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.* tomoae) are not from the genus *Hebeloma*, but are members of *Agrocybe*, *Homophoron*, or *Pholiota*. Recombinations are made. *Hebeloma crustuliniforme* f. microsporum, 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.* radiicosoides (*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).

Katsumoto (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. microsporum, *H.* fimicola, *H.* helvolescens, *H.* humosum, *H.* longicaudum, *H.* luchuense, *H.* mesophaeum, *H.* radiicosoides, *H.* radicosum, *H.* sacchariolens, *H.* sinuosum, *H.* spoliatum, *H.* tomoae, and *H.* vinosophyllum. Katsumoto 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 Katumoto and *Hebeloma lactariolens* are also *Hebeloma microsporum* (one record, no preserved specimen), *Hebeloma leucosarx* (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 June 2021) gives 160 occurrences of *Hebeloma* in Japan. Of these 160 occurrences, 110 reference a preserved specimen and 141 give a species name. Additional to the names given by Katumoto and *Hebeloma lactariolens* are also *Hebeloma microsporum* (one record, no preserved specimen), *Hebeloma leucosarx* (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).
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. tomoae* (Imai 1938); *H. vinosophyllum* (Hongo 1965); *H. crustuliniforme* f. *microspermum* (Hongo 1966); *H. lactariolens* (Clémençon 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 González and Labarère (1998). Sequencing was carried out at LGC Genomics (Berlin). Sequences were edited using Sequencer 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 ALVIEW 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 “Maffit-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 ≥ 80% and ultrafast bootstrap support ≥ 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                                                                 |
|--------------------------|---------------|---------|---------------------------|---------------------------------------------------------------------------|
| *Agrocybe firma*         | TENN RMA17    | USA     | MG663239                  | Matheny, P.B. and Swenie, R.A., unpubl., subm. 10-Dec-2017                 |
| *Agrocybe firma*         | CBS 390.79    | unknown | MN306192                  | Frings et al. 2020                                                        |
| *Agrocybe firma*         | GLM-F045867   | Germany | MZ019447                  | Eberhardt et al., Mycologia, in press                                     |
| *Agrocybe flexuosipes*   | NYS-F-001221  | USA     | MN017805                  | Eberhardt et al., Mycologia, in press                                     |
| *Agrocybe humosa*        | SAPA 1000033  | Japan   | MZ725546                  | Here                                                                      |
| *Agrocybe imaii*         | SAPA 1000036  | Japan   | MZ725547                  | Here                                                                      |
| *Agrocybe pediades*      | LE 262811     | Russia  | JN684798                  | Malysheva and Kiyashko 2011                                              |
| *Agrocybe pediades*      | MO270391      | Mexico  | KY646479                  | Rockefeller, A., unpubl., subm. 23-Feb-2017                              |
| *Agrocybe praecox*       | HJAU 0368     | China   | MN258622                  | Huo, unpubl., subm. 01-Aug-2019                                          |
| *Agrocybe praecox*       | TUF 106288    | Estonia | UDB011682                 | Liiv, 06-Jul-2018                                                        |
| *Agrocybe praecox*       | O-F-21680     | Norway  | UDB036650                 | NORBOL (Norwegian Barcode of Life)                                       |
| *Agrocybe praecox*       | MSC 378486    | UK      | AY194531                  | Hallen et al. 2003                                                       |
| *Agrocybe smithii*       | GLM-F045869   | Germany | MZ019448                  | Eberhardt et al., Mycologia, in press                                     |
| *Agrocybe smithii*       | TROM-F-17213  | Norway  | UDB037131                 | NORBOL                                                                    |
| *Agrocybe smithii*       | O-F-302315    | Norway  | UDB037255                 | NORBOL                                                                    |
| *Agrocybe smithii*       | SMNS-STU-F-0900850 | Norway  | MZ019432                  | Eberhardt et al., Mycologia, in press                                     |
| *Agrocybe putaminum*     | PDD 96108     | New Zealand | KM975434                  | Cooper and Park, unpubl., subm. 15-Oct-2014                              |
| *Agrocybe putaminum*     | MO116752      | USA     | MH285875                  | Rockefeller unpubl., subm. 03-May-2018                                   |
| *Agrocybe smithii*       | UWO T-792, Z-45 | USA     | KC176295                 | Thorn et al. 1996                                                        |
| *Agrocybe smithii*       | UWO T-792, Z-45 | USA     | KC176296                 | Thorn et al. 1996                                                        |
| *Agrocybe smithii*       | TEN 066942 (PBM3793) | USA     | MG663269                 | Matheny et al., unpubl., subm. 11-Dec-2017                               |
| *Agrocybe smithii*       | MO310653      | Canada  | MH558289                  | Matheny and Hobbs, unpubl., subm. 28-Jun-2018                             |
| Environmental sequence   |               |         |                           |                                                                           |
| Fungal isolate           | 2013071701    | Estonia | UDB0575407                | Tedersoo et al. 2020                                                      |
| *Homophron camptopodum*  | TUF 118215    | Estonia | UDB015582                 | Fukasawa, unpubl., subm. 20-Nov-2015                                     |
| *Homophron cernuum*      | BRNM 705614   | Czech Republic | AM712287                 | Vašutová et al. 2008                                                     |
| *Homophron cernuum*      | GB DB2013652266 | Denmark | KJ936932                  | Örstadius et al. 2015                                                    |
| *Homophron helvolescens* | SAPA 1000035  | Japan   | MZ725549                  | Here                                                                      |
| *Homophron spadiceum*    | WUTU-F-023854 | USA     | MZ725550                  | Here                                                                      |
| *Homophron spadiceum*    | TAKK08.11.12.1-2 | Japan   | AB594840                  | Kobayashi and Hoshino, unpubl., subm. 18-Oct-2010                        |
| *Homophron spadiceum*    | BRNM 705613   | Czech Republic | AM712288                 | Vašutová et al. 2008                                                     |
| *Homophron spadiceum*    | GB 981111 Epitype | Germany | DQ389729                 | Larsson and Östadius 2008                                                |
| Species           | Collection no | Country | ITS Genbank/UNITE acc. no | Citation                          |
|-------------------|---------------|---------|---------------------------|-----------------------------------|
| Homophron spadiceum | JCS100905B    | USA     | FJ168610                  | Slot et al. 2010                  |
| Homophron spadiceum | TRTC156998    | Canada  | JN021090                  | Dentinger et al. 2011             |
| Homophron spadiceum | HC-PNNT-106   | Mexico  | KT875089                  | Garibay-Orijel et al., unpubl., subm. 05-Oct-2015 |
| Homophron spadiceum | HC-PNNT-300   | Mexico  | KT875090                  | Garibay-Orijel et al., unpubl., subm. 05-Oct-2016 |
| Homophron spadiceum | CUH AM031     | India   | KU928134                  | Yangdol et al. 2016               |
| Homophron spadiceum | TENN 071834 (PBM4137) | USA | MG773815                  | Matheny et al., unpubl., subm. 07-Dec-2017 |
| Homophron spadiceum | MO111084      | Mexico  | MG993188                  | Rockefeller, unpubl., subm. 24-Feb-2018 |
| Homophron spadiceum | MycoMap7004   | USA     | MK564559                  | Russell, unpubl., subm. 22-Feb-2019 |
| Homophron spadiceum | MO224603      | USA     | MN906125                  | Russell, unpubl., subm. 04-Jan-2020 |
| Homophron spadiceum | MO110531      | USA     | MN906126                  | Russell, unpubl., subm. 04-Jan-2020 |
| Homophron spadiceum | TUF 118222    | Estonia | UDB015406                 | Liiv, 06-Jul-2018                 |
| Homophron spadiceum | TUF 106436    | Estonia | UDB015694                 | Liiv, 06-Jul-2018                 |
| Homophron spadiceum | TUF 118801    | Estonia | UDB019586                 | Liiv, 06-Jul-2018                 |
| Homophron spadiceum | O-F-251569    | Norway  | UDB036170                 | Fonneland, 27-Oct-2018            |
| Homophron spadiceum | O-F-301571    | Norway  | UDB036893                 | Fonneland, 27-Oct-2018            |
| Homophron spadiceum | GLM-F046017   | Germany | MZ724623                  | Here                              |
| Homophron cf. spadiceum | MO377580  | USA     | MT271783                  | Clements, unpubl., subm. 30-Mar-2020 |
| Lacrymaria hypertropicalis | XAL Guzman29585 | Mexico | KC992958                  | Örstadius et al. 2015             |
| Lacrymaria hypertropicalis | MO353205 | USA     | MK346140                  | Rockefeller, unpubl., subm. 29-Dec-2018 |
| Lacrymaria lacrymabunda | GB EL7-03   | Sweden  | DQ389724                  | Larsson and Örstadius 2008        |
| Lacrymaria lacrymabunda | K(M) 234056 | UK      | MZ159649                  | Gaya et al., unpubl., subm. 30-Apr-2021 |
| Pholiota brunnescens | TENN 052897 (TFB5897) | Mexico | KF871789                  | Matheny and Bougher 2017          |
| Pholiota brunnescens | WTU 10337    | USA     | MG735270                  | Matheny et al. 2018               |
| Pholiota brunnescens | GALL37545, WTU 21130 | USA | MG735298                  | Matheny et al. 2018               |
| Pholiota brunnescens | PBMB527, WTU 10342 | USA | MG735299                  | Matheny et al. 2018               |
| Pholiota brunnescens | Szr9021, WTU 10354 | USA | MG735303                  | Matheny et al. 2018               |
| Pholiota brunnescens | MTS4953b, WTU 10343 | USA | MG735305                  | Matheny et al. 2018               |
| Pholiota brunnescens | ET32, TENN 074791, HMJAU 37361 | China | MN209732                  | Tian and Matheny 2021             |
| Pholiota brunnescens | ET22, TENN 074782, HMJAU 37363 | China | MN209733                  | Tian and Matheny 2021             |
| Pholiota brunnescens | TUF 133578    | Pakistan | UDB0780780               | Gohar, 01-Dec-2020                |
| Pholiota brunnescens holotype | AHS3525, MICH 11657 | USA | MG735292                  | Matheny et al. 2018               |
| Pholiota castanea | TENN 071878   | USA     | MH016952                  | Matheny et al. 2018               |
| Pholiota castanea | PBMB4254, TENN 074736 | USA | MN337888                  | Tian and Matheny 2021             |
| Pholiota castanea holotype | TENN 020269 | USA | HQ222025                  | Matheny et al. 2018               |
| Pholiota choceuenensis holotype | PRM 95066  | Czech Republic | NR_155622 | Holec et al. 2014 |
| Pholiota foedata | MIN 47532     | USA     | MZ019457                  | Eberhardt et al., Mycologia, in press |
| Pholiota foedata holotype | NYS-F-001228 | USA | MN017804                  | Eberhardt et al., Mycologia, in press |
| Pholiota gallica | PRM 933232    | France  | LN889967                  | Holec et al. 2016                 |
(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.
| Species          | Database ref | Collection no | Country   | GenBank acc. no. ITS | GenBank acc. no. TEF1a | GenBank acc. no. RPB2 | GenBank acc. no. mitSSU V6 | Published by |
|------------------|--------------|---------------|-----------|----------------------|------------------------|-----------------------|----------------------------|--------------|
| *H. aestivale*   | HJB13626     | HJB13626      | Germany   | KT218447             | KT217675               | KT217767              | Grilli et al. 2016        |
| *H. aestivale*   | HJB13801     | SP-10.11.03   | Spain     | KT218454             | KT217678               | KT217769              | Grilli et al. 2016        |
| *H. aestivale*   | HJB10439     | HJB10439      | UK        | KT218282             | KT217631               | KT217716              | Grilli et al. 2016        |
| *H. albidulum*   | HJB18372     | HJB18372      | USA       | MZ782147             | MZ782953               | MZ782921              | Here                      |
| *H. albidulum*   | HJB16965     | HJB16965      | USA       | MZ782142             | MZ782954               | MZ782922              | Here                      |
| *H. albidulum*   | HJB14702     | HJB14702      | USA       | MZ782105             | MZ782955               | MZ782923              | Here                      |
| *H. ammophilum*  | HJB12374     | GB EL-281-08  | Hungary   | KT217509             | KT216849               | KT216980              | Eberhardt et al. 2016     |
| *H. ammophilum*  | HJB14471     | EL-18861      | Hungary   | MZ782104             | MZ782956               | MZ782924              | MZ782867                  |
| *H. ammophilum*  | HJB15417     | HJB15417      | Italy     | MZ782106             | MZ782957               | MZ782925              | MZ782868                  |
| *H. ammophilum*  | HJB16438     | EG-101029.01  | Italy     | MZ782140             | MZ782958               | MZ782926              | MZ782869                  |
| *H. ammophilum*  | HJB16439     | EG-121019.01  | Italy     | MZ782141             | MZ782959               | MZ782927              | MZ782870                  |
| *H. asperosporum*| HJB16250     | TNS TNS-F-75704| Japan     | MZ782138             | MZ782960               | MZ782928              | MZ782871                  |
| *H. asperosporum*| HJB16251     | TNS TNS-F-75705| (holotype)| MZ782139             | MZ782961               | MZ782929              | MZ782872                  |
| *H. bulbiferum*  | HJB13083     | HJB EC177060  | Croatia   | KT218422             | KT217667               | KT217754              | Grilli et al. 2016        |
| *H. bulbiferum*  | HJB10300     | HJB10300      | Italy     | KT218261             | KT217615               | KT217704              | Grilli et al. 2016        |
| *H. bulbiferum*  | HJB10812     | C JV-03-587   | Italy     | KT218318             | KT217645               | KT217730              | Grilli et al. 2016        |
| *H. cavipes*     | HJB10537     | HJB10537      | France    | KT217402             | KT216799               | KT216916              | KT217198                  |
| *H. cavipes*     | HJB13227     | HJB13227      | Poland    | MZ782102             | MZ782962               | MZ782930              | MZ782873                  |
| *H. cavipes*     | HJB9433      | HJB9433       | Spain     | KT217362             | KT216780               | KT216877              | KT217158                  |
| *H. cavipes*     | HJBNS5357    | NS3537        | USA       | MZ782148             | MZ782963               | MZ782932              | MZ782874                  |
| *H. cavipes*     | HJB14374     | HJB14374      | USA       | MZ782103             | MZ782964               | MZ782931              | MZ782875                  |
| *H. celatum*     | HJB13621     | BR 5020184119676| Germany | KT218446             | KT217674               | KT217766              | Grilli et al. 2016        |
| *H. celatum*     | HJB12857     | MK-MAK 08-10021| North Macedonia| KT218413             | KT217664               | KT217752              | Grilli et al. 2016        |
| *H. celatum*     | HJB13799     | SP-10.11.02   | Spain     | KT218453             | KT217677               | KT217768              | Grilli et al. 2016        |
| *H. cinnamomeum* | HJB16236     | TNS TNS-F-59098| Japan     | MZ782128             | MZ782965               | MZ782933              | MZ782876                  |
| *H. cinnamomeum* | HJB16245     | TNS TNS-F-73984| Japan     | MZ782134             | MZ782966               | MZ782934              | MZ782877                  |
| *H. cinnamomeum* | HJB16246     | TNS TNS-F-74039| Japan     | MZ782135             | MZ782967               | MZ782935              | MZ782878                  |
| *H. cinnamomeum* | HJB15837     | TNS TNS-F-82067| (holotype)| MZ782111             | MZ782968               | MZ782936              | MZ782879                  |
| *H. cinnamomeum* | HJB15838     | HJB15838      | Japan     | MZ782112             | MZ782969               | MZ782937              | MZ782880                  |
| *H. cinnamomeum* | HJB16173     | TNS TNS-F-1387| Japan     | MZ782113             | MZ782113               | Here                  |
| *H. cinnamomeum* | HJB16213     | TNS TNS-F-42284| Japan     | MZ782114             | MZ782114               | Here                  |
| *H. cinnamomeum* | HJB16214     | TNS TNS-F-43723| Japan     | MZ782115             | MZ782115               | Here                  |
| *H. cinnamomeum* | HJB16216     | TNS TNS-F-44535| Japan     | MZ782116             | MZ782116               | Here                  |
| *H. cinnamomeum* | HJB16220     | TNS TNS-F-44863| Japan     | MZ782118             | MZ782118               | Here                  |
| *H. cinnamomeum* | HJB16221     | TNS TNS-F-44864| Japan     | MZ782119             | MZ782119               | Here                  |
| Species                  | Database ref  | Collection no | Country       | GenBank acc. no. ITS | GenBank acc. no. TEF1a | GenBank acc. no. RPB2 | GenBank acc. no. mitSSU V6 | Published by |
|-------------------------|---------------|---------------|---------------|----------------------|------------------------|------------------------|----------------------------|---------------|
| *H. cinnamomeum*        | HJB16226      | TNS TNS-F-46098 | Japan         | MZ782121             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16228      | TNS TNS-F-49380 | Japan         | MZ782122             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16229      | TNS TNS-F-49387 | Japan         | MZ782123             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16230      | TNS TNS-F-49389 | Japan         | MZ782124             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16234      | TNS TNS-F-58915 | Japan         | MZ782126             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16235      | TNS TNS-F-59097 | Japan         | MZ782127             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16238      | TNS TNS-F-60045 | Japan         | MZ782129             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16243      | TNS TNS-F-72963 | Japan         | MZ782132             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16244      | TNS TNS-F-73028 | Japan         | MZ782133             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16247      | TNS TNS-F-74060 | Japan         | MZ782136             |                        |                        |                            | Here          |
| *H. cinnamomeum*        | HJB16199      | TNS TNS-F-38024 | Japan         | MZ782144             |                        |                        |                            | Here          |
| *H. citrisporum*        | HJB15832      | MO255034      | Japan         | MZ782109 MZ782971 MZ782938 |                        |                        |                            | Here          |
| *H. citrisporum*        | HJB15833      | BR 5020214140236 V (holotype) | Japan | MZ782110 MZ782972 MZ782939 |                        |                        |                            | Here          |
| *H. crustuliniforme*    | HJB13713      | BR BR-MYCO-1739 89-68 (epitype) | France | KF309424 KT216860 KF309495 KM390510 |                        |                        |                            | Eberhardt et al. 2015, 2016 |
| *H. crustuliniforme*    | HJB12807      | L WAG-W9581   | Netherlands   | KF309415 KT216854 KF309492 KM390452 |                        |                        |                            | Eberhardt et al. 2015, 2016 |
| *H. crustuliniforme*    | HJB11237      | HJB11237      | Spain         | JN943870 KT216824 KF309480 KM390380 |                        |                        |                            | Schoch et al. 2012; Eberhardt et al. 2015, 2016 |
| *H. echinosporum*       | HJB13524      | BR BR-MYCO 174907-16 (holotype) | France | KT217548 KT216858 KT216993 KT217330 |                        |                        |                            | Eberhardt et al. 2016 |
| *H. erebium*            | HJB11857      | C JV-06-690   | Denmark       | KT218373 KT217657 KT217745 |                        |                        |                            | Grilli et al. 2016 |
| *H. erebium*            | HJB13620      | HJB13620      | Germany       | KT218445 KT217673 KT217765 |                        |                        |                            | Grilli et al. 2016 |
| *H. erebium*            | HJB14180      | LOD IK-H0182  | Poland        | KT218463 KT217682 KT217773 |                        |                        |                            | Grilli et al. 2016 |
| *H. hiemale*            | HJB8890       | HJB8890       | Belgium       | GQ869484 KT216772 KT216867 KT217148 |                        |                        |                            | Beker et al. 2010; Eberhardt et al. 2016 |
| *H. hiemale*            | HJB10758      | HJB10758      | Belgium       | KT217433 KT216814 KT216941 KT217231 |                        |                        |                            | Eberhardt et al. 2016 |
| *H. hiemale*            | HJB11704      | BR BR-MYCO 174905-14 (epitype) | France | GQ869505 KT216833 KT216964 KT217279 |                        |                        |                            | Eberhardt et al. 2016 |
| *H. hiemale*            | HJB17443      | C C-F-106776 | Greenland     | MW45625 MZ782975 MZ782943 MZ782881 |                        |                        |                            | Eberhardt et al. 2016 |
| *H. hiemale*            | HJB9384       | HJB9384       | UK            | GQ869482 KT216778 KT216875 KT217156 |                        |                        |                            | Beker et al. 2010; Eberhardt et al. 2016 |
| *H. incarnatum*         | HJB10132      | HJB10132      | Finland       | KT218239 KT217606 KT217695 |                        |                        |                            | Grilli et al. 2016 |
| Species               | Database ref | Collection no | Country    | GenBank acc. no. ITS | GenBank acc. no. TEF1a | GenBank acc. no. RPB2 | GenBank acc. no. mitSSU V6 | Published by |
|-----------------------|--------------|---------------|------------|----------------------|------------------------|------------------------|-----------------------------|---------------|
| H. incarnatulum       | HJB10139     | HJB10139     | Finland    | KT218246             | KT217607               | KT217697               | Grilli et al. 2016          |               |
| H. incarnatulum       | HJB13589     | HJB13589     | Germany    | KT218441             | KT217672               | KT217764               | Grilli et al. 2016          |               |
| H. leucosarx          | HJB11694     | HJB11694     | Belgium    | KT218361             | KT217652               | KT217740               | Grilli et al. 2016          |               |
| H. leucosarx          | HJB10140     | HJB10140     | Finland    | KT218247             | KT217608               | KT217698               | Grilli et al. 2016          |               |
| H. leucosarx          | HJB9289      | HJB9289      | UK         | KT218219             | KT217599               | KT217687               | Grilli et al. 2016          |               |
| H. matritense         | HJB9485      | BR BR-MYCO-174910-19 (holotype) | Spain | KT217364 | KT216781 | KT216879 | KT217160 | Eberhardt et al. 2016 |
| H. matritense         | HJB9486      | HJB9486      | Spain      | KT217365             | MZ782976               | KT216880               | Eberhardt et al. 2016; here |
| H. populinum          | HJB14114     | HJB GK-5803  | Greece     | KT217563             | KT216862               | KT217002               | Eberhardt et al. 2016       |               |
| H. populinum          | HJB13758     | HJB13758     | UK         | KT217560             | KT216861               | KT217000               | Eberhardt et al. 2016       |               |
| H. quercetorum        | HJB13497     | HJB13497     | Cyprus     | KT218437             | KT217670               | KT217761               | Grilli et al. 2016          |               |
| H. quercetorum        | HJB10327     | HJB10327     | Italy      | KT218268             | KT217620               | KT217708               | Grilli et al. 2016          |               |
| H. sacchariolens      | HJB13418     | HJB13418     | Spain      | KT218435             | KT217669               | KT217760               | Grilli et al. 2016          |               |
| H. sacchariolens      | HJB10321     | HJB10321     | Italy      | KT218266             | KT217618               | KT217706               | Grilli et al. 2016          |               |
| H. sinapizans         | HJB10360     | HJB10360     | Belgium    | KT218216             | KT217597               | KT217684               | Grilli et al. 2016          |               |
| H. sinapizans         | HJB13530     | BR 5020184118648 | France | KT218440 | KT217671 | KT217763 | Grilli et al. 2016 |
| H. sinapizans         | HJB10628     | HJB10628     | UK         | QJ751191             | KT217637               | KT217721               | Eberhardt et al. 2013; Grilli et al. 2016 |
| H. sordidulum         | HJB15800     | UWO          | Canada     | MZ782108             | MZ782977               | MZ782947               | MZ782882 | Here |
| H. sordidulum         | HJB12269     | HJB12269     | USA        | MZ782101             | MZ782978               | MZ782944               | MZ782883 | Here |
| H. sordidulum         | HJB12287     | HJB12287     | USA        | MZ782100             | MZ782979               | MZ782945               | MZ782884 | Here |
| H. sordidulum         | HJB15700     | HJB15700     | USA        | MZ782107             | MZ782980               | MZ782946               | MZ782885 | Here |
| H. sordidulum         | HJB16978     | HJB16978     | USA        | MZ782143             | MZ782981               | MZ782948               | MZ782886 | Here |
| H. subconcolor        | HJB17065     | C C-F-8242   | Greenland  | MW445847             | MZ782982               | MZ782949               | Eberhardt et al. 2021b; here |
| H. subconcolor        | HJB11114     | HJB11114     | Switzerland | KT218330 | KT217646 | KT217732 | Grilli et al. 2016 |
| H. subconcolor        | HJB11142     | HJB11142     | Switzerland | KT218332 | KT217647 | KT217734 | Grilli et al. 2016 |
| H. vaccinum           | HJB9965      | HJB9965      | Belgium    | KT217371             | KT216784               | KT216883               | KT217167 | Eberhardt et al. 2016 |
| H. vaccinum           | HJB10067     | HJB10067     | Belgium    | KT217373             | KT216785               | KT216885               | KT217169 | Eberhardt et al. 2016 |
| H. vaccinum           | HJB17492     | C C-F-106767 | Greenland  | MW445830             | MZ782983               | MZ782952               | MZ782887 | Eberhardt et al. 2021b; here |
Results

None of the four species described by Imai (1938), *Hebeloma fimbicola*, *H. helvolescens*, *H. humosum*, and *H. tomoae* belong to *Hebeloma* as recognized today. They belong to the genera *Agrocybe*, *Homophoron*, and *Pholiota* and are recombined in the Taxonomy section with a short summary of their main characters. *Hebeloma crustuliniforme* s. *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. fimbicola*) is placed in a clade with sequences identified as *A. pediades*.

The alignment for *Homophoron* includes 35 ITS sequences and 708 positions. *Homophoron 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 “*Homophoron 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. tomoae* 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. Clepsy-droida*, 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. Clepsy-droida*, 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 *TEFla*, alignment 717 positions) have been employed to
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. ammonium*, *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. *Clepsydroida* 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
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 tomoae in a taxonomic context. Support values are from 1000 replicates of SH-like approximate likelihood ratio tests and ultrafast bootstrap. Support values ≥ 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.

**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 × 7.7 μm, 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 10–11.5 × 7–8 μm. This matches most closely with our measurements for SAPA 10000033 (10.1–13.3 × 6.9–9.5 μm, av. 11.1 × 7.7 μm, 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 × 8.9 μm (11.8–14.7 × 8.0–10.1 μm), 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 (11–13.5 × 6.5–8 μm respectively 12.1 × 7.7 μm) 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 10–13 × 5–7 μm, 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.

**Basionym:** Hebeloma fimicola [as “fimicolum”] 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 × 8.9 µm, 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 µm long, indextrinoid and with 0.005

Fig. 5 Maximum Likelihood result of concatenated ITS, RPB2, TEF1a, and mitSSU V6 sequences of members of Hebeloma sect. Denudata, subsects. Clepsyroida and Crustuliniiformia, rooted with members of H. subsect. Echinospora. Relationships that include conflicting data are indicated by dashed lines. Support values ≥ 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.
consistently loosening perispore distinguishes this species from other known members of *H. section Denudata*.

**Etymology:** From asper (Latin) meaning rough and spora (Latin) to emphasize the rough spores.

**Typification:** 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, Holotype (TNS-F-75705), database record HJB16251). GenBank ITS = MZ782138.

**Description:** Pileus (21) 29–52 (58) mm diameter, hemispherical, convex often umbonate; margin often crenulate or eroded, often spotting, not hygrophanous; usually almost unicolored with color at center clay-buff, honey or dark pinkish buff, paler at margin. Lamellae emarginate, white, cream to brown, with strongly white fimbriate edge and droplets visible with the naked eye, number of full-length lamellae 70–72. Stipe (26) 32–56 (77) mm long, (6) 7–10 (13) mm diameter at median, widening towards a clavate base, surface cream, ivory to pale brown but discoloring from the base.

**Fig. 6** Maximum Likelihood result of concatenated ITS, *RPB2*, and *TEF1a* sequences of members of *Hebeloma* sect. *Sinapizantia*. Relationships that include conflicting data are indicated by dashed lines. Support values ≥ 80% (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.
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 \( 9.0 \)–\( 10.8 \times 5.4 \)–\( 6.6 \) \( \mu \)m, with median \( 9.5 \times 5.9 \) \( \mu \)m and av. \( 9.6 \times 5.9 \) \( \mu \)m with S. D. length 0.6 \( \mu \)m and width 0.35 \( \mu \)m; \( Q \) value 5\% to 95\% percentile range \( 1.53 \)–\( 1.77 \), with median 1.60 and av. 1.62 with S. D. 0.08; spore size based on two collections, medians \( 9.5 \)–\( 10.1 \times 5.9 \)–\( 6.3 \) \( \mu \)m and av. \( 9.6 \)–\( 10.0 \times 5.9 \)–\( 6.2 \) \( \mu \)m with av. S. D. length 0.565 \( \mu \)m and width 0.33 \( \mu \)m, av. \( Q \) 1.61–1.62, 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
every mature spore and indextrinoid hardly changing color in Melzer’s reagent (O3/4; P3; D0); spore color under the microscope brown. Basidia 22–30 × 6–8 µm, with av. Q 3.2–3.6 µm, cylindrical to clavate, without pigmentation, 4–spored. Cheilocystidium width near apex holotype 5% to 95% percentile range 5.7–9.2 µm, with median 7.7 µm and av. 7.6 µm with S. D. 1.1 µm; across two collections median 7.4–7.7 µm and av. 7.4–7.6 µm; examining approx. 20 selected cheilocystidia of each of the two collections yields a range for the avs. of 44–45 × 7.4–7.6 × 3.9–4.3 × 5.3–6.0 µm and 44 × 7.6 × 4.3 × 6.0 µm 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 capititate 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 µm long. Pileipellis is an ixocutis with an epicutis up to 150 µm thick, with gelatinized, often encrusted hypheae up to 6 µm 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 µm 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-Oshima.

**Additional collections examined:** Japan, Kagoshima, Amami-Oshima Island, Yamato, Amami Forest Polis Park (approx. 28.316056N, 129.344778E, alt. approx. 214 m aisl.) 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. *Clepsyroida* 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 µm 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 µm, 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, Nakanagatanii (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) 21–46 (51) mm diameter, hemispherical, often convex, occasionally umbonate; margin involute, particularly when young, not hygrophanous; usually almost unicolored, 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, sometimes 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 22–33 × 6–8 µm, with av. Q 3.0–3.9 µm, cylindrical to
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 avs. of 50–61 × 5.0–6.6 × 3.3–3.9 × 4.6–7.0 µm and 54 × 6.6 × 3.7 × 4.9 µm 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
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. 36.1015N, 140.1131E, 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 evergreen *Quercus* spp., 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.), 5 Nov 2014, K. Nishibori (TNS-F-79263, 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-74060, 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, Nakanagatan (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, Fuiyosenda, 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. sect. Clepsydroida* within *H. sect. Demudata*. 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. sect. Clepsydroida*) rather than with *H. crustuliniforme* (the type of *H. sect. Crustuliniformia*) or *H. hiemale* (the type of *H. sect. Hiemalia*). Within *H. sect. Demudata*, 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, 2006)
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...
cheilocystidia with average width near the apex greater than 6.5 µm 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 a.s.l.) in urban pond-side roadside under *Quercus myrsinfolia* 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 umboed, 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 medium, 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 10.4–13.1 × 6.2–7.4 µm, with median 11.6 × 6.9 µm and av. 11.6 × 6.8 µm with S. D. length 0.86 µm and width 0.40 µm; *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 11.3–12.3 × 6.6–7.1 µm and av. 11.3–12.1 × 6.7–7.0 µm with av. S. D. length 0.82 µm and width 0.37 µm, 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. Basidium 26–36 × 7–9 µm, with av. *Q* 3.4–3.6 µm, cylindrical to clavate, without pigmentation, 4-sспорed. Cheilocystidium width near apex holotype 5% to 95% percentile range 4.8–8.4 µm, with median 6.6 µm and av. 6.6 µm with S. D. 0.54 µm; across 5 collections median 6.6–8.9 µm and av. 6.6–9.1 µm; examining approx. 20 selected cheilocystidia of each of the 5 collections yields a range for the avs. of 54–68 × 6.6–9.1 × 5.7–3.9 × 5.3–7.0 µm and 54 × 6.6 × 4.7 × 5.3 µm 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 µm long. Pileipellis is an ixocutis with an epicutis up to 115 µm thick, with gelatinized, often encrusted hyphae up to 7 µm wide. Subcutis yellow brown and the trama below the cutis made up of cylindrical or thickly sausage-shaped cells up to 18 µm 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 a.s.l.) under *Quercus* sp., 8 Nov 2011, K. Hosaka KH-JPN11-529 (TNS-F-44560, HJB16217); Ibaraki, Tsukuba (approx. 36.086858N, 140.119679E, alt. approx. 25 m a.s.l.) in urban pond-side roadside under *Quercus myrsinfolia* and *Quercus serrata*, 4 Oct 2016, U. Kawasaki UK267 (MO255034, HJB15832); Ibaraki, Tsukuba (approx. 36.085N, 140.12E, alt. approx. 25 m a.s.l.) in mixed woodland, 20 Oct 2017, U. Kawasaki UK338 (MO295075, HJB17412); Ibaraki, Tsukuba (approx. 36.085N, 140.12E, alt. approx. 25 m a.s.l.), 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 citiform 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 cheilocystidia with average width near the apex greater than 6.5 µm and average ratio of basal width to median width (B/M) at most 1.35, distinguish this species. While citiform 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 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 SH195151.08FU, 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)–9.5 × 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. helvellescens is indeed a later synonym of Ho. spadiceum.

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

MB840291

**Basionym:** *Hebeloma tomoae* 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 1000031), 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 × 4.9 μm, with av. spore Q 1.56, while for SAPA 1000032 they are on av. 7.9 × 4.8 μm, 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 1000031 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. tomoae* are in good agreement with *Pholiota brunnescens*, which is associated with burnt soil or wood (Matheny et al. 2018). It appears likely that *P. tomoae* 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. helvellescens* with *Ho. spadiceum*, and *P. tomae* 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. subsects. Clepsydroida, Crustulinaformia, 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. helvolecsens, H. humosum, H. tomoae), which are not Hebeloma. Additionally, it may be safer to reject H. longicaudum and H. sinusum that should be regarded as dubious names and without material to examine, it is difficult to assign them. Hebeloma crustuliniforme f. microsporum 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. (2020).

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 (Kõljalg et al. 2005; Johnson et al. 2008; Nilsson et al. 2019) for sequence data from Japan strongly suggest that H. sordeascens (AB848488, Miyamoto et al. 2014) and H. rostratum (MT596467, Favorol-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. incarnatum 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. melleur 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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