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Research Article

Identification and phylogenetic analysis of two newly recorded *Hebeloma* species (Basidiomycota) from Türkiye

Ayşenur Kalmer[1], Sedat Kesici[2]* Ayten Tekpınar[1], Yusuf Uzun[3]

[1]*Van Yüzüncü Yıl University, Department of Molecular Biology and Genetics, Van, Türkiye*
[2]*Hakkâri University, Department of Plant and Animal Production, Hakkâri, Türkiye*
[3]*Van Yüzüncü Yıl University, Faculty of Pharmacy, Department of Pharmaceutical Sciences, Van, Türkiye*

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Abstract

Hebeloma species are ectomycorrhizal fungi that are widely distributed in nature and grow in a wide variety of habitats. *Hebeloma* spp. are difficult to identify and distinguish due to high morphological similarity between species. In this study, two newly recorded *Hebeloma* (Fr.) P. Kumm. species (*H. minus* Bruchet and *H. rostratum* Beker, Vesterh. & U. Eberh.) from Türkiye were described and photographed. Specimens were identified using morphological and molecular methods. Phylogenies based on the internal transcribed spacer (ITS) and translation elongation factor 1-alpha (TEF1-α) regions of the genome were constructed employing the Maximum-Likelihood method. In conclusion, a technique that combines morphological and molecular data provides a robust approach to assessing the taxonomic status of *Hebeloma* spp. Descriptions and photographs of the species are also presented.

Özet

Hebeloma türleri doğada geniş yayılım gösteren ektomikorizal mantarlardır ve çok çeşitli habitatlarda yetişirler**.** *Hebeloma* türleri, türler arasındaki yüksek morfolojik benzerlik nedeniyle tanımlanması ve ayırt edilmesi zordur. Bu çalışmada, Türkiye'den iki *Hebeloma* (Fr.) P. Kumm. türü (*H. minus* Bruchet ve *H. rostratum* Beker, Vesterh. & U. Eberh.) tanımlanmış ve fotoğraflanmıştır. Örnekler, moleküler ve morfolojik yöntemler kullanılarak belirlenmiştir. İç transkripsiyon aralayıcı (ITS) ve translasyon uzatma faktörü 1-alfa (TEF1-α) bölgelerinin filogenisi Maksimum Olasılık yöntemi kullanılarak oluşturulmuştur. Sonuç olarak, moleküler veriler ve morfolojinin birleşimi, *Hebeloma* türlerinin taksonomik durumunu değerlendirmek için sağlam bir yaklaşım sunmuştur. Türlerin ayrıntılı açıklamaları ve çizimleri verilmiştir.

Keywords: fungal systematics, ITS, molecular taxonomy, phylogeny, TEF1-α

Introduction

Hebeloma (Fr.) P. Kumm. (Basidiomycota, Hymenogastraceae) is a fungal genus growing widely over varying habitats and forming symbiotic relationships with various tree species (Cripps et al., 2019). Currently, more than 500 *Hebeloma* species have been recognized globally (https://www.indexfungorum.org), including a few undocumented ones. Beker et al. (2016) conducted a worldwide study and documented this genus comprehensively. In the *Hebeloma* monograph published by Beker et al. (2016), 84 species were recognized based on morphological and molecular characters. Additionally, 51 species were identified in other studies conducted by the Beker group (Cripps et al., 2019; Eberhardt et al., 2020; Eberhardt et al., 2021a, 2021b; Eberhardt et al., 2022a, 2022b, 2022c). In total, 135 species have been recorded globally

Edited by: *Boris Assyov*
***Corresponding Author:** Sedat Kesici, **E-mail:** sedatkesici@hakkari.edu.tr*
***ORCID iDs of the authors:** AK. 0000-0001-6176-8812, SK. 0000-0002-0284-1247, AT. 0000-0002-0578-5092, YU. 0000-0002-0537-4517*

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using morpho–molecular analysis, of which 35 have been identified in Türkiye (Dizkırıcı et al., 2019, 2022; Sesli et al., 2020; Acar et al., 2021, 2022, 2024; Solak & Türkoğlu, 2022; Lambert et al., 2024). Among them, only eight have been studied using molecular data (Dizkırıcı et al., 2019, 2022; Acar et al., 2021, 2022, 2024; Lambert et al., 2024).

Hebeloma species are morphologically characterized by a bicolored convex pileus, mostly yellowish–brown lamellae, a veil, and abundant cheilocystidia (Eberhardt et al., 2015, 2021b, 2022b; Beker et al., 2016). However, as identifying the species within this genus remains challenging, infrageneric classification requires both morphological and molecular data (Beker et al., 2016). The internal transcribed spacer (ITS) region is considered one of the most vital DNA barcodes applicable for species-level identification in fungal taxonomy (Schoch et al., 2012). It is commonly used in phylogenetic studies due to easy amplification, the availability of vast amounts of related data in the GenBank database, and a distinct barcode gap for species determination (Schoch et al., 2012). It can be utilized alone or in combination with protein-coding genes like the translation elongation factor 1-alpha (TEF1-α) to improve precision in the molecular identification of fungi (Tekpinar & Kalmer, 2019).

This study aimed to report and document two new records, *H. minus* Bruchet and *H. rostratum* Beker, Vesterh. & U. Eberh. from Türkiye, identified based on morphological features and molecular data. It also evaluates the phylogenetic affinities of the two species.

Materials and Methods

Fungal Materials and Morphological Observations

The *Hebeloma* specimens were collected from Hakkâri province of Türkiye. The samples were photographed in the field using an EOS 60D camera (Canon, Tokyo, Japan) equipped with an AT-X 100 mm macro lens (Tokina, Tokyo, Japan). The macroscopic characteristics were determined based on field notes and photographs. For microscopic examinations, thin cuttings from the lamellae and basidiomata surfaces were obtained with razor blades. They were then treated with distilled water and Melzer's reagent. The material was microscopically examined underwater to count basidiospores, cystidia, and basidia, and to determine other vital features, but in Melzer's solution to assay the dextrinoid reactions (Vesterholt, 2005; Beker et al., 2016). At least 50 spores, 40 basidia, and cheilocystidia were measured from each specimen of each recorded species. Observations were made using a DM500 research microscope (Leica Microsystems), and images were captured utilizing the Leica Application Suite (version 3.4.0). The length–width ratio of the basidiospores is referred to as "Q" in the text. The dextrinoid reaction of spores in the Melzer's reagent (Atom scientific) is mentioned as "D." The loosening of the spore perisporium in Melzer's reagent is noted as "P." The ornamentation of the spore is recorded as "O." All materials studied were preserved in the Fungarium of the Van Yüzüncü Yıl University, Van, Türkiye.

DNA Isolation and Sequencing

CTAB Doyle & Doyle, 1987). The ITS and TEF1-α regions were polymerase chain reaction (PCR)-amplified using the primer sets N-nc18S10/C26A (Wen & Zimmer, 1996) and EF1-983F/EF1-1567R (Rehner & Buckley, 2005). PCR was performed in a total volume of 25 µL, containing genomic DNA (10 ng/µL), 10X Buffer, $MgCl_2$ (25 mM), dNTP mix (10 mM), primer pair (10 µM), Taq Pol (5U/µL), and sterile water. The thermocycling conditions included, an initial denaturation at 94°C for 3 min, followed by 35 cycles of denaturation at 95°C for 1 min, annealing at 51°C (52°C for TEF1-α) for 35 s, and extension at 72°C for 40 s, with a final extension at 72°C for 5 min. The amplicons were separated using 1% TAE agarose gel and stained with Gelred dye. The positive reactions were bidirectionally sequenced using the same primer pairs on an ABI 3730XL automated sequencer at BM Labosis Inc., Ankara, Türkiye. The sequences generated were submitted to the GenBank, and their accession numbers are listed in Table 1.

Phylogenetic Analysis

The chromatograms were visualized using Finch TV (http://www.geospiza.com). Consensus sequences were generated and utilized for BLAST alignment against the sequences available in the National Center for Biotechnology Information (NCBI) database (https://www.ncbi.nlm.nih.gov/). The novel sequences were submitted to the NCBI and related taxa identified were downloaded to establish the phylogenetic relationships (Table 1). *H. mesophaeum* (Pers.) Quél. and *H. sacchariolens* Quél. were chosen as the outgroup taxa. All sequences were aligned using CLUSTALW (Thompson et al., 1994) and refined with the Mesquite v3.70 software (Maddison & Maddison, 2021).

Phylogenetic analyses utilized a concatenated ITS/TEF1-α dataset, and the Maximum-Likelihood (ML) method was applied. The best substitution model for each partition was calculated via the Modelfinder algorithm (Kalyaanamoorthy et al., 2017). ML analysis was performed with IQ-TREE v.1.6.12 (Nguyen et al., 2015) employing the K2P + R2 model. Branch support was assessed through 1,000 replicates of the ultrafast bootstrap (Hoang et al., 2018) and Shimodaira–Hasegawa-like approximate likelihood ratio tests (Guindon et al., 2010). The phylograms were visualized using Figtree v1.4.3 (Rambaut 2016).

Results

Taxonomy

Descriptions, locations, collection dates, fungarium numbers, and illustrations of the identified taxa are provided below.

***Hymenogastraceae* Vittad.**

Hebeloma* sect. *Denudata* subsect. *Crustliniformia

***H. minus* Bruchet, *Bull. Mens. Soc. Linn. Lyon* 39 (suppl. 6): 126 (1970), (Figure 1)**

Description: Pileus: 10–25(30) mm, shape convex to umbonate; generally bicolored, yellow–brown or dark brown in center, margin

Table 1. The species studied, along with their NCBI accession numbers, country of origin, voucher numbers, and citations.

Taxa	NCBI accession number (ITS)	NCBI accession number (TEF1-α)	Country/Voucher	References
Hebeloma ammophilum	KT217509	MZ782958	Hungary/HJB12374	Eberhardt et al. (2016)
Hebeloma alpinum	KM390654	KT216819	Switzerland/HJB12502	Eberhardt et al. (2015)
Hebeloma alpinum	MW445565	KT216820	Greenland/CF106775	Eberhardt et al. (2021b)
Hebeloma arcticum	MW445588	MW452585	Greenland/HJB17680	
Hebeloma aurantioumbrinum	MW445900	MW452577	Greenland/CF137117	
Hebeloma cavipes	KX905028	KT216780	Germany/KRM0044143	Direct submission
Hebeloma cavipes	KT217555	KT216799	United Kingdom/HJB13725	Eberhardt et al. (2016)
Hebeloma cinnamomeum	MZ782134	MZ782965	Japan/HJB16245	Eberhardt et al. (2022a)
Hebeloma crustuliniforme	KF309409	KT216854	England/HJB11215	Eberhardt et al. (2015)
Hebeloma crustuliniforme	KF309417	KT216824	Cyprus/HJB13430	
Hebeloma eburneum	JN943863	KT216777	Belgium/HJB11687	Direct submission
Hebeloma eburneum	KM390744	KT216853	Macedonia/HJB12772	Eberhardt et al. (2015)
Hebeloma geminatum	KM390554	KT216769	United Kingdom/HJB10766	
Hebeloma geminatum	KM390584	KT216815	Belgium/BRBELVJ03073	
Hebeloma helodes	MW445873	KT216810	Greenland/HJB15780	Eberhardt et al. (2021b)
Hebeloma hiemale	GQ869521	KT216848	Norway/HJB11964	Direct submission
Hebeloma lutense	KM390631	KT216798	United Kingdom/HJB12917	Eberhardt et al. (2015)
Hebeloma mesophaeum	MK961995	ON167781	Iceland/HJB11050	Eberhardt et al. (2020)
Hebeloma minus	KM390751	KT216842	France/LYBR6915	Eberhardt et al. (2015)
Hebeloma minus	JN943872	KT216818	Iceland/ue3984	Direct submission
Hebeloma minus	KM390664	KT216816	France/LWBS9630	Eberhardt et al. (2015)
Hebeloma minus	PV124179	PV156016	Türkiye/16SDT	This study
Hebeloma minus	PV124180	PV156017	Türkiye/4SDT	
Hebeloma minus	PV124181	PV156018	Türkiye/5SDT	
Hebeloma pallidolabiatum	KM390703	KT216840	Norway/HJB11992	Eberhardt et al. (2015)
Hebeloma pallidolabiatum	KM390713	KT216846	Norway/HJB12059	
Hebeloma populinum	KT217560	KT216861	United Kingdom/HJB13758	Eberhardt et al. (2016)
Hebeloma populinum	KT217563	KT216862	Greece/HJB14114	
Hebeloma pusillum	KM390665	KT216835	France/HJB12515	Eberhardt et al. (2015)
Hebeloma rostratum	KT217532	KT216829	Germany/HJB13009	Eberhardt et al. (2016)
Hebeloma rostratum	KT217534	KT216855	Italy/TUR177056	
Hebeloma rostratum	KT217535	KT216774	France/HJB13139	
Hebeloma rostratum	PV124182	PV156019	Türkiye/50SDT	This study
Hebeloma rostratum	PV124183	PV156020	Türkiye/178SDT	
Hebeloma sacchariolens	KT218266	KT217618	Italy/HJB10321	Grilli et al. (2016)
Hebeloma salicicola	KM390682	KT216788	Netherlands/HJB12533	Eberhardt et al. (2015)
Hebeloma vaccinum	MF039237	MZ782984	Belgium/HJB11578	Eberhardt et al. (2018)
Hebeloma vaccinum	MW445835	MZ782985	Greenland/HJB17076	Eberhardt et al. (2021b)

ITS = internal transcribed spacer; NCBI = National Center for Biotechnology Information; TEF1-α = translation elongation factor 1-alpha

smooth, sometimes curly. **Lamellae:** emarginate, occasionally adnate, L = 26–40. Cortina absent. **Stipe:** 10–30(40) × 2–8 mm, generally cylindrical, clavate, often pruinose. **Odor:** absent or slightly radish-like. **Basidiospores:** (8.6)9–15 × 5–7(7.9) µm (n = 50), on average 12.8 × 6.4 ± 0.9 (length), ± 0.4 (width); Q = 1.6–1.91, amygdaliform, brown or yellow–brown, ornamentation distinct (O2–O3), no loosening perispore (P0–P1), slightly dextrinoid (D1–D2). **Basidia:** 27–40 × 7–15 µm (n = 40), four-

Figure 1. *Hebeloma minus.* (a–c) basidiomata; (d) basidia; (e) spores (H_2O); (f) spores (Melzer); (g–h) cheilocystidia.

spored. **Cheilocystidia:** 35–70(80) × 7(8)–10(14) × 3–7 × 2–7(8) µm (n = 40), on average 40–62 × 7–10 (apex) × 3–5 (middle) × 3–6 (base) µm, usually clavate–stipitate, often capitate–stipitate, contents yellow. **Caulocystidia:** like cheilocystidia, up to 100 µm.

Specimen examined: Hakkâri, Yüksekova, Adaklı Village, meadow area, 37°31′34″N and 44°10′12″E, elev. 1,870 m a.s.l., 03.11.2012; VANF4, leg. S. Kesici. 37°31′39″N and 44°10′04″E, elev. 1,872 m a.s.l., 03.11.2012; VANF5, leg. S. Kesici. 37°31′35″N and 44°10′11″E, elev. 1,868 m a.s.l., 03.11.2012; VANF16, leg. S. Kesici.

Notes: *H. minus* is classified within the *Denudata* section with its clavate cheilocystidia (Beker et al., 2016). The species is distinguished from other members of the section by its mostly ornamented basidiospores. The monograph by Beker et al. (2016) states that the species prefers Arctic tundra habitats with mossy soils. Eastern Anatolia and its environs are included in the Irano–Turanian phytogeographical region of Türkiye. The Irano–Anatolian region is a mountainous area, and Parolly (2004) classified it as high mountain grasslands. *H. minus* specimens have also been found in the high mountain grassland areas of Türkiye.

Hebeloma sect. *Denudata* subsect. *Echinospora*

H. rostratum Beker, Vesterh. & U. Eberh., *Fungal Biol.* 120: 96 (2015), (Figure 2)

Description: Pileus: 16–35(40) mm, shape convex, sometimes umbonate, generally bicolored; yellow–brown, cream-brown, cream, dark brown in center, margin curly, sometimes smooth. **Lamellae:** generally emarginate, adnate, L = 30–65. Cortina absent. **Stipe:** 20–45(50) × 2–6 mm, cylindrical at the base, clavate, floccose at the apex. **Odor:** absent or slightly radish-like. **Basidiospores:** 6–13(14.6) × (5.5)6–8(8.7) µm (n = 50), on average 11.2 × 6.7 ± 0.7 (length), ± 0.33 (width); Q = 1.62–1.95, amygdaliform, yellow–brown; strongly ornamented (O3–O4), loosening perisporium (P2–P3), strongly dextrinoid (D3–D4). **Basidia:** 24−45 × 6−10 µm (n = 40), four-spored. **Cheilocystidia:** 40–60(90) × 3(4)–7 × 3–6(8) × 4–10(12) µm (n = 40), on average 44–65 × 5–7 (apex) × 4–6 (middle) × 6–9 (base) µm, often clavate–lageniform or clavate–ventricose, bifurcate, rostrate, contents yellow. **Caulocystidia:** like cheilocystidia, larger, up to 120 µm.

Specimen examined: Hakkâri, Yüksekova, Gürdere Village, under *Populus* spp., 37°29′48″N and 44°12′53″E, elev. 1,962 m a.s.l., 06.11.2012; VANF50, leg. S. Kesici. 37°30′08″N and

Figure 2. *Hebeloma rostratum*. (a–b) basidiomata; (c) basidia; (d) spores (H_2O); (e) spores (Melzer); (f) cheilocystidia.

44°12′50″E, elev. 1,894 m a.s.l., 03.11.2013; VANF178, leg. S. Kesici.

Notes: This species of the *Denudata* section is distinguished from other members by its rostrate-shaped cheilocystidia and cheilocystidia apex measuring up to 98 µm (Beker et al., 2016). According to the monograph of Beker et al. (2016), *H. rostratum* prefers grassy or marshy soils. The most recorded associations of this species were with *Populus* spp. (Beker et al., 2016). Turkish specimens have also been found under *Populus* spp.

Phylogenetic Analyses

The DNA sequences of the ITS and TEF1-α genomic regions of *H. minus and H. rostratum* specimens were deposited in the GenBank database. After removing the missing data and ambiguous regions, the final ITS and TEF1-α datasets were 567 and 524 bp long, respectively. In total, 127 and 89 variable sites were identified in the ITS and TEF1-α datasets, respectively. The length of the concatenated sequence was ~1,158 bp, comprising 176 variable sites.

The combined dataset consisting of 38 sequences, including the five studied here and two outgroups, was utilized to construct the phylogenetic tree. It illustrated the phylogenetic relations and taxonomic positions of the species studied (Figure 3). Members of the *Denudata* section formed a monophyletic clade with robust support (100%). The section was subdivided into two main clusters: the newly recorded *H. minus* species clustered within clade A (subsect. *Crustuliniformia*) with reference sequences of the same species with robust support (99%), and *H. rostratum* grouped closely with its representatives in clade B (subsect. *Echinospora*) with high support (99%). These results provide strong evidence for the taxonomic classification of both species within the section *Denudata* with high bootstrap values.

Discussion

The present study provided morphological descriptions of two newly recorded species of the *Hebeloma* genus from Türkiye. They were identified based on morphological features and then verified using molecular data. After confirmation, the phylogenetic relationships of these species with close relatives within the genus were established.

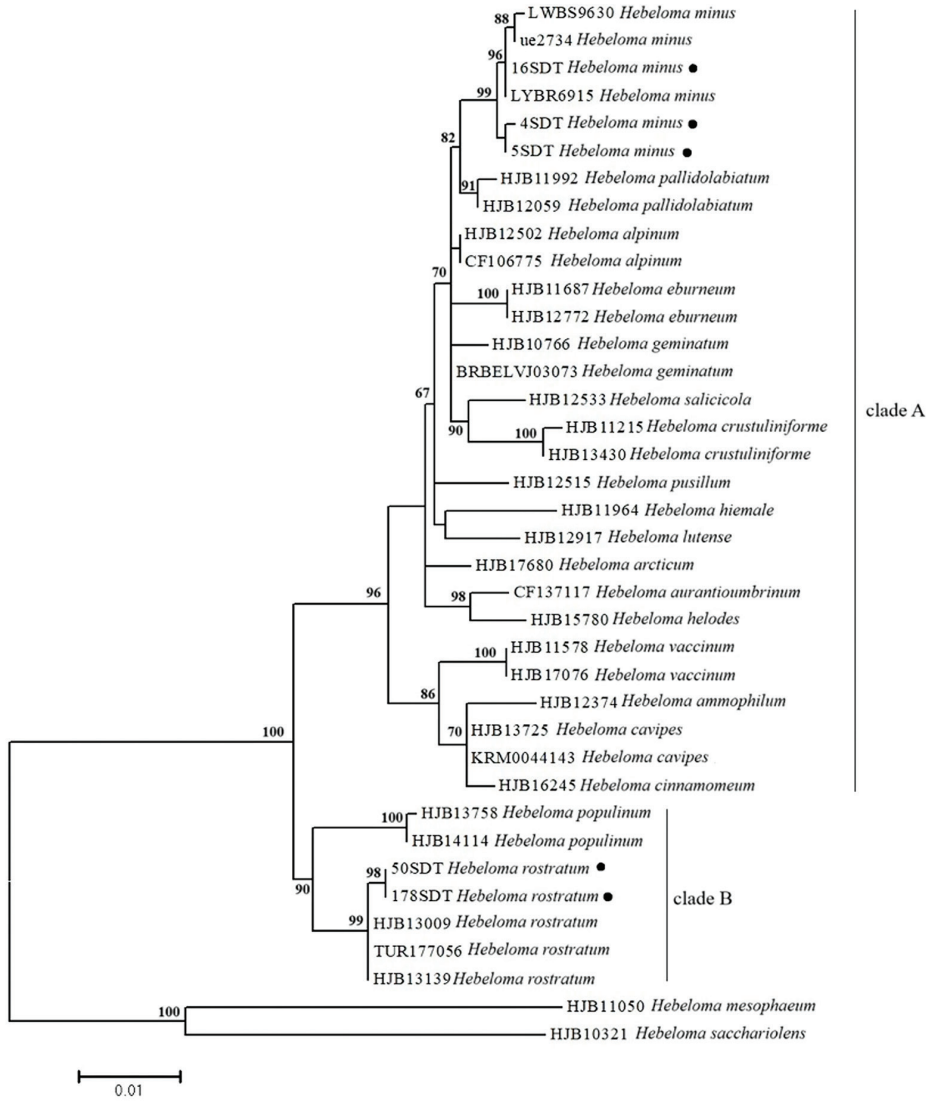

Figure 3. Phylogram of the Maximum-Likelihood analysis using the combined ITS + TEF1-α dataset. The newly generated sequences were marked with black circles. The numbers representing the likelihood bootstrap support (≥ 60%) are shown above the nodes.

The species presented in this study were included in the *Denudata* section, which is the largest within the *Hebeloma* genus. The most important feature of this section is the cheilocystidia morphology, with swollen apices and constricted midsections. Members of this section generally lack a cortina, and their odor is usually described as radish-like. The lamellae typically have clear droplets. Basidiospores are usually almond-shaped. The spore codes were O1–3; P0–2; and D1–3, on an average. The average spore size was 9−12 × 5−7.5 µm, and the mean Q value was 1.60−2.10. The average length of the cheilocystidia was between 40 and 75 µm (Beker et al., 2016). Eberhardt et al. (2016) recognized four subsections: *Crustuliniformia*, *Clepsydroida*, *Hiemalia*, and *Echinospora* within this section. *Crustuliniformia* is characterized by clavate–stipitate and clavate–capitate cheilocystidia. Clavate–stipitate to clavate–ventricose cheilocystidia indicate that a species is from *Echinospora* (Beker et al., 2016; Eberhardt et al., 2016).

The phylogeny presented in this work confirmed that *H. minus* belongs to *Crustuliniformia*. It can be distinguished from other members by its highly ornamented spores (Eberhardt et al., 2016). *H. minus* occupied a clearly distinct position in the phylogenetic tree and was closely related to *H. pallidolabiatum* Beker & U. Eberh. These two species resembled one another, but could be distinguished microscopically based on the shape of cheilocystidia and ornamentation of the spores, which were often capitate–stipitate and O2–3 for *H. minus* but clavate–lageniform and O2 for *H. pallidolabiatum* (Beker et al., 2016). *H. minus* was also macroscopically similar to *H. alpinum* (J. Favre) Bruchet. However, detailed examinations revealed that *H. minus* had smaller basidiomes with a darker coloration and fewer full-length lamellae, with counts < 40. This was in contrast to *H. alpinum,* which consistently exhibited ≥ 40 full-length lamellae (Cripps et al., 2019; Eberhardt et al., 2021b).

H. rostratum belongs to *Echinospora* and is characterized by clavate–ventricose cheilocystidia and amygdaliform-shaped spores (Eberhardt et al., 2016). It draws attention via its rostrate cheilocystidia that distinguish it from other species within the section when examined microscopically. The species was first collected in Italy by Eberhardt et al. (2016) and reported to grow under *Salix* and *Populus* spp. *H. rostratum* occupied a clearly distinct position in the phylogram and was closely related to *H. populinum* Romagn. The *H. rostratum* specimens studied can be differentiated based on highly warty spores and cheilocystidia apex with dimensions averaging < 7.5 µm.

Conclusion

Türkiye harbors a noticeable climatic and phytogeographical diversity, supporting a wide variety of vegetation. It is hypothesized that many fungal species are yet to be discovered in this country. The fact that species belonging to *Hebeloma* have been studied extensively across the globe has enabled the construction of a comprehensive database. It allows us to cluster a newly discovered species into collections with similar characteristics and to compare the collection parameters within the same phylogenetic clade. Considering such a situation, the lack of data for this genus in Türkiye is a serious scientific lacuna. Being aware of this deficiency, we performed diagnostic studies on the samples collected during every field study and accumulated data for *Hebeloma*. Based on the data collected in the present work, we report two new species from Türkiye and present them to the scientific community.

Ethics

Ethics Committee Approval: Since the article does not contain any studies with human or animal subject, its approval to the ethics committee was not required.

Data Sharing Statement: Data available on reasonable request.

Footnotes

Author Contributions: Conceptualization: A.K.; Design/methodology: A.K.; Execution/investigation: A.K.; Resources/materials: S.K., and Y.U.; Data acquisition: A.K.; Data analysis/interpretation: A.K.; Writing – original draft: A.K., and A.T.; Writing – review & editing/critical revision: A.T.

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