Revision of collections of *Hebeloma* spp. from the high-altitude Altay Mountains (Altay Republic) and report of a new to Russia species of *H. excedens*

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Abstract. Eight *Hebeloma* specimens from the high-altitude zone of Altai Mountains (West Siberia) were analyzed using morphological and molecular methods. Three species were identified (*H. alpinum*, *H. dunense*, *H. excedens*), including the previously unreported in Russia species *H. excedens*. The detailed morphological description and ecological data on *H. excedens* based on the studied collections are provided.

Keywords: Agaricales, Hymenogastraceae, taxonomy, West Siberia.

Ревизия ряда коллекций рода *Hebeloma* из высокогорья Алтая с описанием новой для России находки *H. excedens*

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Резюме. Восемь образцов рода *Hebeloma* из высокогорий Горного Алтая (Западная Сибирь) были проанализированы с использованием морфологических и молекулярных методов. Идентифицированы три вида (*H. alpinum*, *H. dunense*, *H. excedens*), включая ранее не отмечавшийся в России вид *H. excedens*. В статье представлено подробное морфологическое описание и экология *H. excedens*, основанные на изученных коллекциях.

Ключевые слова: Agaricales, Hymenogastraceae, таксономия, Западная Сибирь.

The genus *Hebeloma* (Fr.) P. Kumm. is a widely distributed group of ectomycorrhizal agaricoid fungi forming symbiotic associations with various species of trees and shrubs. This genus is challenging to identify at the species level, not only through morphological features, but through using molecular phylogeny approach (Eberhardt *et al.*, 2021). According to the latest classification based on current molecular and morphological data, *Hebeloma* is placed within the family Hymenogastraceae, order Agaricales (Matheny *et al.*, 2006; Knudsen, Vesterholt, 2018; Bartlett *et al.*, 2022). The species of the genus are generally characterized by a smooth cap (with rare exceptions), presence or absence of cortina, brown spores that may be either smooth or rough, absence of a germ pore and pleurocystidia, and presence of cheilocystidia.

The current taxonomic classification of the genus *Hebeloma* includes 17 sections. The section *Hebeloma* (Fr.) P. Kumm. is characterized by a visible cortina in young basidiomes and cheilocystidia, which are consistently lageniform or ventricose. This section includes 23 species, eight of which, referred to as the *H. mesophaeum* complex, have ellipsoid, indextrinoid or slightly dextrinoid spores: *Hebeloma alpinicola* A. H. Sm., V. S. Evenson et Mitchel, *H. colvinii* (Peck) Sacc., *H. dunense* L. Corb. et R. Heim, *H. excedens* (Peck) Sacc., *H. marginatulum* (J. Favre) Bruchet, *H. mesophaeum* (Pers.) Quél., *H. pascuense* Peck, *H. pubescens* Beker et U. Eberh. The section *Denudata* (Fr.) Sacc is characterized by absence of cortina, universal veil only visible in primordia, and cheilocystidia narrowly to broadly clavate or capitate, and comprises about 14 species, including *Hebeloma alpinum* (J. Favre) Bruchet (Vesterholt, 2005; Eberhardt *et al.*, 2021; Bartlett *et al.*, 2022).

Many *Hebeloma* species are commonly found in arctic and alpine habitats, where they play a significant role as mycorrhizal symbionts for plants such as *Salix* L., *Betula* L., *Bistorta* (L.) Scop., and *Dryas* L. (Miller, 1998; Beker *et al.*, 2010, 2018; Eberhardt *et al.*, 2015, 2021; Cripps *et al.*, 2019; Bolshakov *et al.*, 2021; *etc.*). In the Altai Republic, four species from the section *Hebeloma* (*H. alpinicola*, *H. dunense*, *H. marginatulum*, *H. mesophaeum*)

https://doi.org/10.31111/nsnr/2025.59.1.F33
Received: 5 February 2025 Accepted: 31 March 2025 Published: 6 April 2025

were previously recorded in the high-mountain belts (Bolshakov *et al.*, 2021; Kotkova *et al.*, 2024). However, no revision, combining morphological and molecular phylogenetic approaches, has been carried out so far. In this study, we analyzed eight specimens collected during expeditions in the high-mountain belts of the Plato Ukok and Severo-Chuisky Range. Most of the specimens examined belong to the *H. mesophaeum* complex that includes morphologically similar species, which are difficult to identify.

Morphological and phylogenetic analyses have revealed a species not previously recorded in Russia (*Hebeloma excedens*). This species was originally described by North American mycologist C. H. Peck as *Agaricus excedens* Peck (Peck, 1872), found in sandy woodlands under *Pinus* sp. For a long period, *H. excedens* was known only from continental North America, later recorded in Greenland with isolated findings in France and Turkey (Cripps *et al.*, 2019; Eberhardt *et al.*, 2021, 2022; Bartlett *et al.*, 2022; Dizkirici, 2022). As the first record across a large Asian continent, we consider that it merits a detailed description in present publication.

The article also presents characteristics of microstructures and photographs of basidiomata of the other identified species of *Hebeloma*, namely *Hebeloma alpinum*, *H. excedens*, and *H. dunense*. To confirm species identification, phylogenetic analysis was performed using a nuclear ribosomal DNA marker (ITS region).

Materials and Methods

Fresh basidiomata of *Hebeloma* were collected in a mountain tundras in June–July 2015, 2019 in the Kosh-Agach District, Plato Ukok and near the village Chagan-Uzun (2000–2200 m a. s. l.), the Altai Republic.

Morphological study

Collected specimens were photographed *in situ* using a Lumix camera. Macromorphological characters were described based on the field notes and color photographs of fresh basidiomata. The specimens were dried using standard methods (Clémençon, 2009). The dried specimens were examined microscopically following Vesterholt (2005) and Bartlett *et al.* (2022).

The morphological description of the basidiomata is based on examination of fresh and dried material. A standard set of reagents (5–10% KOH, 1% Congo Red solution, Melzer's reagent) and a microscope (Zeiss AxioStar Plus) with a digital camera (AxioCam ERc5s) were used for microscopic examination. The dimensions of microstructures are given as (minimum) average minimum – average maximum (maximum). The cheilocystidia dimensions given as length × width at base × width in the middle × width at the apex. The microscopic measurements were made using the Zeiss AxioVision 4.8.2 software. The diagnostic characters of spores (dextrinoidity, ornamentation and degree of loosening of the perispore) were abbreviated according to Vesterholt (2005) with "D" indicating the degree of basidiospore dextrinoidity in Melzer's, "P" the degree of loosening of the basidiospore perisporium in Melzer's, and "O" the degree of basidiospore surface ornamentation.

The specimens are stored in the M. G. Popov Herbarium of the Central Siberian Botanical Garden, Siberian Branch of the Russian Academy of Sciences (NSK), and their duplicates are kept in the Fungarium of the Yugra State University (YSU-F). The information about the specimens is stored in the Specify collection information system (http://specify.ugrasu.ru/). Collection data, including specimen photographs, and obtained sequences, are available for searching and downloading through GBIF (Gorbunova, Filippova, 2025).

Specimens examined

Hebeloma alpinum: **Russia, Republic of Altai,** Kosh-Agach District, Plato Ukok, 49°16′14.4″N, 87°48′50.4″E, 2100 m a. s. l., grass tundras with *Salix glauca,* 30 VII 2019, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013038, YSU-F-13983 (GenBank PP277316); *ibid*., 49°16′14.4″N, 87°48′50.4″E, 2200 m a. s. l., dryad tundras, on soil, 30 VII 2019, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013032, YSU-F-13972 (GenBank PP264692); *ibid*., nearby Chagan-Uzun village, 50°04′17.2″N, 88°12′43.1″E, 2200 m a. s. l., dryad tundras, on soil, 23 VI 2015, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013044, YSU-F-14010 (GenBank PP277323).

Hebeloma dunense: **Russia, Republic of Altai,** Kosh-Agach District, Plato Ukok, 49°16′14.4″N, 87°48′50.4″E, 2200 m a. s. l., grass tundras with *Salix glauca* L., on soil, 30 VII 2019, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013047, YSU-F-13963 (GenBank PP277318); *ibid*., 49°16′14.4″N, 87°48′50.4″E, 2100 m a. s. l., grass tundras with *Salix glauca*, on soil, 30 VII 2019, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013039, YSU-F-13976 (GenBank PP264693); *ibid*., Plato Ukok, 49°16′14.4″N, 87°48′50.4″E, m a. s. l., dryad tundras, on soil, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013057, YSU-F-14011 (GenBank PP277324).

Hebeloma excedens: **Russia, Republic of Altai,** Kosh-Agach District, nearby Chagan-Uzun village, 50°04′17.2″N, 88°12′43.1″E, 2200 m a. s. l., dryad tundras, on soil, scattered, 24 VI 2015, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013033, YSU-F-13980 (GenBank PP264694); *ibid*., Plato Ukok, 49°16′13.8″N, 87°48′50.4″E, 2100 m a. s. l., grass tundras with *Salix glauca*, on soil, scattered, 30 VII 2019, *Gorbunova*, det. *Gorbunova, Filippova*, NSK 1013055, YSU-F-13981 (GenBank PP277319).

Molecular techniques

The PCR was made using the TransDirect® Plant Tissue PCR Kit without DNA extraction. PCR reactions were performed in 20 µL of reaction mixtures containing 4 µL of ScreenMix (Evrogen), 0.2 µL of each PCR primer, 14 µL of deionized H_2O, and 1.6 µL of template DNA. For amplification of the nrITS region the primers ITS1-F (Gardes, Bruns, 1993) and ITS4 (White *et al.*, 1990) were used. PCR cycle parameters were as follows: initial denaturation for 5 min at 95 °C, 30 cycles (denaturation for 20 sec at 95 °C, primers annealing for 30 sec at 54°C, extend DNA for 60 sec at 72 °C), final extension for 7 min at 72 °C. PCR and sequence reaction products were purified using CleanMag DNA (Evrogen) and Dynabeads™ Sequencing Clean-Up kits. Sequencing was performed with BrilliantDye™ Terminator (v3.1) Cycle Sequencing kit (NimaGen) using Applied Biosystems® Sanger Sequencing 3500 Series Genetic Analyzer. Newly generated sequences were deposited in the GenBank.

Phylogenetic analyses

Raw data were edited and assembled using Molecular Evolutionary Genetics Analysis Version 11 (MEGA11) software (Koichiro *et al.*, 2021). Additionally, 61 ITS sequences were retrieved from GenBank following previous publications (Cripps *et al.*, 2019; Eberhardt *et al.*, 2021). Sequences were aligned with the MAFFT version 7 web tool (Kazutaka *et al.*, 2019) using the E-INS-i option (iterative refinement method recommended for < 200 sequences with one conserved domain and long gaps). The best-fit substitution model (TPM2u+F+G4) was estimated based on the Bayesian Information Criterion (BIC) using ModelFinder (Kalyaanamoorthy *et al.*, 2017). Maximum likelihood (ML) phylogenetic reconstruction was performed in IQTREE 1.6.12 (Nguyen *et al.*, 2015). The support was tested by 1000 ultrafast bootstraps (BS) (Hoang *et al.*, 2017), as well as the Shimodaira-Hasegawa-like approximate likelihood-ratio test (Guindon *et al.*, 2010). BS consensus tree was constructed from 1000 bootstrap trees (Nguyen *et al.*, 2015). The final technical formatting of the resulting tree was made in FigTree (Rambaut, 2008–2018) and InkScape (https://inkscape.org) software. Similarity percentage of the sequences was calculated in Basic Local Alignment Search Tool (BLAST) at NCBI portal (https://blast.ncbi.nlm.nih.gov/Blast.cgi) (Altschul *et al.*, 1990).

Results

Molecular phylogeny

The final nrITS dataset contains 69 sequences (749 characters including gaps), including two sequences of *Galerina pruinatipes* A. H. Sm., *G. pseudocamerina* Singer as an outgroup; 15 sequences of seven species without cortina (*Hebeloma avellaneum* Kauffman, *H. vaccinum* Romagn., *H. aurantioumbrinum* Beker, Vesterh. et U. Eberh., *H. subconcolor* Bruchet, *H. hiemale* Bres., *H. velutipes* Bruchet, *H. alpinum*), and 52 sequences of eight species from *Hebeloma* section (*H. alpinicola, H. colvinii, H. mesophaeum, H. pubsecens, H. excedens, H. dunense, H. marginatulum, H. pascuense*) (Fig. 1; Electronic supplement[1]).

In the first group (without cortina), seven species formed separate clades. Specimens identified by us as *H. alpinum* clustered with reliable voucher specimens of the same species.

In *Hebeloma* section, our sequences clustered with eleven other reliable voucher specimens of *H. excedens* and *H. dunense*. However, the *H. mesophaeum* complex was poorly resolved and represented a complex group.

Morphology

A study of the micro-morphological features of the specimens revealed tree species: *Hebeloma alpinum* (with amygdaloid, large, ornamented spores and capitate cystidia), *H. excedens* and *H. dunense* (with ellipsoidal spores and cylindrical cystidia). Detailed measurements and photographs of the microstructures are presented in Table 1 and Fig. 2, 3.

Of these, *Hebeloma excedens* is listed for the first time for Russia.

Hebeloma excedens (Peck) Sacc., 1887, *Syll. Fung.* 5: 806. (Fig. 3A, C, D)

Pileus 25–35 mm in diam., convex then almost applanate, slightly umbonate, viscid when moist, clay-buff, yellow brown, or cream-brown when young, later darkening, dark brown in the center, lighter at margin, with hygrophanous spots, with white velar remnants on the edges. Margin extending beyond the lamellae. Cortina present. Lamellae sinuate, attached by a tooth, cream when young, later pale brown, edges white, without watery droplets, number of full-length lamellae (L) 36–40. Stipe 20–30 × 2–2.5 mm, cylindrical, straight or curved, whitish, pruinose above cortina zone, dark brown

[1] Electronic supplement is available at the end of the article page on the journal website (https://doi.org/10.31111/nsnr/2025.59.1.F33).

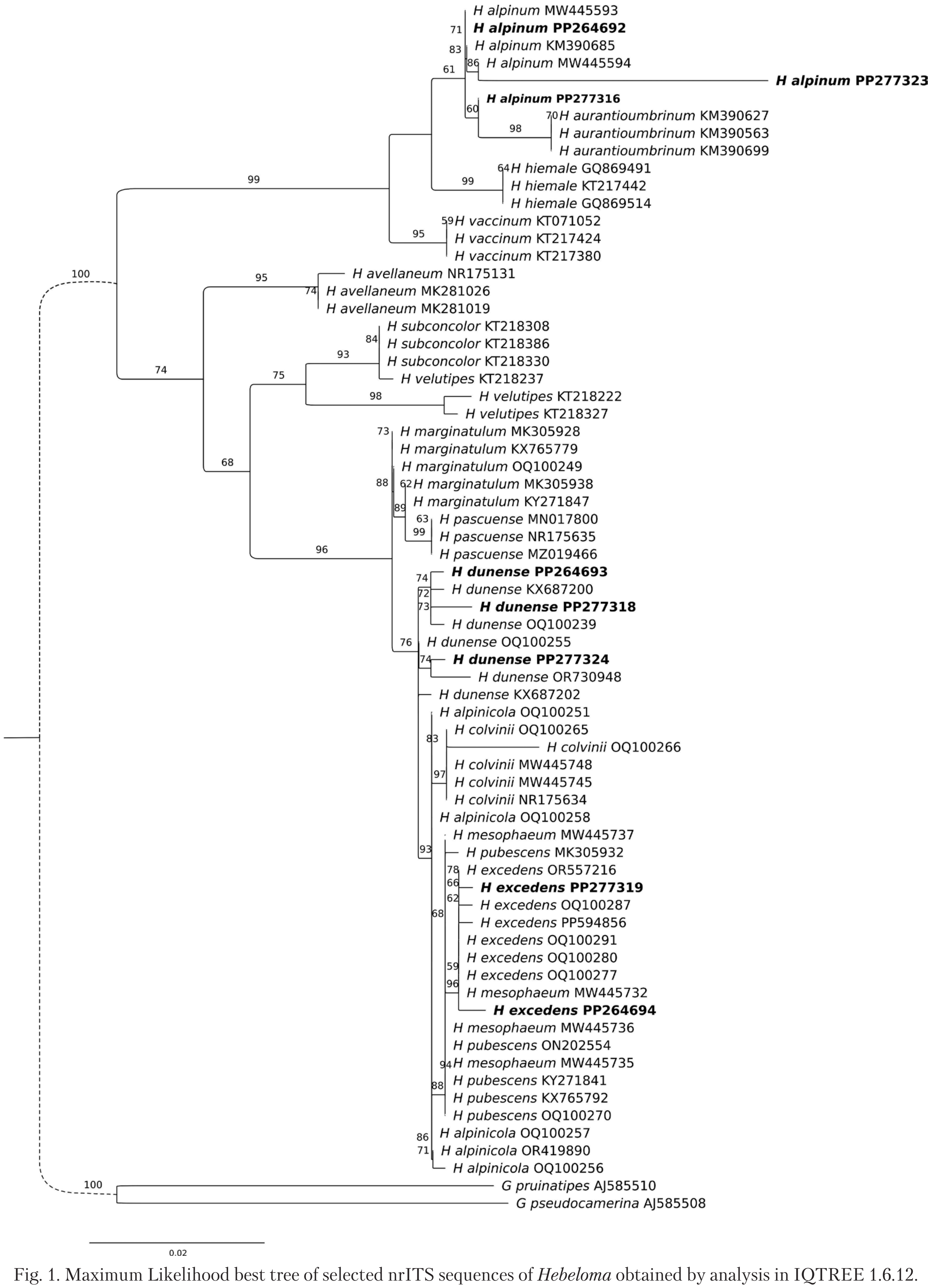

Fig. 1. Maximum Likelihood best tree of selected nrITS sequences of *Hebeloma* obtained by analysis in IQTREE 1.6.12. The bootstrap support is provided above the branches (values below 60 are not shown in the picture). The newly generated sequences marked in bold type. The branches at the base of the tree were shortened to reduce the image width (dotted line).

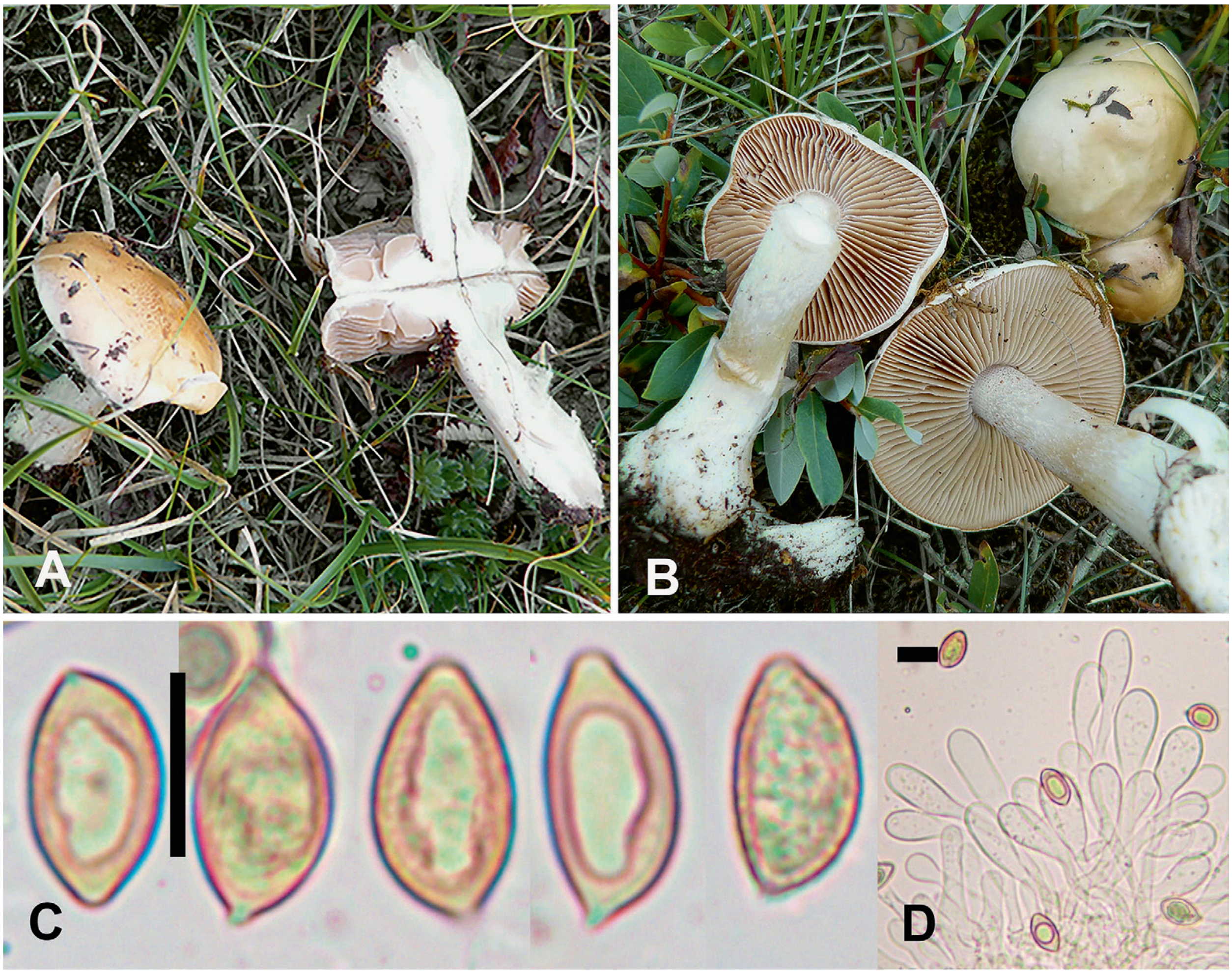

Fig. 2. Macro- and microscopical features of studied specimens of *Hebeloma alpinum*.
A, B — photo of basidiocarps *in situ* (YSU-F-14010, YSU-F-13983); C, D — basidiospores and cheilocystidia (YSU-F-13972). Scale bars: 10 µm.

below, with zones of brown fibrils, blackening towards base. Context firm, whitish in pileus and stipe apex and brown in lower part of stipe, almost blackish at base. Smell raphanoid. Spore print brownish. Exsiccate pale brown, not dark.

Basidiospore (8.7)9.9–11.0(12.6) × (5.0)5.4–6.0(6.7) µm, Q = 1.8 (1.6–2.2) (n = 45, two specimens), ellipsoid to slightly amygdaloid, ovoid, light yellow, grey yellow, almost smooth (O1), slightly dextrinoid (D1, D2), perispore not loosening (P0). Basidia 15–30 × 7–12 µm, clavate, mostly 4-spored, some with yellow-brown contents in KOH. Pleurocystidia absent. Cheilocystidia (32)41–52(64) × (6)8–12(16) × (4.5)5–6(7) × (4.5)5.5–5.6(7.0) µm (n = 45, two specimens), narrowly lageniform with long neck, rarely subcapitate or septate. Pileipellis exocutis, made of brownish hyphae.

Discussion

Eight specimens of the genus *Hebeloma* collected in the Altai highlands have been studied. The analysis based on molecular phylogeny showed that specimens from the Altai Mountains cluster well with the previously described species *Hebeloma alpinum*, *H. excedens* and *H. dunense*. *Hebeloma alpinum* (*Hebeloma* section *Denudata* (Fr.) Sacc) differs well from the others in the form of spores and cheilocystidia. Our specimens have some similarity to *H. vaccinum*. However, phylogenetic analysis showed that our specimens clustered well with voucher specimens of *H. alpinum* collected in Greenland (Fig. 1).

The *Hebeloma mesophaeum* complex has poor resolution on the phylogenetic tree, as previously shown by some authors (Cripps *et al.*, 2019; Eberhardt *et al.*, 2021). Three our specimens clustered with voucher specimens of *H. dunense*, and two with *H. excedens*. The support for these clades is weak, but previous authors consider them as separate taxa.

Hebeloma excedens is widely distributed across North America, occurring in various habitats, primarily in forest communities. It forms symbiotic relationships with a variety of trees, including

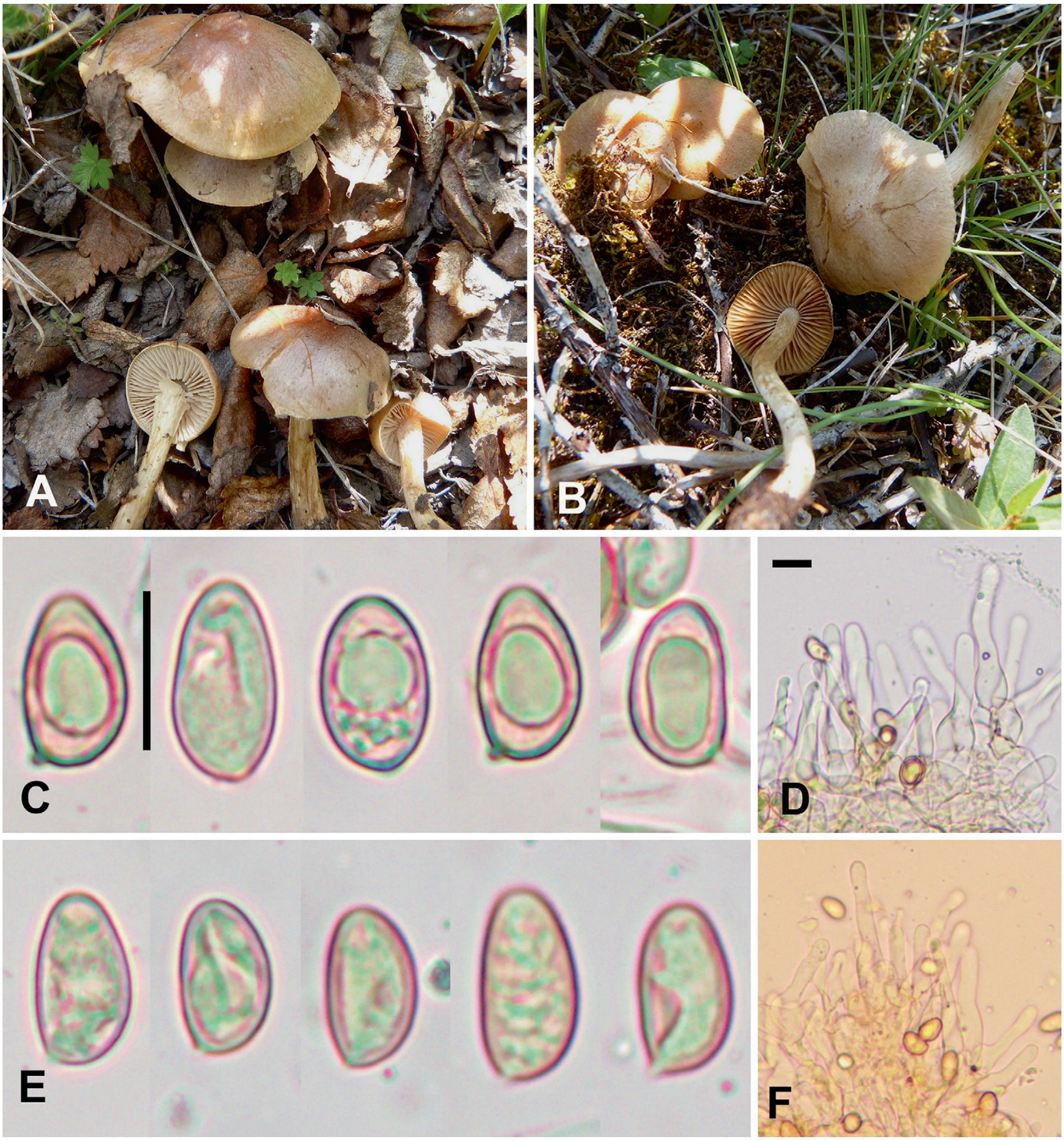

Fig. 3. Macro- and microscopical features of studied specimens of *Hebeloma excedens* and *H. dunense*. A — photo of *H. excedens* basidiocarps *in situ* (YSU-F-13980); B — photo of *H. dunense* basidiocarps *in situ* (YSU-F-13976); C, D — basidiospores and cheilocystidia of *H. excedens* (YSU-F-13981); E, F — basidiospores and cheilocystidia of *H. dunense* (YSU-F-13976). Scale bars:10 µm.

Picea A. Dietr., *Salix*, *Betula*, *Populus* L., *Tilia* L., *Quercus* L., *Abies* Mill., *Tsuga* (Endl.) Carrière, *Alnus* Mill. and *Larix* Mill. Notably. *Hebeloma excedens* is more common in eastern North America compared to *H. mesophaeum* (Bartlett *et al.*, 2022).

While it was previously thought that *Hebeloma excedens* species did not grow in arctic and alpine environments, it has since been discovered in Alaska in alpine meadows, in Greenland in arctic shrubland, and in the Rocky Mountain alpine belt (Colorado) (Cripps *et al.*, 2019; Eberhardt *et al.*, 2021; Bartlett *et al.*, 2022). In these arctic-alpine habitats, *H. excedens* forms mycorrhizal associations with various *Salix* species and, less commonly, with *Dryas*. In present study, this species was found in the tundra-steppe landscapes of high-altitude Altai Mountains, at 2100–2200 m a. s. l., in tundras with *Dryas oxyodonta* Juz., and grass tundras with *Salix glauca*. It is possible that this species also grows at lower elevations in forest communities but was previously identified as *H. mesophaeum*.

Table 1

Specimen numbers, GenBank accession numbers, and morphological parameters of the studied specimens of *Hebeloma*

Species	Herbarium numbers	GenBank accession number	Cheilocystidia size* and shape	Spores size* and shape
H. alpinum	YSU-F-13983 NSK 1013038	PP277316**	30.0–68.0 × 3.5–7.2 × 3.1–7.4 × 4.0–10.5 µm (n = 22), clavate	12.2–15.0 × 6.3–7.6 µm, Q = 1.7–2.1 (n = 21), amygdaloid to limoniform, weak ornamentation
H. alpinum	YSU-F-13972, NSK 1013032***	PP264692**	34.0–78.0 × 3.6–7.6 × 3.4–8.4 × 4.3–12.5 µm (n = 42), clavate	11.6–15.1 × 5.9–7.8 µm, Q = 1.7–2.2 (n = 24), amygdaloid to limoniform, weak ornamentation
H. alpinum	YSU-F-14010 NSK 1013044	PP277323	47.0–76.0 × 4.4–8.7 × 3.8–6.7 × 5.8–10.6 µm (n = 35), clavate	11.6–16.1 × 6.3–7.8 µm, Q = 1.6–2.4 (n = 49), amygdaloid to limoniform, weak ornamentation
H. dunense	YSU-F-13976, NSK 1013039	PP264693**	40.0–56.7 × 7.1–10.0 × 4.7–6.8 × 4.4–6.2 µm (n = 11), narrowly lageniform with long neck	9.1–12.2 × 5.2–6.3 µm, Q = 1.6–2.0 (n = 30), ellipsoid to slightly amygdaloid, smooth
H. dunense	YSU-F-13963 NSK 1013047	PP277318**	45.0–56.0 × 8.0–12.0 × 4.5–6.0 × 5.0–7.0 µm (n = 7), narrowly lageniform with long neck	9.6–12.5 × 5.4–6.6 µm, Q = 1.6–2.0 (n = 25), ellipsoid to slightly amygdaloid, smooth
H. dunense	YSU-F-14011 NSK 1013057	PP277324	32.0–55.0 × 6.7–9.7 × 4.0–6.0 × 3.5–6.2 µm (n = 26), narrowly lageniform with long neck	8.5–11.1 × 4.9–6.5 µm, Q = 1.6–2.0 (n = 30), ellipsoid, smooth
H. excedens	YSU-F-13980, NSK 1013033	PP264694**	32.5–55.0 × 6.3–10.3 × 4.5–6.7 × 4.5–7.2 µm (n = 27), narrowly lageniform with long neck	8.7–11.5 × 5.0–6.3 µm, Q = 1.6–2.0 (n = 22), ellipsoid to slightly amygdaloid, smooth
H. excedens	YSU-F-13981, NSK 1013055	PP277319	43.0–64.0 × 8.0–16.0 × 5.0–7.0 × 5.0–7.0 µm (n = 23), narrowly lageniform with long neck	10.0–12.6 × 5.1–6.7 µm, Q = 1.6–2.2 (n = 25), ellipsoid to slightly amygdaloid, smooth

* — all dimensions are given as minimum–maximum of values; ** — assembled sequences — made by sequencing forward and reverse reads and assembling a contig; *** — the specimen YSU-F-13972 (NSK 1013032) was published earlier as *Hebeloma dunense* (Kotkova *et al.*, 2024); this was our mistake (the sequences were mixed up).

Morphologically, *Hebeloma excedens* is similar to species of *H. mesophaeum* complex. C. H. Peck suggests that the pileus margin extending beyond the lamellae is a distinguishing field characteristic of *H. excedens* from other species (Bartlett *et al.*, 2022). This feature was as well observed in some specimens from the Republic of Altai, but not everyone. The pileus and stipe of *H. excedens* are darker in color compared to *H. dunense* and more closely resemble the basidiomata of *H. mesophaeum*. Distinguishing morphological feature of *H. excedens* and *H. dunense* is pale yellow spores in KOH. In *H. dunense*, some cheilocystidia have thick yellow contents.

Acknowledgments

The article used materials from the collection of the Central Scientific Library of the Siberian Branch of the Russian Academy of Sciences of the UNU Herbarium of Higher Vascular Plants, Lichens and Fungi (NSK). N. V. Filippova was supported by a grant from the federal budget for the implementation of the state assignment Molecular-genetic methods in the study and assessment of biodiversity in the Northern regions (FENG-2024-0003). The work of I. A. Gorbunova was carried out within the framework of the state assignment of the Central Library Science Center of the Siberian Branch of the Russian Academy of Sciences under project No AAAA-A21-121011290024-5.

Author Contributions. I. A. Gorbunova — collection of samples, morphological analysis, sequencing of samples, literature analysis, and writing the article; N. V. Filippova — molecular phylogenetic analysis, literature analysis, and writing the article. All authors have read and agreed to the final version of the manuscript.

Conflicts of Interest. The authors declare no conflict of interest.

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