TEF1a</i>	GenBank acc. no. <i>RPB2</i>	GenBank acc. no. mitSSU V6	Published by
<i>H. vaccinum</i>	HJB17310	DUKE 0351073	USA	MT157290	MZ782984	MZ782951	MZ782888	Here
<i>H. vaccinum</i>	HJB15327	MONT CLC1881	USA	MK281113	MZ782985	MZ782950	MZ782889	Cripps et al. 2019; here
<i>H. velutipes</i>	HJB10350	HJB10350	Belgium	KT218274	KT217626	KT217712		Grilli et al. 2016
<i>H. velutipes</i>	HJB11756	HJB11756	France	KT218364	KT217653	KT217741		Grilli et al. 2016
<i>H. velutipes</i>	HJB10329	C C-F-44818	Italy	EU570173	KT217622	JQ751093		Eberhardt et al. 2009, 2013; Grilli et al. 2016
<i>H. velutipes</i>	HJB11315	HJB11315	Portugal	KT218342	KT217649	KT217737		Grilli et al. 2016
<i>H. velutipes</i>	HJB11951	HJB11951	Svalbard	KT218376	KT217658	KT217746		Grilli et al. 2016
<i>H. velutipes</i>	HJB10588	HJB10588	UK	KT218294	KT217635	KT217719		Grilli et al. 2016

Results

None of the four species described by Imai (1938), *Hebeloma fimicola*, *H. helvolescens*, *H. humosum*, and *H. tomoeae* belong to *Hebeloma* as recognized today. They belong to the genera *Agrocybe*, *Homophron*, and *Pholiota* and are recombined in the Taxonomy section with a short summary of their main characters. *Hebeloma crustuliniforme* f. *microspermum* is synonymized with *H. nanum* based on morphology (no sequence data obtained). Three new species of *Hebeloma* were discovered in the course of this study, two of these species, *H. asperosporum* and *H. cinnamomeum*, are members of *H. sect. Denudata* while the third species *H. citrisporum* belongs to *H. sect. Velutipes*.

The alignment for *Agrocybe* includes 24 ITS sequences and 717 positions. The result of the analysis is shown in Fig. 2. The topology is rooted with *Agrocybe firma* at a branch receiving 100/100 support (support not shown because branch used for rooting). The type species of *Agrocybe* is *A. praecox*, which is represented in the alignment by five sequences of different authors. The lectotype ITS of *Agrocybe humosa* (*Hebeloma humosum*) is placed in an unsupported clade together with sequences identified as *A. smithii*; the holotype ITS of *A. imaii* (*H. fimicola*) is placed in a clade with sequences identified as *A. pediades*.

The alignment for *Homophron* includes 35 ITS sequences and 708 positions. *Homophron spadiceum* is the type species of the genus. We have made an effort to sample all variation from UNITE SH1186588.08FU (which includes the epitype

of *Ho. spadiceum*), because it was not possible to see the species limits of *Ho. spadiceum*. The result of the analysis is shown in Fig. 3. The topology is rooted with *Lacrymaria* spp. The clade indicated as “*Homophron spadiceum* s.l.” consists of a number of subclades, some appear to be geographically restricted, among which *Ho. helvolescens* is in a subclade with sequences from Japan and India.

The alignment for *Pholiota* (*P. sect. Flammuloides* in Tian and Matheny 2021) includes 26 ITS sequences and 771 positions. The result of the analysis is shown in Fig. 4. The sequences of the two syntypes (one designated as lectotype below) of *P. tomoeae* are within the *P. brunnescens* clade, which includes sequences from America, Asia, and Europe.

Hebeloma asperosporum is morphologically and molecularly distinct from all other described *Hebeloma* species. Morphologically, it is a member of *H. subsect. Clepsydroida*, distinguished by its small, strongly ornamented spores, on average less than 10.5 µm long, indextrinoid and with consistently loosening perispore.

Likewise, *Hebeloma cinnamomeum* is morphologically and molecularly distinct from all other described *Hebeloma* species. Morphologically, it is a member of *H. subsect. Clepsydroida*, distinguished by its cinnamon-colored pileus and the spores with average *Q* less than 1.85 and the cheilocystidia with average width near the apex of less than 6.5 µm.

Four loci (ITS, alignment 708 positions; mitSSU V6, alignment 476 positions; *RPB2*, alignment 779 positions; and *TEF1a*, alignment 717 positions) have been employed to

Fig. 1 Measuring cystidia width of apex (A), width at narrowest point in central region (M), and maximum width in lower half (B) illustrated on left to right gently clavate, clavate-stipitate and clavate-ventricose cystidia

infer the phylogenetic relationships of taxa in *Hebeloma* sect. *Denudata* (Fig. 5). The topology is rooted with members of *H.* subsect. *Echinospora*. All loci analyzed individually resolved the two available sequences of *H. asperosporum* as monophyletic with high support (min. 94% SH-like approximate likelihood ratio test and 97% ultrafast bootstrap support, in most loci higher), but it was on a long branch and the position of the species within the section was unresolved. The sequences obtained for *H. cinnamomeum* form an independent lineage only in the ITS (support 92%/99%) and V6

(84%/–). An ITS tree with all *H. cinnamomeum* sequences (not shown) is available via TreeBase. In the *TEF1a* result, *H. cinnamomeum* is paraphyletic in relation to *H. ammophilum*, *H. cavipes*, and *H. sordidulum* and in the *RPB2* result also in relation to *H. vaccinum*.

Only ITS and V6 resolve *H. asperosporum* and *H. cinnamomeum* sequences as species clades in relation to other members of *H.* sect. *Denudata*, with SH-like approximate likelihood ratio test support above 90% and ultrafast bootstrap support above 95% in ITS, and with approximately 100% in both tests for *H. asperosporum* and with 87% SH-like approximate likelihood ratio test support, but without relevant ultrafast bootstrap support, for *H. cinnamomeum* in V6.

The topologies obtained for the different loci (see Treebase submission) were in conflict. This was largely due to *H. asperosporum* and *H. matritense* being placed with relevant support by one or both support criteria as sister to different species clades in the results for different loci. The result of the analysis of the concatenated alignment is shown in Fig. 5. The topology is rooted with *H. echinosporum* and *H. populinum*. Here, *H. asperosporum* receives 100% support by both criteria and *H. cinnamomeum* 94%/97% support. The inclusion of members of *H.* sect. *Clepsydroidea* in two reciprocally monophyletic groups is weakly (86% in the lesser supported clade) supported by SH-like approximate likelihood ratio tests. However, conflicts between the evolutionary hypothesis of different loci concern this part of the tree.

Hebeloma citrisporum is morphologically and molecularly distinct from all other described *Hebeloma* species. The predominantly gently clavate cheilocystidia suggest that this

Fig. 2 Maximum likelihood result (ITS) for placing *Agroclybe humosa* and *A. imaii* in a taxonomic context. Support values are from 1000 replicates of SH-like approximate likelihood ratio tests

and ultrafast bootstrap. Support values $\geq 85\%$ (SH-like approximate likelihood ratio tests) or 95% (ultrafast bootstrap) are shown. The last two letters indicate the country of origin

Fig. 3 Maximum Likelihood result (ITS) for placing *Homophron helvolens* in a taxonomic context. Support values are from 1000 replicates of SH-like approximate likelihood ratio tests and ultrafast bootstrap. Support values $\geq 85\%$ (SH-like approximate

likelihood ratio tests) or 95% (ultrafast bootstrap) are shown. Branches with at least one of the support values above the thresholds are thick lined. * Type collection included in clade. The last two letters indicate the country of origin

species belongs in *H. sect. Velutipes*, which is supported by molecular results (Fig. 6).

Three loci (ITS, alignment 715 positions; *RPB2*, alignment 779 positions; and *TEF1a*, alignment 712 positions) have been employed to infer the phylogenetic relationships of taxa in *Hebeloma* sect. *Velutipes*. Sequences of *H. citrisporum* are monophyletic in all single locus trees and the branch supported by 90–97%/95–100%. The only conflict among the single locus results (see Treebase submission) is between *TEF1a* and the *RPB2* in the placement of *H. erebium*, paraphyletic as sister of *H. celatum* (*TEF1a*) or as sister to *H. celatum*, *H. citrisporum*, and *H. quercetorum* (*RPB2*). The ITS does not resolve *H. celatum*, *H. erebium*, and *H. quercetorum* in separate clusters. The result of the analysis of the concatenated data is shown in Fig. 6. Here, the lineage of *H. citrisporum* receives 100%/100% support

and is supported as sister taxon of *H. quercetorum* as in the single locus results of *RPB2* and *TEF1a*.

In addition to the species mentioned above (*H. nanum*, *H. asperosporum*, *H. cinnamomeum*, *H. citrisporum*), and *H. danicum* (often recorded as *H. spoliatum*), *H. luchuense* and *H. radicosoides* (*H. sect. Scabrispora*), *H. sagarae* (*H. sect. Myxocybe*) and *H. lactariolens* and *H. vinosophyllum* (*H. sect. Porphyrospora*), the following taxa were identified from the Japanese material examined: *H. cavipes* (e.g., TNS-F-44988; GenBank ITS = MZ782120), *H. eburneum* (TNS-F-38029; no DNA sequence data obtained), *H. hygrophilum* (TNS-F-61595; GenBank ITS = MZ782130), *H. subtortum* (TNS-F-61666; GenBank ITS = MZ782131), and *H. velutipes* (TNS-F-75075; GenBank ITS = MZ782137). This gives a total of 15 species that we can confirm are present in Japan.

Fig. 4 Maximum likelihood result (ITS) for placing *Pholiota tomoeae* in a taxonomic context. Support values are from 1000 replicates of SH-like approximate likelihood ratio tests and ultrafast bootstrap. Support values $\geq 85\%$ (SH-like approximate likelihood ratio tests) or 95% (ultrafast

bootstrap) are shown. Branches with at least one of the support values above the thresholds are thick lined. * Type collection included in clade. The last two letters indicate the country of origin

Taxonomy

Agrocybe humosa (S. Imai) Beker & U. Eberh., comb. nov.
MB840285

Basionym: *Hebeloma humosum* S. Imai, Journal of the Faculty of Agriculture of the Hokkaido Imperial University 43(2): 230 (1938).

Typification: Japan, Hokkaido, Sapporo, Ishikari, on badly decayed wood or on humus in gardens, 25 Jun 1935, S. Imai, Syntypes (SAPA 10000033 and SAPA 10000034). **Lectotype designated here** (MBT10001751, SAPA 10000033), database record HJB1000376. GenBank ITS = MZ725546.

Description of the lectotype: Spores elliptical, smooth, pale brown, thick-walled, with a conspicuous germ pore, on av. $11.1 \times 7.7 \mu\text{m}$, with av. spore Q 1.44. The cheilocystidia are ventricose; the pleurocystidia are similar.

Japanese name: Ki-wakafusa-take (Imai 1938).

Remarks: There are two collections (SAPA 10000033 and SAPA 10000034) at SAPA, marked as syntypes. The material selected as lectotype fits the original description by Imai (1938) who gives the spore size as $10\text{--}11.5 \times 7\text{--}8 \mu\text{m}$. This matches most closely with our measurements for SAPA 10000033 ($10.1\text{--}13.3 \times 6.9\text{--}9.5 \mu\text{m}$, av. $11.1 \times 7.7 \mu\text{m}$, av. Q 1.44) for which we also have an ITS sequence. The other collection, SAPA 10000034, also appears to be an *Agrocybe*, with elliptical, smooth, pale brown, thick-walled spores, with a conspicuous germ pore, on av. $13.3 \times 8.9 \mu\text{m}$

($11.8\text{--}14.7 \times 8.0\text{--}10.1 \mu\text{m}$), with av. spore Q 1.50. The cheilocystidia are ventricose; the pleurocystidia are similar.

The spores of *A. smithii* (Watling and Bigelow 1983) and of the type of *A. flexuosipes* (Eberhardt et al., in press) are around the same size ($11\text{--}13.5 \times 6.5\text{--}8 \mu\text{m}$ respectively $12.1 \times 7.7 \mu\text{m}$) as the spores of *A. humosa*. Whereas the spores of the former two species are described as (indistinctly) ornamented, the spores observed in the lectotype of *A. humosa* are smooth. The spores of *A. putaminum* are described as $10\text{--}13 \times 5\text{--}7 \mu\text{m}$, thus somewhat narrower than in *A. humosa*, but also smooth (Maire 1913).

Both morphology (without annulus, yellowish tones in pileus, spore size, and prominent germ pore) and sequence data (Fig. 2) suggest that *A. humosa* is closely related with *A. smithii*, *A. putaminum*, or other related species (Nauta 2005). Another closely related species is *A. flexuosipes* (Eberhardt et al., in press). However, none of these species matches the type of *A. humosa* sufficiently closely for synonymization.

Agrocybe imaii Beker & U. Eberh., nom. nov.
MB840286

Basionym: *Hebeloma fimicola* [as “fimiculum”] S. Imai, Journal of the Faculty of Agriculture of the Hokkaido Imperial University 43(2): 227 (1938); non *Agrocybe fimicola* (Speg.) Singer, Lilloa 23: 209 (1952).

Etymology: In honor of S. Imai, the describer of this species.

Typification: Japan, Hokkaido, Sapporo, Ishikari, on horse dung under trees, Jun 1935, S. Imai, Holotype (SAPA 10000036), database record HJB1000377. GenBank ITS = MZ725547.

Description of the holotype: The spores are elliptical, smooth, pale brown, thick-walled, with a conspicuous germ pore, on av. $12.9 \times 8.9 \mu\text{m}$, with av. spore Q 1.44. The cheilocystidia are ventricose; pleurocystidia only near lamella edge. The pileipellis has a thin gelatinous layer, with small pieces of hypha embedded within it.

Japanese name: Baba-wakafusa-take (Imai 1938).

Remarks: *Hebeloma fimicola* is an *Agrocybe*. Our examination of the type material was in close agreement with the description of Imai (1938). It is possible, even likely, that

A. imaii is a later synonym of *A. pediades* s.l., and, given its habitat on dung, may be *A. pediades* var. *fimicola* (Speg.) Nauta (*Agrocybe fimicola* (Speg) Sing.) (Nauta 2005), but we rather leave it to experts on the genus based on multilocus sequence data to come to a conclusion. Based on ITS data, *Agrocybe pediades* occurs in many countries including China, India, Iraq, Pakistan, and Sri Lanka (see Fig. 2 and UNITE SH2290413.08FU).

Hebeloma asperosporum Beker & U. Eberh., sp. nov., Figs. 7 and 8, Mycobank MB840287

Diagnosis: The small, strongly ornamented spores, on average less than $10.5 \mu\text{m}$ long, indextrinoid and with

Fig. 5 Maximum Likelihood result of concatenated ITS, *RPB2*, *TEF1a*, and mitSSU V6 sequences of members of *Hebeloma* sect. *Denudata*, subsects. *Clepsydroidea* and *Crustuliniformia*, rooted with members of *H.* subsect. *Echinospora*. Relationships that include conflicting data are indicated by dashed lines. Support values $\geq 85\%$ (SH-like approximate

likelihood ratio tests) or 95% (ultrafast bootstrap) are shown. In some places support values 85–99% (SH-like approximate likelihood ratio tests) or 95–99% (ultrafast bootstrap) are represented by “*” and values of 100% by “#”. Branches with at least one of the support values above its threshold are thick lined. The last two letters indicate the country of origin

Fig. 7 *Hebeloma asperosporum* holotype (TNS-F-75705). Photo K. Hosaka

upwards, fibrillose, at apex pruinose. Context in pileus white to cream, firm, in stipe stuffed; taste and smell not recorded. Spore deposit color not recorded.

Basidiospores based on $n = 45$ spores of the holotype, 5% to 95% percentile range $9.0\text{--}10.8 \times 5.4\text{--}6.6 \mu\text{m}$, with median $9.5 \times 5.9 \mu\text{m}$ and av. $9.6 \times 5.9 \mu\text{m}$ with S. D. length $0.6 \mu\text{m}$ and width $0.35 \mu\text{m}$; Q value 5% to 95% percentile range $1.53\text{--}1.77$, with median 1.60 and av. 1.62 with S. D. 0.08 ; spore size based on two collections, medians $9.5\text{--}10.1 \times 5.9\text{--}6.3 \mu\text{m}$ and av. $9.6\text{--}10.0 \times 5.9\text{--}6.2 \mu\text{m}$ with av. S. D. length $0.565 \mu\text{m}$ and width $0.33 \mu\text{m}$, av. Q $1.61\text{--}1.62$, amygdaloid or limoniform, with small apiculus and rounded apically, with a distinct thinning of the apical wall and a strongly prominent papilla, guttulate with one or sometimes more oily drops, usually very distinctly ornamented (ornamentation visible at low magnification), with a strongly loosening perispore on almost

Fig. 8 *Hebeloma asperosporum* holotype (TNS-F-75705) **a** spores and **b** spore ornamentation in Melzer's reagent $\times 1600$, **c** basidium in Melzer's reagent $\times 1000$, **d** spores and **e** spore ornamentation in KOH $\times 1600$, **f** cheilocystidia in KOH $\times 1000$, **g** cheilocystidia in KOH $\times 1000$, **h** cheilocystidia in Melzer's reagent $\times 1000$, **i** caulocystidia in KOH $\times 500$, **j** cutis in KOH $\times 125$, **k** subcutis in KOH $\times 500$, and **l** caulocystidia in KOH $\times 1000$. Scale bars $10 \mu\text{m}$, in **j** $100 \mu\text{m}$. Photos H.J. Beker

every mature spore and indextrinoid hardly changing color in Melzer's reagent (O3/4; P3; D0); spore color under the microscope brown. Basidia $22\text{--}30 \times 6\text{--}8 \mu\text{m}$, with av. Q $3.2\text{--}3.6 \mu\text{m}$, cylindrical to clavate, without pigmentation, 4-spored. Cheilocystidium width near apex holotype 5% to 95% percentile range $5.7\text{--}9.2 \mu\text{m}$, with median $7.7 \mu\text{m}$ and av. $7.6 \mu\text{m}$ with S. D. $1.1 \mu\text{m}$; across two collections median $7.4\text{--}7.7 \mu\text{m}$ and av. $7.4\text{--}7.6 \mu\text{m}$; examining approx. 20 selected cheilocystidia of each of the two collections yields a range for the avs. of $44\text{--}45 \times 7.4\text{--}7.6 \times 3.9\text{--}4.3 \times 5.3\text{--}6.0 \mu\text{m}$ and $44 \times 7.6 \times 4.3 \times 6.0 \mu\text{m}$ av. for holotype. Cheilocystidium av. ratios A/M: 1.79–1.91, A/B: 1.30–1.49, B/M: 1.36–1.41, mainly clavate-ventricose, often capitate stipitate or clavate stipitate, sometimes with one or two septa (occasionally clamped) often with thickening of the median wall. Pleurocystidia absent. Caulocystidia similar to cheilocystidia but larger, up to $110 \mu\text{m}$ long. Pileipellis is an ixocutis with an epicutis up to $150 \mu\text{m}$ thick, with gelatinized, often encrusted hyphae up to $6 \mu\text{m}$ wide. Subcutis pale yellow under the microscope and the trama below the cutis made up of cylindrical or thickly sausage-shaped cells up to $16 \mu\text{m}$ wide. Clamp connections present throughout the basidiome.

Ecology and distribution: In mixed woodlands with *Pinus*, *Quercus* and *Castanopsis*. The growth habit was caespitose to scattered. To date, *Hebeloma asperosporum* is recorded only from the island Amami-Ōshima.

Additional collections examined: Japan, Kagoshima, Amami-Ōshima Island, Yamato, Amami Forest Polis Park (approx. 28.316056N , 129.344778E , alt. approx. 214 m asl.) under *Castanopsis sieboldii*, *Pinus luchuensis* and *Quercus glauca*, 17 Nov 2015, K. Hosaka (TNS-F-75704, HJB16250).

Japanese name: Amami-wakafusa-take (newly proposed here).

Remarks: The mainly clavate-ventricose cheilocystidia together with distinctly to strongly ornamented spores support the placement of this taxon in *H.* subsect. *Clepsydroidea* within *H.* sect. *Denudata*. The occasional presence of cystidia with thickening of the wall in the middle is further evidence of this placement. Molecularly, the position of the species within *H.* sect. *Denudata* is supported, but its assignment to subsection is not. Within *H.* sect. *Denudata*, the small spores, on average less than $10.5 \mu\text{m}$ long, indextrinoid but strongly ornamented and with consistently loosening perispore distinguishes this species from all other known members of *H.* section *Denudata*. While the description is based on just two collections, its morphological and molecular separation, from all known species of *Hebeloma*, leave us in no doubt that this should be regarded as a distinct species.

Of course, our description and knowledge of this taxon is limited to just these two collections from the same locality, hence our concept of this species is limited. A sequence published from

China as *H. alpinum* (MW554385, Zouh, unpublished, submitted 26 Jan 2021; no UNITE SH to date) is, apart from obvious editing errors, identical to our *H. asperosporum* sequences. It is hoped that publishing this description will encourage other mycologists to search for this taxon.

Hebeloma cinnamomeum Beker & U. Eberh., sp. nov., Figs. 9 and 10, Mycobank MB840288

Diagnosis: The cinnamon-colored pileus, the spores with average Q less than 1.85 and the cheilocystidia with average width near the apex of less than $6.5 \mu\text{m}$, are characters that separate this species from others in *H.* sect. *Denudata*.

Etymology: From cinnamomeus (adj. Latin) describing the cinnamon-colored pileus.

Typification: Japan, Ishikawa, Wajima, Mii, Nakanagatani (approx. 37.39059N , 136.899196E , alt. approx. 229 m asl.), under *Pinus densiflora*, *Quercus serrata* and *Q. variabilis*, 16 Oct 2016, T. Kasuya TKB3261, Holotype (TNS-F-82067), database record HJB15837. Genbank ITS = MZ782111.

Description: Pileus (20) $21\text{--}46$ (51) mm diameter, hemispherical, often convex, occasionally umbonate; margin involute, particularly when young, not hygrophanous; usually almost unicolorous, usually cinnamon, rarely more brick colored, sometimes slightly paler towards margin. Lamellae emarginate, depth up to 4 mm , white, cream to brown, with white fimbriate edge but without droplets on the lamella edge, number of full-length lamellae $52\text{--}64$. Stipe (24) $30\text{--}60$ (64) mm long, $4\text{--}8$ (11) mm diameter at median, often widening towards a clavate base, surface cream, ivory to pale brown rarely weakly discoloring from the base upwards, velvete, at apex pruinose. Context in pileus white to cream, firm, in stipe stuffed; taste and smell not recorded. Spore deposit color not recorded.

Basidiospores based on $n = 90$ spores of the holotype, 5% to 95% percentile range $9.1\text{--}12.5 \times 5.4\text{--}7.1 \mu\text{m}$, with median $10.2 \times 6.0 \mu\text{m}$ and av. $10.5 \times 6.1 \mu\text{m}$ with S. D. length $1.1 \mu\text{m}$ and width $0.59 \mu\text{m}$; Q value 5% to 95% percentile range $1.49\text{--}1.97$, with median 1.70 and av. 1.72 with S. D. 0.16 ; spore size based on 23 collections, medians $9.5\text{--}11.2 \times 5.7\text{--}6.3 \mu\text{m}$ and av. $9.6\text{--}11.2 \times 5.8\text{--}6.3 \mu\text{m}$ with av. S. D. length $0.76 \mu\text{m}$ and width $0.45 \mu\text{m}$, av. Q $1.60\text{--}1.83$, amygdaloid, occasionally limoniform, with small apiculus and rounded apically, with a distinct thinning of the apical wall and sometimes a weak papilla, usually guttulate with one or sometimes more oily drops, weakly to distinctly ornamented (ornamentation not conspicuous at low magnification), with a perispore hardly loosening and weakly but sometimes distinctly dextrinoid, becoming at most pale brown or yellow brown in Melzer's reagent, (O2/3; P0/1; D1/2); spore color under the microscope yellow brown. Basidia $22\text{--}33 \times 6\text{--}8 \mu\text{m}$, with av. Q $3.0\text{--}3.9 \mu\text{m}$, cylindrical to

Fig. 9 *Hebeloma cinnamomeum* holotype (TNS-F-82067). Photo T. Kasuya

clavate, without pigmentation, 4-spored. Cheilocystidium width near apex holotype 5% to 95% percentile range 5.9–7.5 μm , with median 6.7 μm and av. 6.6 μm with S.D.

0.54 μm ; across 23 collections median 5.0–6.7 μm and av. 5.0–6.6 μm ; examining approx. 20 selected cheilocystidia of each of the 23 collections yields a range for the av. of $50\text{--}61 \times 5.0\text{--}6.6 \times 3.3\text{--}3.9 \times 4.6\text{--}7.0 \mu\text{m}$ and $54 \times 6.6 \times 3.7 \times 4.9 \mu\text{m}$ av. for holotype. Cheilocystidium av. ratios A/M: 1.42–1.81, A/B: 0.86–1.37, B/M: 1.35–1.86, mainly clavate-ventricose, rarely clavate stipitate, sometimes with one or two septa (occasionally clamped) often with thickening of the median wall, rarely with thick yellow content. Pleurocystidia absent. Caulocystidia similar to cheilocystidia but larger, up to 110 μm long. Pileipellis is an ixocutis with an epicutis up to 160 μm thick, with gelatinized, often encrusted hyphae up to 6 μm wide. Subcutis cinnamon colored and the trama below the cutis made up of cylindrical or ellipsoid, often thickly sausage-shaped cells up to 12 μm wide. Clamp connections present throughout the basidiome.

Ecology and distribution: In deciduous or mixed woodlands apparently associated with *Quercus* or *Pinus*, but

Fig. 10 *Hebeloma cinnamomeum* holotype (TNS-F-82067) **a** spores and **b** spore ornamentation in Melzer's reagent $\times 1600$, **c** spores and **d** spore ornamentation in KOH $\times 1600$, **e** cheilocystidia in Melzer's reagent $\times 1000$, **f** cheilocystidia in KOH $\times 1000$, **g** basidia in KOH $\times 1000$, **h** cheilocystidia in KOH $\times 1000$, **i** caulocystidia in KOH $\times 1000$, **j** caulocystidia in KOH $\times 500$, **k** epicutis hyphae and **l** subcutis in KOH $\times 500$, and **m** cutis in KOH $\times 125$. Scale bars 10 μm , in **m** 100 μm . Photos H.J. Beker

occasionally *Carpinus* and *Fagus* were also present. The growth habit was mainly scattered, but occasionally caespitose and rarely solitary. To date, all collections of *Hebeloma cinnamomeum* have been recorded only from the Japanese island of Honshu.

Additional collections examined: Japan, Ibaraki, Tsukuba, Tsukuba Botanical Garden, (approx. 36.1015N, 140.1131E, alt. approx. 40 m asl.), 16 Oct 2000, D. Yoshioka (TNS-F-1387, HJB16173); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Evergreen Broad-leaved Forest Section,” (approx. 36.101518N, 140.11308E, alt. approx. 40 m asl.) on soil under *Quercus myrsinifolia* and other evergreen *Quercus* spp., 27 Oct 2011, Y. Muramatsu (TNS-F-42284, HJB16213); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Evergreen Broad-leaved Forest Section” (approx. 36.101518N, 140.11308E, alt. approx. 40 m asl.) on soil under *Quercus myrsinifolia* and other evergreen *Quercus* spp., 9 Nov 2011, Matsumoto (TNS-F-43723, HJB16214); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Evergreen Broad-leaved Forest Section” (approx. 36.101518N, 140.11308E, alt. approx. 40 m asl.) on soil under *Quercus myrsinifolia* and other evergreen *Quercus* spp., 4 Dec 2011, not recorded (TNS-F-44535, HJB16216); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Evergreen Broad-leaved Forest Section” (approx. 36.1015N, 140.1131E, alt. approx. 40 m asl.) on soil under *Quercus myrsinifolia* and other evergreen *Quercus* spp., 1 Nov 2012, K. Nishibori (TNS-F-49380, HJB16228); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Rockeries Section (High Altitudes)” (approx. 36.101513N, 140.113035E, alt. approx. 40 m asl.) on soil under evergreen *Quercus* spp., 1 Nov 2012, N.P. Thao (TNS-F-49387, HJB16229); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Evergreen Broad-leaved Forest Section” (approx. 36.1015N, 140.1131E, alt. approx. 40 m asl.) on soil under *Quercus myrsinifolia* and other evergreen *Quercus* spp., 1 Nov 2012, N.P. Thao (TNS-F-49389, HJB16230); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Fern Section” (approx. 36.1008N, 140.1126E, alt. approx. 38 m asl.), 10 Oct 2013, Dawa (TNS-F-58915, HJB16234); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Fern Section” (approx. 36.10078N, 140.112572E, alt. approx. 38 m asl.) on soil under *Quercus* sp., 13 Nov 2013, K. Hosaka (TNS-F-59097, HJB16235); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Fern Section” (approx. 36.10078N, 140.112572E, alt. approx. 38 m asl.) on soil under *Quercus* sp., 13 Nov 2013, K. Hosaka (TNS-F-59098, HJB16236); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Fern Section” (approx. 36.1008N, 140.1126E, alt. approx. 38 m asl.), 5 Nov 2014, K. Nishibori (TNS-F-72963, HJB16243); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Cool-temperate Deciduous Broad-leaved Forest Section” (approx. 36.103102N, 140.111201E, alt. approx. 43 m asl.) on soil in deciduous woodland under *Carpinus* sp. and *Fagus* sp., 13 Nov 2014, K. Hosaka (TNS-F-73028, HJB16244); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Warm-temperate Deciduous Broad-leaved Forest Section” (approx. 36.102944N,

140.11268E, alt. approx. 35 m asl.) on soil in deciduous woodland, 22 Oct 2015, K. Nishibori (TNS-F-73984, HJB16245); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Fern Section” (approx. 36.1008N, 140.1126E, alt. approx. 38 m asl.) on soil, 18 Nov 2015, J. Yamazaki (TNS-F-74039, HJB16246); Ibaraki, Tsukuba, Tsukuba Botanical Garden “Endangered Species Section” (approx. 36.1015N, 140.1131E, alt. approx. 40 m asl.) on soil, 25 Nov 2015, J. Yamazaki (TNS-F-74060, HJB16247); Ibaraki, Tsukuba, Usui, Tsukuba-Fureai-no-Sato (approx. 36.201127N, 140.108664E, alt. approx. 90 m asl.), 16 Oct 2005, collector not recorded (TNS-F-11893, HJB16177); Ishikawa, Nomi, Tatsunokuchi, Ishikawa Zoo (approx. 36.433759N, 136.545712E, alt. approx. 50 m asl.) under *Quercus serrata*, 4 Oct 2001, H. Mori (TNS-F-38024, HJB16199); Ishikawa, Wajima, Mii, Nakanagatani (approx. 37.39059N, 136.899196E, alt. approx. 40 m asl.), 16 Oct 2016, T. Kasuya (HJB15838); Tottori, Daisen, Mt. Daisen (approx. 36.314665N, 139.800149E, alt. approx. 35 m asl.), 12 Oct 2008, Y. Taneyama (TNS-F-44863, HJB16220); Tottori, Daisen, Mt. Daisen (approx. 36.314665N, 139.800149E, alt. approx. 35 m asl.), 12 Oct 2008, M. Nabe (TNS-F-44864, HJB16221); Yamanashi, Kofu, Atago, Mt. Atago, Kodomono-kuni (approx. 35.6702N, 138.5803E, alt. approx. 410 m asl.) under *Pinus densiflora* and *Pinus resinosa*, 11 Nov 2011, K. Hosaka (TNS-F-46098, HJB16226); Yamanashi, Fujiyoshida, Yamanashi Institute of Environmental Sciences (approx. 35.477904N, 138.795091E, alt. approx. 839 m asl.) under *Pinus densiflora*, 19 Sep 2013, K. Hosaka (TNS-F-60045, HJB16238).

Japanese name: Mizuho-wakafusa-take (newly proposed here).

Remarks: The mainly clavate-ventricose cheilocystidia together with distinctly ornamented spores support the placement of this taxon in *H.* subsect. *Clepsydroidea* within *H.* sect. *Denudata*. The occasional presence of cystidia with thickening of the wall in the middle is further evidence of this placement. All loci apart from mitSSU V6 support a shared lineage of *H. cinnamomeum* with *H. cavipes* (the type species of *H.* subsect. *Clepsydroidea*) rather than with *H. crustuliniforme* (the type of *H.* subsect. *Crustuliniformia*) or *H. hiemale* (the type of *H.* subsect. *Hiemalia*). Within *H.* sect. *Denudata*, the spores with average Q less than 1.85, the cheilocystidia with average width near the apex of less than 6.5 μm and the cinnamon-colored pileus are characters that separate this species from others within this subsection. The pileus color is an eye-catching feature that may well enable field identification, or at least a reasonable suspicion of determination, of this species.

While our morphological description is based on 23 collections, many (but not all) are from a relatively confined area within the Tsukuba Botanical Garden, which is planted with endogenous plants from Japan. The description provided may be too narrow, given the similar habitat for many of these collections. In addition, a sequence from a *Quercus dentata* root tip collected in Hokkaido (LC068995, Arai et al. unpublished,

Fig. 11 *Hebeloma citrisporum* holotype (BR 5020214140236 V). Photo U. Kawasaki

submitted 27-Jul-2015) clusters in ML analyses (not shown) with *H. cinnamomeum* sequences, supporting the assumptions on associates and adding evidence that it is an endogenous species in Japan. This sequence currently (9 June 2021) forms a singleton UNITE SH hypothesis (SH2292369.08FU) at the < 0.5% level, but owing to probable editing errors in this sequence this SH has to be treated with caution.

Note that cited collection TNS-F-44863 was originally identified as *Hebeloma microsporum*, the name under which it is recorded on GBIF, and which was mentioned in the introduction.

Hebeloma citrisporum Beker & U. Eberh., sp. nov. Figs. 11 and 12, Mycobank MB840289

Diagnosis: The citriform spores, distinctly ornamented and rather strongly dextrinoid but with the perispore only somewhat loosening in a few spores, with average width less than 7.5 μm , and the predominantly gently clavate

Fig. 12 *Hebeloma citrisporum* holotype (BR 5020214140236 V) **a** spores and **b** spore ornamentation in KOH $\times$ 1600, **c** basidium in KOH $\times$ 1000, **d** spores and **e** spore ornamentation in Melzer's reagent $\times$ 1600, **f** cheilocystidium in KOH $\times$ 1000, **g** caulocystidia in KOH $\times$ 1000, **h** epicutis hyphae in KOH $\times$ 500, **i** cheilocystidium in KOH $\times$ 1000, **j** caulocystidia in KOH $\times$ 500, **k** subcutis in KOH $\times$ 500, and **l** cutis in KOH $\times$ 125. Scale bars 10 μm , in **l** 100 μm . Photos H.J. Beker

cheilocystidia with average width near the apex greater than $6.5\ \mu\text{m}$ and average ratio of basal width to median width (B/M) at most 1.35, distinguish this species from other *Hebeloma*.

Etymology: From citrus (noun, Latin) meaning lemon, lemon tree and spora (Latin) to emphasize the limoniform spores.

Typification: Japan, Ibaraki, Tsukuba, (approx. 36.0869N, 140.1197E, alt. approx. 30 m asl.) in urban pond-side roadside under *Quercus myrsinifolia* and *Q. serrata*, 24 Oct 2016, U. Kawasaki UK270, MO258729, Holotype (BR 5020214140236 V), database record HJB15833. GenBank ITS = MZ782110.

Description: Pileus (21) 28–63 (68) mm diameter, hemispherical, often umbonate, occasionally convex; margin usually smooth, occasionally involute or wavy, not hygrophanous; usually bicolored, usually clay buff, distinctly paler towards margin. Lamellae emarginate, white, cream to brown, with white fimbriate edge but without droplets on the lamella edge, number of full-length lamellae 52–64. Stipe (22) 31–64 (84) mm long, (6) 7–9 (10) mm diameter at median, widening towards a bulbous base, surface cream, ivory to pale brown not discoloring on handling, velute, slightly fibrillose, at apex pruinose to floccose. Context in pileus and stipe white to cream, firm; taste and smell not recorded. Spore deposit color not recorded.

Basidiospores based on $n = 90$ spores of the holotype, 5% to 95% percentile range $10.4\text{--}13.1 \times 6.2\text{--}7.4\ \mu\text{m}$, with median $11.6 \times 6.9\ \mu\text{m}$ and av. $11.6 \times 6.8\ \mu\text{m}$ with S. D. length $0.86\ \mu\text{m}$ and width $0.40\ \mu\text{m}$; Q value 5% to 95% percentile range 1.53–1.90, with median 1.69 and av. 1.70 with S. D. 0.11; spore size based on 5 collections, medians $11.3\text{--}12.3 \times 6.6\text{--}7.1\ \mu\text{m}$ and av. $11.3\text{--}12.1 \times 6.7\text{--}7.0\ \mu\text{m}$ with av. S. D. length $0.82\ \mu\text{m}$ and width $0.37\ \mu\text{m}$, av. Q 1.61–1.83, amygdaloid or limoniform, with small apiculus and rounded apically, with a distinct thinning of the apical wall and a very strong, very prominent papilla, usually guttulate with one or sometimes more oily drops, weakly to distinctly ornamented (ornamentation not conspicuous at low magnification), with a perispore somewhat to distinctly loosening in many spores and rather strongly dextrinoid, becoming medium brown in Melzer's reagent, (O2/3; P1/2; D3); spore color under the microscope yellow to yellow brown. Basidia $26\text{--}36 \times 7\text{--}9\ \mu\text{m}$, with av. Q $3.4\text{--}3.6\ \mu\text{m}$, cylindrical to clavate, without pigmentation, 4-spored. Cheilocystidium width near apex holotype 5% to 95% percentile range $4.8\text{--}8.4\ \mu\text{m}$, with median $6.6\ \mu\text{m}$ and av. $6.6\ \mu\text{m}$ with S. D. $0.54\ \mu\text{m}$; across 5 collections median $6.6\text{--}8.9\ \mu\text{m}$ and av. $6.6\text{--}9.1\ \mu\text{m}$; examining approx. 20 selected cheilocystidia of each of the 5 collections yields a range for the avs. of $54\text{--}68 \times 6.6\text{--}9.1 \times 5.7\text{--}3.9 \times 5.3\text{--}7.0\ \mu\text{m}$ and $54 \times 6.6 \times 4.7 \times 5.3\ \mu\text{m}$ av. for holotype. Cheilocystidium av. ratios A/M: 1.31–1.58, A/B: 1.08–1.38,

B/M: 1.12–1.35, mainly gently clavate, occasionally clavate-ventricose or ventricose, sometimes with one or two septa. Pleurocystidia absent. Caulocystidia similar to cheilocystidia but larger, up to $135\ \mu\text{m}$ long. Pileipellis is an ixocutis with an epicutis up to $115\ \mu\text{m}$ thick, with gelatinized, often encrusted hyphae up to $7\ \mu\text{m}$ wide. Subcutis yellow brown and the trama below the cutis made up of cylindrical or thickly sausage-shaped cells up to $18\ \mu\text{m}$ wide. Clamp connections present throughout the basidiome.

Ecology and distribution: All records to date suggest *Quercus* as the most likely ectomycorrhizal host. The growth habit was mainly scattered, but occasionally caespitose. To date, all collections of *Hebeloma citrisporum* have been recorded only from the Japanese island of Honshu, in the vicinity of Tokyo.

Additional collections examined: Japan, Tokyo, Shibuya, Yoyogi, Meiji Shrine (approx. 35.6781N, 139.6999E, alt. approx. 60 m asl.) under *Quercus* sp., 8 Nov 2011, K. Hosaka KH-JPN11-529 (TNS-F-44560, HJB16217); Ibaraki, Tsukuba (approx. 36.086858N, 140.119679E, alt. approx. 29 m asl.) in urban pond-side roadside under *Quercus myrsinifolia* and *Quercus serrata*, 4 Oct 2016, U. Kawasaki UK267 (MO255034, HJB15832); Ibaraki, Tsukuba (approx. 36.085N, 140.12E, alt. approx. 25 m asl.) in mixed woodland, 20 Oct 2017, U. Kawasaki UK338 (MO295075, HJB17412); Ibaraki, Tsukuba (approx. 36.085N, 140.12E, alt. approx. 25 m asl.), 27 Oct 2017, U. Kawasaki UK350 (MO299321, HJB17414).

Japanese name: Tokiwa-wakafusa-take (newly proposed here).

Remarks: The predominantly gently clavate towards the apex cheilocystidia, with a few ventricose or clavate-ventricose, supports the placement of *H. citrisporum* in *H. sect. Velutipes*. Within this section, the citriform spores, distinctly ornamented and rather strongly dextrinoid but with the perispore only somewhat loosening in a few spores, with average width less than $7.5\ \mu\text{m}$, and the cheilocystidia with average width near the apex greater than $6.5\ \mu\text{m}$ and average ratio of basal width to median width (B/M) at most 1.35, distinguish this species. While citriform spores are commonly found within species of *H. sect. Velutipes*, rarely are they as regular and eye-catching as for this species. The species and its placement in *H. sect. Velutipes* are supported by molecular data (Fig. 6).

The description is based on just five collections from a relatively small geographic area around Tokyo. We would suspect that it is far more widespread, at least on Honshu Island. A *Quercus dentata* root tip sequence from Hokkaido (AB979728, Arai et al. 2017) might have been formed by *H. citrisporum*. Currently (9 June 2021), the sequence forms a singleton UNITE SH (SH1235508.08FU) at the 3% level. It differs from our *H. citrisporum* sequences by three indels,

two singleton deletions and one 15 bp insertion which we have not observed in our material.

Hebeloma danicum Gröger, Z. Mykol. 53(1): 53 (1987).

Japanese name: Ashinaga-numeri (Kawamura 1954).

Remarks: A detailed description and molecular analyses including this species are provided in Beker et al. (2016). In Eberhardt et al. (2020b) the authors commented that Japanese collections studied that were referred to *H. spoliatum* were similar to or conspecific with *H. danicum*, but that further research was necessary to decide upon any conspecificity. Following further morphological and molecular analysis using multiple loci, we cannot see any reason to differentiate the Japanese collections, albeit for some of the collections (but importantly not all), there are some minor morphological differences. Specifically, the range for the number of complete lamellae for our European collections is 58–64, while for the Japanese collections this is 60–72, and the range of spore lengths for our European collections is 9.5–10.3 µm while the range for our Japanese collections is 8.5–10.0 µm. Both these parameters affect the use of the dichotomous key provided in Beker et al. (2016), and might therefore lead to some confusion with other species of *H. sect. Scabrispora*, in particular *H. laterinum*, *H. melleum*, or *H. pumilum*. However, all three of these species can be straightforwardly distinguished: *H. laterinum* with its blackening stipe, *H. melleum* with its smaller basidiomes and *H. pumilum*, with its consistently loosening and very well visible perispore.

Hebeloma nanum Velen., Novitates mycologicae: 117 (1939).

= *Hebeloma crustuliniforme* f. *microspermum* Hongo, Journal of Japanese Botany 41: 169 (1966).

Japanese name: Kotsubu-o-wakafusa-take (Hongo 1966).

Remarks: A detailed description of *H. nanum* and molecular analyses of *H. sect. Naviculospora* are provided in Beker et al. (2016). The holotype of *Hebeloma crustuliniforme* f. *microspermum* has small (av. 7.9 × 4.8 µm) spores, prompting the choice of name. The spores, however, are weakly ornamented and strongly dextrinoid (unlike *H. crustuliniforme*). The cheilocystidia are very irregular, subclavate to subcylindrical, again very unlike *H. crustuliniforme*, but typical for *H. sect. Naviculospora*, as is Hongo's description of the pileus: "viscid, pale tan, often tinged brownish-alutaceous, especially on the disc, sometimes irregularly cracked." Within this section, the narrow spores and rarely ventricose cheilocystidia are typical for *H. nanum*, with which this taxon is certainly conspecific. We were not able to generate any molecular data from the type material. *Hebeloma crustuliniforme* f. *microspermum*

was described by Hongo (1966) from pine forests in Akibayama, Niitsu, Niigata Prefecture. We have examined and sequenced another collection of *H. nanum* from Japan (TNS-F-55100; GenBank ITS = MZ782125).

Hebeloma nanum is widespread across the globe and as well as in Japan and northern Europe; we are aware of confirmed collections from India, Canada, China, and the USA (unpublished results). The species probably corresponds to UNITE species hypothesis SH1951515.08FU, including the type (from Czechia) and, in addition to the above, sequence data from Pakistan. It appears that *H. nanum* most commonly occurs on sandy soil, in post-fire regenerating boreal and temperate, coniferous forests (Beker et al. 2016; Hughes et al. 2020).

Homophron helvolescens (S. Imai) Beker & U. Eberh., comb. nov.

MB840290

Basionym: *Hebeloma helvolescens* S. Imai, Journal of the Faculty of Agriculture of the Hokkaido Imperial University 43(2): 229 (1938).

Typification: Japan, Hokkaido, Sapporo Botanic Garden, 4 Jul 1932, on the ground around the tree trunks in open woods, S. Imai, Holotype (SAPA 10000035), database record HJB1000374. GenBank ITS = MZ725549.

Description of type: The spores are elliptical to cylindrical, sometimes fabiform, smooth, pale brown, without a germ pore, on av. 9.9 × 5.3 µm, with av. spore *Q* 1.87. The cheilocystidia are metuloid; the pleurocystidia are similar.

Japanese name: Ko-wakafusa-take (Imai 1938).

Remarks: Our examination of the type material is in good agreement with the description given by Imai (1938). Imai also mentions the caespitose habit of this species, and the presence of crystals on the cystidia. Morphologically, it appears to be closely related or even conspecific with *Ho. spadiceum*.

Spore size of *Ho. spadiceum* is, according to Vašutová (2008), 8–9.5 × 4–5 µm, average 8.7 × 4.7 µm, *Q* 1.6–2.2 (–2.3) and according to Enderle (1989) who later collected the specimen that was selected as epitype by Örstadius (2001) (8.0)9–10.2(11) × 4.2–5.2(5.6) µm. Both authors stress the light spore colour of the species, under the microscope in water and in the spore deposit, according to Vašutová (2008) brick-beige (S40Y60M5, Küppers 1999). Vašutová (2008) suspected that Smith (1972) concept of *Psathyrella spadicea* might not coincide with what is called *Ho. spadiceum* in Europe, citing a difference in spore deposit colour as indication. Imai (1938) described the spores of *Ho. helvolescens* as cinnamon; S40Y60M5 (Küppers 1999) is lighter and more greenish than cinnamon; under the microscope the spores of *Ho. helvolescens* appear distinctly colored.

The ITS of the epitype of *Ho. spadiceum* is sequenced, as is the holotype of *Ho. helvolescens* and both are included in

the “*Homophron spadiceum* s.l.” clade of Fig. 3. This clade includes a number of supported (and unsupported) subclades that appear to have restricted geographical distributions. However, the sequence variation underlying these clades is so small (see scale in Fig. 3) and the data is only from a single locus that we hesitate to recognize them as hypotheses of distinct species. Vašutová et al. (2008) stressed that ITS is not sufficient for delimiting species in the *Psathyrellaceae*. Thus, it is not clear whether *Ho. helvolens* is indeed a later synonym of *Ho. spadiceum*.

Pholiota tomoeae (S. Imai) Beker & U. Eberh. comb. nov.

MB840291

Basionym: *Hebeloma tomoeae* S. Imai, Journal of the Faculty of Agriculture of the Hokkaido Imperial University 43(2): 226 (1938).

Typification: Japan, Hokkaido, Sapporo, 14 Oct 1937, on the humus ground or decayed wood under trees, in gardens or roadsides, S. Imai, Syntypes (SAPA 10000031 and SAPA 10000032). **Lectotype designated here** (MBT10001755, SAPA 10000031), database record HJB1000379. GenBank ITS = MZ724681.

Description of syntypes: The spores are smooth, ellipsoid to ovate, yellowish brown to brown and with a very small indistinct germ pore. For SAPA 1000031 the spores are on av. $7.6 \times 4.9 \mu\text{m}$, with av. spore Q 1.56, while for SAPA 1000032 they are on av. $7.9 \times 4.8 \mu\text{m}$, with av. spore Q 1.63. In both cases, the pleurocystidia are mainly ventricose, hyaline to yellowish in 5% KOH, while the cheilocystidia are more utriform in shape.

Japanese name: Tomoe-take (Imai 1938).

Remarks: Based on morphology and ITS sequence data (Fig. 4), the syntypes represent the same taxon. Although neither of the syntypes is in particularly good condition, of the two collections, SAPA 10000031 yielded better sequence data.

The description is in good agreement with the description given by Imai (1938). Although Imai does not mention burnt ground as the habitat, morphologically and molecularly both syntypes of *H. tomoeae* are in good agreement with *Pholiota brunnescens*, which is associated with burnt soil or wood (Matheny et al. 2018). It appears likely that *P. tomoeae* is a later synonym of *P. brunnescens*; we rather leave it to *Pholiota* experts to synonymize the two species, also considering that the phylograms based on several loci published by Matheny et al. (2018) and Tian and Matheny (2021) suggest that *P. brunnescens* s.l. may be rather variable and is not supported by bootstrap (Tian and Matheny 2021).

Discussion

For the newly described species as well as for the species described by Imai (1938), we had both morphological and molecular data available and the conclusions from both kinds of data supported each other. With regard to Imai's species, it is clear that, at the time he described these four species, the concepts of brown-spored genera were rather different from today. We cannot be sure that all of the new combinations are indeed non-redundant species. It is beyond the scope of this study to explore the limits of species from genera other than *Hebeloma*. We only have ITS data available for the types which may not be sufficient to distinguish species in *Agrocybe*, around *Homophron spadiceum* or *Pholiota brunnescens*. This situation leads to a dilemma between different principles of best taxonomic practices formulated by Aime et al. (2021): On the one hand, the publication of superfluous names ought to be avoided, on the other we view the recombination into the genus we consider the correct one as the most efficient means to communicate our findings to the experts for the respective genera. The experts, in our view, should make the decision on the synonymy or otherwise of *A. imaii* with *A. pediades*, *A. humosa* with *A. smithii*, *Ho. helvolens* with *Ho. spadiceum*, and *P. tomoeae* with *P. brunnescens*.

Based on the almost completed study of *Hebeloma* types worldwide, we are confident that the new *Hebeloma* species, *H. asperosporum*, *H. cinnamomeum*, and *H. citrisporum*, are good species and all of them can, based on our current knowledge, be identified by ITS alone.

The presence of conflicts between single locus results in the genus *Hebeloma* was previously known. Conflicts have been discussed earlier by Grilli et al. (2016) for *H. sect. Velutipes* and by Eberhardt et al. (2016) for *H. sect. Clepsydroida*. The recent recognition of additional taxa in *H. sect. Clepsydroida*, i.e., *H. asperosporum*, *H. cinnamomeum*, and *H. sordidulum* (Eberhardt et al., submitted) appears to have increased the conflict. While more advanced analysis methods might have given a better representation than concatenation, of what the available data suggest about species relationships, it would not have changed the fact that additional loci are needed to resolve infrageneric relationships. In the case of *H. sect. Denudata*, additional loci are also needed for the delimitation of subsections. Currently, we do not have molecular support that the morphological characters that are used for distinguishing and delimiting *H. subsections. Clepsydroida, Crustuliniformia, and Hiemalia* have evolved concertedly among the members of each subsection.

We are not aware of any records outside of Japan of the three new species described here (but note the remark made above with regard to a possible collection of *H. asperosporum* from China). The species may be endemic to these islands, but more collections, particularly of *H. asperosporum* and *H. citrisporum*, are needed before such a hypothesis could be either accepted or rejected.

With regard to the list of *Hebeloma* for Japan produced by Katumoto (2010) which listed 15 species, we can remove the four Imai species (*H. fimicola*, *H. helvolescens*, *H. humosum*, *H. tomoeae*), which are not *Hebeloma*. Additionally, it may be safer to reject *H. longicaudum* and *H. sinuosum* that should be regarded as dubious names and without material to examine, it is difficult to assign them. *Hebeloma crustuliniforme* f. *microspermum* is *H. nanum*, a species for which we have another collection, confirming its presence in Japan. Collections previously referred to *H. spoliatum* should likely be referred to *H. danicum* as discussed above. Collections previously referred to *H. radicosum* should likely be referred to *H. sagarae* as discussed in Eberhardt et al. (2020b).

We are unable to confirm the presence, in Japan, of *H. crustuliniforme*, *H. mesophaeum*, and *H. sacchariolens*. It is possible that those collections which were called *H. crustuliniforme* in the past are *H. cavipes* or *H. velutipes*, both of which have often been mistakenly determined as *H. crustuliniforme* (Vesterholt et al. 2014). It is likely that species previously determined as *H. sacchariolens* did indeed belong to *H. sect. Sacchariolentia* but during our studies, we have not identified any collections from this section. Four collections recorded as *H. sacchariolens* were in fact *Pholiota* sp., *H. danicum* and *H. vinosophyllum* (2). With regard to *H. mesophaeum*, again it is likely that species previously determined as *H. mesophaeum* did indeed belong to *H. sect. Hebeloma* but during our studies, the only species from this section that we have encountered is *H. hygrophilum*. The final three species Katumoto mentioned (*H. luchuense*, *H. radicosoides*, *H. vinosophyllum*) are certainly present in Japan and as yet the first two of these have not been recorded from anywhere outside Japan.

In summary, we can add, as verified for Japan, *H. cavipes*, *H. eburneum*, *H. hygrophilum*, *H. subtortum*, and *H. velutipes*, as well as the three new species described here, bringing the total number of *Hebeloma* species that we can confirm to be present in Japan to fifteen.

Searches in GenBank and UNITE (Köljal et al. 2005; Johnson et al. 2008; Nilsson et al. 2019) for sequence data from Japan strongly suggest that *H. sordescens* (AB848488, Miyamoto et al. 2014) and *H. rostratum* (MT596467, Faverol-Longo et al. unpublished, direct submission 08-Jun-2020) occur in the country, while sequences from *H. sect. Hebeloma* (e.g., AB211272 or AB327182, Nara 2006; Obase et al. 2007) could belong to various species of the *H. mesophaeum* complex; AB211274 (Nara 2006) might be *H. helodes* or

H. aurantiotumbrinum; AB848487 (Miyamoto et al. 2014) or some others could be *H. incarnatulum* rather than *H. velutipes* and EU711239 (Roy et al. 2009) or some others could be *H. leucosarx* rather than *H. velutipes*. LC009707 (Maeno and Sagara, unpublished, direct submission 6 Nov 2014) might be *H. melleum* or a closely related taxon.

Given the, relatively, small number of collections available for this study, it can be assumed that there are many more species of *Hebeloma* to be discovered from the islands of Japan. We hope that this publication will encourage the collection and determination of *Hebeloma* in the country. In lieu of a key for *Hebeloma* in Japan (which would be deficient, based on too few collections), we refer to an interactive identification tool for *Hebeloma* that is currently under development (Bartlett et al. 2021).

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Data availability The majority of the material was obtained through public collections or, in the case of the private collection of H.J.B., will be accessioned to a public collection when the project is finished. Sequence data were submitted to GenBank. Alignments and trees were submitted to TreeBASE.

Code availability Not applicable.

Declarations

Conflict of interest None.

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