www.tujns.org

Expanding the diversity of *Genea* Vittad. (Ascomycota, Pezizales) in Türkiye: Morphological and molecular insights into newly recorded species

● Eda Kumru¹, ● Gülce Edis^{1,2,3}, ● Ergin Sahin^{4,5}, ● Emre Keskin^{2,3,6}, ● Ilgaz Akata^{7*}

¹Ankara University, Graduate School of Natural and Applied Sciences, Ankara, Türkiye

²Ankara University, Faculty of Agriculture, Department of Fisheries and Aquaculture, Evolutionary Genetics Laboratory, Ankara, Türkiye

³AgriGenomics Hub Animal and Plant Genomics Research Innovation Centre, Ankara, Türkiye

⁴Dokuz Eylül University, Faculty of Science, Department of Biology, İzmir, Türkiye

⁵Dokuz Eylül University, Fauna and Flora Research and Application Center, İzmir, Türkiye

⁶Ankara University, Aquaculture Research and Application Center, Ankara, Türkiye

⁷Ankara University, Faculty of Science, Department of Biology, Ankara, Türkiye

Cite this article as: Kumru, E., Ediş, G., Şahin, E., Keskin, E., & Akata, I. (2025). Expanding the diversity of *Genea* Vittad. (Ascomycota, Pezizales) in Türkiye: Morphological and molecular insights into newly recorded species. *Trakya University Journal of Natural Sciences*, 26(2), 106–117. https://doi.org/10.23902/trkjnat.1640957

Abstract

Despite their ecological significance, the diversity of Genea Vittad. species in Türkiye remains underexplored, highlighting the need for further research. The current study aims to expand the known distribution of Genea species in Türkiye by integrating morphological and molecular analyses of new collections. Fungal specimens were collected from Edirne and Kırklareli provinces between October and December 2022. Morphological characteristics were documented using light and scanning electron microscopy, and molecular phylogenetic analyses were conducted using nrITS (rDNA) sequences to confirm species identity. The studies identified the new Turkish collections as Genea fragrans (Wallroth) Saccardo, Genea pseudobalsleyi Agnello, Bratek & Cabero, Genea pseudoverrucosa Bratek, Konstant. & Van Vooren, and Genea vagans Mattir., each exhibiting over 99% sequence similarity. This study provides the first records of these species in Türkiye, offering detailed descriptions of their morphological features, habitats, and phylogenetic placement.

Özet

Ekolojik önemlerine rağmen, Türkiye'deki Genea Vittad. türlerinin çeşitliliği yeterince keşfedilmemiştir ve bu durum daha fazla araştırma yapılması gerektiğini vurgulamaktadır. Bu çalışma, morfolojik ve moleküler analizleri entegre ederek Genea türlerinin Türkiye'deki bilinen dağılımını genişletmeyi amaçlamaktadır. Mantar örnekleri Ekim ve Aralık 2022 tarihleri arasında Edirne ve Kırklareli illerinden toplanmıştır. Morfolojik özellikler ışık ve taramalı elektron mikroskobu kullanılarak belgelenirken, tür kimliğini doğrulamak için nrITS dizileri kullanılarak moleküler filogenetik analizler yapılmıştır. Çalışmalar, yeni Türk koleksiyonlarını Genea fragrans (Wallroth) Saccardo, Genea pseudobalsleyi Agnello, Bratek & Cabero, Genea pseudoverrucosa Bratek, Konstantinidis & Van Vooren ve Genea vagans Mattirolo olarak tanımladı ve her biri % 99'un üzerinde dizi benzerliği sergiledi. Bu çalışma, bu türlerin Türkiye'deki ilk kayıtlarını sunmakta ve morfolojik özellikleri, habitatları ve filogenetik yerleşimleri hakkında ayrıntılı tanımlar sunmaktadır.

Keywords: subterranean fungi, truffles, mycobiota, European part of Türkiye

Edited by: Boris Assyov

*Corresponding Author: Ilgaz Akata, E-mail: akata@science.ankara.edu.tr

ORCID iDs of the authors: EK. 0009-0000-7417-6197, GE. 0000-0001-7038-9865, EŞ. 0000-0003-1711-738X,

EmK. 0000-0002-7279-313X0, IA. 0000-0002-1731-1302



Received: 16 February 2025, Accepted: 14 May 2025, Online First: 18 May 2025, Published: 15 October 2025





Introduction

The genus *Genea* Vittad., established by Vittadini (1831), represents a group of subterranean fungi within the Ascomycota division. The name of the genus honours the distinguished zoologist Dr. Joseph Gené, with *G. verrucosa* Vittad. and *G. papillosa* Vittad. serving as the original taxa. While *Genea* is predominantly found throughout the Mediterranean region, it has not received the same scientific attention as the genus *Tuber* P. Micheli ex F.H. Wigg, which is widely recognised for its economically and gastronomically valuable truffles. It continues to dominate research priorities in mycology (Alvarado et al., 2014).

The taxonomic classification of *Genea* has undergone considerable revisions over time, reflecting advancements in understanding its phylogenetic relationships. Initially placed within the order Tuberales, the genus was reclassified under Pezizales by Trappe (1979), who retained its inclusion in the subterranean family Geneaceae due to unresolved connections with other taxa in the order. However, subsequent studies by Pfister (1984) highlighted shared structural and morphological features among *Genea* species, including similarities in excipulum architecture, pigmentation patterns, and spore ornamentation, which ultimately led to the dissolution of Geneaceae as a family and the reassignment of *Genea* to Pyronemataceae.

Morphologically, *Genea* species are characterized by hypogeous, hollow, spherical to subspherical ascomata, which are typically black, reddish-brown, or yellowish, often adorned with warts and featuring an apical opening (Læssøe & Hansen, 2007). The ascomata may possess surface hairs and typically exhibit a tuft of basal hyphae. The gleba is divided into chambers containing a ptycothecium arranged in a palisade and an epithecium formed by paraphyses at the peridial junction (Alvarado et al., 2016). Asci are hyaline, inamyloid, and contain eight uniseriate warted spores (Alvarado et al., 2014).

The genus exhibits broad ecological associations with a diverse array of host trees, including fir, larch, pine, oak, beech, birch, chestnut, hazel, hemlock, hornbeam, linden, rockrose, and Douglas fir (Zhang, 1991; Moreno-Arroyo et al., 1998; Smith, 2007; Guevara-Guerrero et al., 2012; Alvarado et al., 2014, 2016, 2021; Agnello et al., 2016; Paz et al., 2016, 2019; Ribes et al., 2016; Kaounas et al., 2016; Crous et al., 2021). Unlike specific, closely related genera, *Genea* has adapted to abandon the mechanism of active spore ejection, opting instead for dispersal facilitated by animals. The ripe ascomata emit volatile chemical signals to lure small mammals, including flying squirrels, voles, and mice. These animals consume the ascomata, and their digestive processes facilitate the effective distribution of the spores (Smith et al., 2006).

The genus exhibits broad ecological associations with a diverse array of host trees, including fir, larch, pine, oak, beech, birch, chestnut, hazel, hemlock, hornbeam, linden, rockrose, and Douglas fir (Zhang, 1991; Moreno-Arroyo et al., 1998; Smith, 2007; Guevara-Guerrero et al., 2012; Alvarado et al., 2014, 2016, 2021;

Agnello et al., 2016; Paz et al., 2016, 2019; Ribes et al., 2016; Kaounas et al., 2016; Crous et al., 2021). Unlike specific, closely related genera, *Genea* has adapted to abandon the mechanism of active spore ejection, opting instead for dispersal facilitated by animals. The ripe ascomata emit volatile chemical signals to lure small mammals, including flying squirrels, voles, and mice. These animals consume the ascomata, and their digestive processes facilitate the effective distribution of the spores (Smith et al., 2006).

Currently, the genus includes 49 formally recognized species, described through contributions spanning nearly two centuries (Vittadini, 1831; Berkeley & Broome, 1846; Tulasne & Tulasne, 1851; Corda, 1854; Saccardo, 1889; Bresadola, 1893; Harkness, 1899; Mattirolo, 1900a, 1900b; Velenovský, 1922; Imai, 1933; Gilkey, 1939; Cribb, 1960; Trappe & Guzmán, 1971; Stewart & Heblack, 1979; Trappe, 1979; Zhang, 1991; Moreno-Arroyo et al., 1998; Smith et al., 2006; Smith, 2007; Guevara-Guerrero et al., 2012; Alvarado et al., 2014, 2016, 2021; Agnello et al., 2016; Kaounas et al., 2016; Paz et al., 2016, 2019; Crous et al., 2021). In Türkiye, five Genea species have been documented to date through morphological analyses carried out by various researchers. Specifically, G. hispidula Berk. ex Tul. & C. Tul. was reported from Trabzon, G. klotzschii Berk. & Broome from Samsun, G. lobulata (Mor.-Arr., J. Gómez & Calonge) P. Alvarado & Mor.-Arr. from Niğde, G. sphaerica Tul. & C. Tul. from İzmir, and G. verrucosa Vittad. from Muğla, with detailed descriptions provided in the studies by Uzun & Kaya (2019), Berber et al. (2019), and Türkoğlu & Castellano (2014). These findings were compiled and included in the Turkish truffles checklist by Akata et al. (2022).

The present study documents and characterizes these four newly recorded *Genea* species in Türkiye, thereby contributing to a deeper understanding of the genus diversity and distribution across the country.

Materials and Methods

Field Study

The Genea specimens were systematically collected from various forest habitats, including pine-dominated woodlands in the Uzunköprü district of Edirne and oak forests in the Demirköy and Pinarhisar districts of Kirklareli, employing trained Lagotto Romagnolo truffle dogs as part of the collection process (Figure 1). Extensive field investigations were conducted to document the macroscopic and ecological characteristics of the collected specimens, facilitating a detailed assessment of their morphological variability and environmental preferences. Highresolution imaging was performed using a Nikon D810 camera fitted with an AF-S NIKKOR 105 mm f/1.4E ED lens, ensuring the capture of intricate structural details essential for taxonomic analysis. Simultaneously, a comprehensive dataset was compiled, systematically recording vital metadata, including collection dates, precise geographical coordinates, habitat descriptions, and unique specimen identifiers.

Morphological Study

The samples were examined using light microscopy (LM) and scanning electron microscopy (SEM). For LM (Euromex Oxion), visualization was achieved with distilled water, 5% KOH, and Congo red. The dimensions of ascospores were assessed by measuring at least 30 randomly selected spores outside the asci, while the length-to-width ratio, noted as Q, was calculated independently of ornamentation. Spore sizes were reported without ornamentation, with the ornamentation width defined with the base of the warts. For SEM, sections of the gleba were affixed to stubs using double-sided tape and coated with gold particles to enhance conductivity. Imaging was conducted using a ZEISS EVO 40 SEM at an acceleration voltage of 20 kV. The specimens were then prepared for long-term preservation and stored in the Fungarium of the Faculty of Science at Ankara University (ANK).

Molecular Study

Determination of Internal Transcribed Spacer (ITS) rDNA Sequences

The nuclear ribosomal ITS (nrITS) rDNA region was amplified from genomic DNA isolated from *Genea* specimens using the

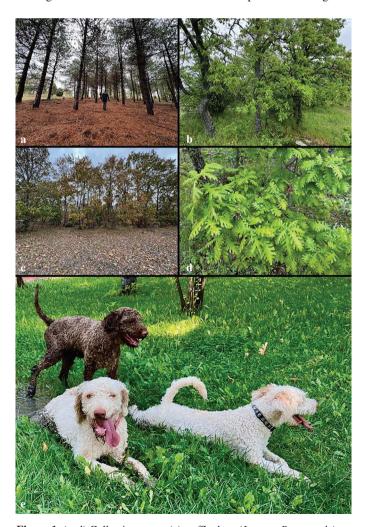


Figure 1. (a-d) Collection areas; (e) truffle dogs (Lagotto Romagnolo).

polymerase chain reaction (PCR) method. This amplification strictly adhered to established and well-validated methodologies outlined in previous studies (Akata et al., 2023a, 2023b, 2024a, 2024b). These standardized protocols ensured the accuracy and reproducibility of the molecular data generated, thus providing a robust foundation for subsequent analyses.

Molecular Phylogenetic Analysis

The phylogenetic relationships among the fungal samples were meticulously analyzed with the MEGA-X software (Kumar et al., 2018), using nucleotide sequences obtained directly from the specimens. The reference sequences were selected from GenBank using a rigorous screening process that designates closely related taxa as the ingroup and more distantly related sequences as the outgroup, using NCBI BLAST searches. Multiple sequence alignment was performed with the MUSCLE algorithm (Edgar, 2004) to optimize accuracy and consistency. Following these alignments, K2+G+I was determined as the most suitable nucleotide substitution model to guide the construction of phylogenetic trees. The Neighbour-Joining method was employed to infer evolutionary relationships, and the robustness of the branching patterns was assessed with 1,000 bootstrap replicates. This analytical approach aligned with established methodologies outlined in previous research (Akata et al., 2024a, 2024b, 2024c, 2024d), ensuring methodological rigour and comparability.

Results

This study assessed the macroscopic and microscopic characteristics of the samples and evaluated their ribosomal DNA (rDNA) sequences using ITS sequencing.

Taxonomy

Phylum ASCOMYCOTA (Berk) Caval.-Sm.

Ordo Pezizales J. Schöt.

Family Pezizaceae Dumort.

Genus Genea Vittad.

Genea fragrans (Wallr.) Sacc. (1889), (Figures 2, 6a, and 6b). **Material examined:** Türkiye-Kırklareli, Pınarhisar, under oak, 350 m, 41°41′ N, 27°42′ E, 4 Oct. 2022, ANK Akata TT 098; ibid., 417 m, 41°41′ N, 27°38′ E, 18 Nov. 2022, ANK Akata TT 207.

Macroscopic and Microscopic Features

Ascomata 7–8 mm across, hypogeous, hollow, subglobose and lobed, with a peridium surface displaying a brownish-black hue and covered by tiny, blunt, inconspicuous dark warts; a small tuft of hyphae occupies the base. Peridium up to $150\,\mu m$ thick, with an outer surface brownish-black and exhibiting small, blunt, inconspicuous dark warts, composed of a single layer of pseudoparenchymatous tissue, comprising hyaline to light brownish angular to subglobose cells measuring $15–35\,\mu m$ in width. Internal chamber consists of unique, winding chambers leading to a gleba with a labyrinth-like configuration, and the chamber walls lined with a black epithecium, up to $70\,\mu m$, formed by brownish to dark brown angular cells

measuring 20–45 µm wide. Asci 240–300 \times 25–30 µm, 8-spored, cylindrical, with a short peduncle. Paraphyses cylindrical, thread-like, 3–6 µm broad, septate, with some swollen cells. Ascospores (29)31–41(43) \times (27)28–36(38) µm, (mean: 38 \times 34), [(n = 30), Q = (1.02)1.06–1.22(1.31), Qav = 1.14], subglobose to broadly ellipsoid, hyaline to pale yellow, ornamented with truncated warts, measuring 1.5–4 \times 2–4.5 µm, mixed with micro-warts.

Ecology and Distribution

Genea fragrans is typically found from September to December, mainly beneath deciduous trees like oak, beech, hornbeam, and common hazel, and less frequently associated with chestnut, poplar, willow, blackthorn, and European hop-hornbeam (Venturella et al., 2006; Riva, 2009; Zotti et al., 2010; Kajevska et al., 2013; Landi et al., 2015; Alvarado et al., 2016). Its known distribution covers Greece, Germany, Hungary, France, Italy, Macedonia, Serbia, Spain, and Morocco (Venturella et al., 2006; Diamandis & Perlerou, 2008; Saitta et al., 2008; Bratek et al., 2013; Kajevska et al., 2013; Alvarado et al., 2016, 2021; Savić et al., 2018).

Genea pseudobalsleyi Agnello, Bratek & J. Cabero (2014), (Figures 3, 6c, and 6d).

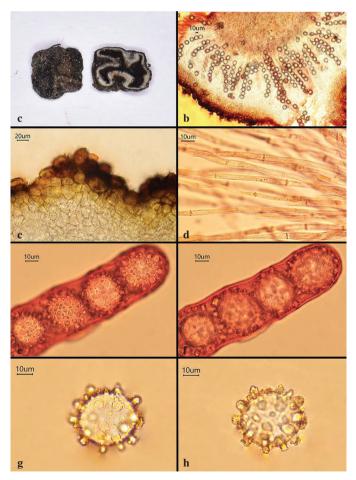


Figure 2. *Genea fragrans.* (a) ascomata; (b) microscopic cross-section of ascomata; (c) peridium; (d) septa of paraphyses; (e, f) spores contained within the ascus; (g, h) single ascospore.

Material examined: Türkiye- Kırklareli, Pınarhisar, under oak, 480 m, 41°44′ N, 27°34′ E, 5 Oct. 2022, ANK Akata TT 127; ibid., 312 m, 41°39′ N, 27°36′ E, 5 Dec. 2022, ANK Akata TT 281; Edirne, Uzunköprü, under pine, 106 m, 41°12′ N, 26°44′ E, 7 Dec. 2022, ANK Akata TT 350. Alvarado et al. (2014) offered a comprehensive overview of the type specimens from the original collection.

Macroscopic and Microscopic Features

Ascomata 7-9 mm across, hypogeous, hollow, subglobose to moderately lobed, with a uniformly warted peridium surface adorned with small polygonal black warts; a small tuft of hyphae occupies the base. Peridium consisting of a single layer of pseudoparenchymatic tissue up to 160 µm thick, composed of hyaline, subglobose cells measuring 15-45 µm in diam., transitioning towards the outer layer into angular cells with thicker, darker walls. Internal chamber displaying variability, ranging from a single chamber to multiple sinuous chambers formed by wall projections, producing a brain-like appearance; chamber walls lined with a blackish or brown-black epithecium up to 60 µm thick, comprising pseudoparenchymatous tissue with angular cells featuring thick, melanized walls measuring 15-40 µm in width. Asci 180–240 \times 35–40 μ m, eight-spored, somewhat cylindrical with a short peduncle. Paraphyses cylindrical, septate, 4-9 µm diam., with some cells appearing swollen. Ascospores (24)25–29 $(31) \times 23-26 \mu m$, (mean: 28×24), [(n = 30), Q = 1.1-1.26, Qav]= 1.18], spherical to broadly ellipsoid, pale yellow, containing prominent, unevenly positioned oil droplets; surface ornamented with truncated warts, occasionally featuring small digitations at the top, measuring $2-3.5 \times 2-2.5 \mu m$.

Ecology and Distribution

Genea pseudobalsleyi is primarily observed between June and December and is mainly associated with oak trees, particularly Quercus ilex L. and Q. pyrenaica Willd. Its geographical distribution encompasses France, Hungary, Italy, and Spain (Alvarado et al., 2014; Perez, 2024).

Genea pseudoverrucosa Bratek, Konstant. & Van Vooren (2014), (Figures 4, 6e, and 6f). Material examined: Türkiye-Kırklareli, Pınarhisar, under oak, 14 m, 41°44′ N, 27°34′ E, 5 Oct. 2022, ANK Akata TT 124. Alvarado et al. (2014) presented a thorough account of the type specimens from the original collection.

Macroscopic and Microscopic Features

Ascomata 10–12 mm across, hypogeous, hollow, spherical to extensively lobed, peridium surface black and adorned with tiny, rounded warts, with an inconspicuous basal tuft of dark hyphae. Peridium consisting of a single layer of pseudoparenchymatic tissue up to 200 μm thick, made up of light brownish angular cells measuring 18–35 μm in width. Internal chamber slightly partitioned yet primarily intact, coated with a dark epithecium resembling the peridium, epithecium structure pseudoparenchymatous made of isodiametric cells up to 160 μm . Asci 200–250 \times 30–35 μm , 8-spored, somewhat cylindrical. Paraphyses 4–8 μm broad, cylindrical, septate, with some swollen cells. Ascospores (26–)28–

33 (-34) × (23–) 24–28(–29) µm, (mean: 31×26), [(n = 30), Q = (1.05)1.1–1.32 (1.4), Qav = 1.2], subglobose to broadly ellipsoid, hyaline, ornamented with conical-truncated to irregular warts, measuring 2–4 × 1.5–3 µm.

Ecology and Distribution

Genea pseudoverrucosa is typically found from July to January in temperate deciduous forests associated with oak, hornbeam, linden, and common hazel. It also thrives in Mediterranean habitats featuring oaks (*Quercus ilex* L. and *Q. coccifera* L.). Its distribution spans Greece, Hungary, France, Romania, and Morocco (Alvarado et al., 2014).

Genea vagans Mattir. (1900), (Figures 5, 6g, and 6h). Material examined: Türkiye-Kırklareli, Demirköy, under oak, 14 m, 41°51′ N, 27°56′ E, 8 Oct. 2022, ANK Akata TT 163.

Macroscopic and Microscopic Features

Ascomata 10–15 mm across, hypogeous, hollow, subglobose to moderately lobed, with an apical pore and a tuft of brownish hairs at the base, peridium black, finely verrucose, surface adorned with small polygonal black warts. Peridium consisting of a single layer of pseudoparenchymatic tissue up to 300 μ m thick, composed

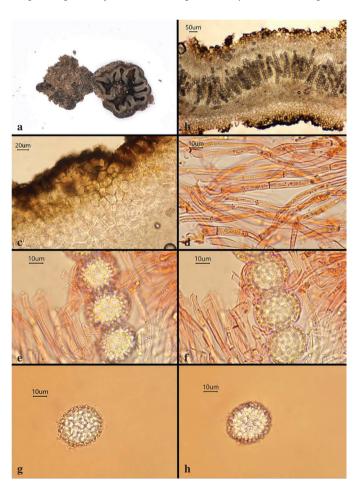


Figure 3. *Genea pseudobalsleyi.* (a) ascomata; (b) microscopic cross-section of ascomata; (c) peridium; (d) septa of paraphyses; (e, f) spores contained within the ascus; (g, h) single ascospore.

of hyaline, angular cells measuring 25–50 µm in width. Internal chamber usually solitary, occasionally divided, coated with a dark epithecium, up to 150 µm thick, comprising pseudoparenchymatous tissue with angular cells measuring 20–40 µm wide. Asci 220–250 \times 30–40 µm, 8-spored, somewhat cylindrical with a long peduncle. Paraphyses cylindrical, septate, 5–10 µm diam., with some swollen cells. Ascospores (29)31–38(39) \times (25)27–30(31) µm, (mean: 35 \times 29), [(n = 30), Q = (1.1)1.15–1.22(1.3), Qav = 1.18], broadly ellipsoid to ellipsoid, hyaline, ornamented with conical or conical-truncated warts, measuring 4–6 \times 3–5 µm, sometimes showing single digitations at the top.

Ecology and Distribution

Genea vagans is typically observed in autumn, particularly beneath trees such as fir and beech, with a tentative association with chestnuts, as indicated in early studies (Mattirolo, 1900b). Recent research has documented its presence under oak, beech, alder, common hazel, and hornbeam (Alvarado et al., 2016, 2021; Savić et al., 2018). Geographically, the species is distributed across Italy, France, Spain, Russia, and Serbia, as evidenced by studies spanning over a century (Mattirolo, 1900a; Bucholtz, 1901; Ceruti, 1960; Vidal, 1997; Alvarado et al., 2014, 2016, 2018, 2021; Kaounas et al., 2016; Ribes et al., 2016; Savić et al., 2018).

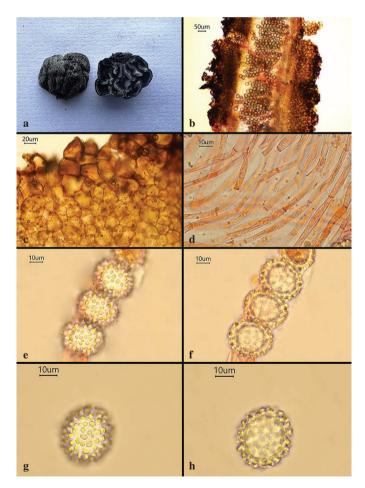


Figure 4. *Genea pseudoverrucosa.* (a) ascomata; (b) microscopic cross-section of ascomata; (c) peridium; (d) septa of paraphyses; (e, f) spores contained within the ascus; (g, h) single ascospore.

Evolutionary History of the Genea Specimens

The evolutionary lineages of the specimens ANK Akata TT 098, ANK Akata TT 124, ANK Akata TT 127, ANK Akata TT 163, ANK Akata TT 207, ANK Akata TT 281, and ANK Akata TT 350 were examined based on their nrITS rDNA sequences, which were obtained using standard molecular techniques and stored in the NCBI GenBank under the accession numbers provided in Table 1. To infer their evolutionary relationships, nrITS rDNA sequences from various members of Genea were selected for comparison, using a sequence of Scutellinia verruculosa M. Zeng, Q. Zhao & K.D. Hyde as outgroup. Our molecular phylogenetic analysis identified eight distinct clades (Figure 7). While Clade 1 comprised different isolates of G. vagans and the specimen ANK Akata TT 163, Clade 2 included an isolate of G. pseudobalsleyi, which clustered with the specimens ANK Akata TT 127, ANK Akata TT 281, and ANK Akata TT 350. In contrast, Clade 3 contained various isolates of G. fragrans, alongside the specimens ANK Akata TT 098 and ANK Akata TT 207. Lastly, the specimen ANK Akata TT 124 grouped with different isolates of G. pseudoverrucosa in a well-supported Clade 4. The remaining clades (Clades 5-8) incorporated other

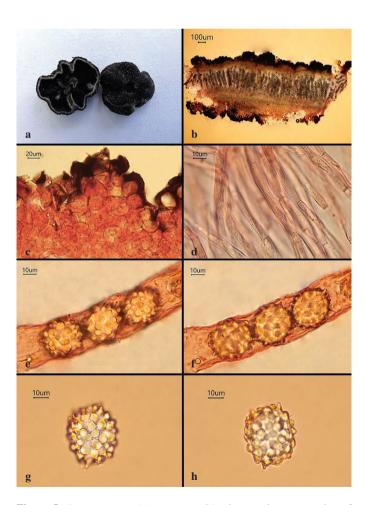


Figure 5. *Genea vagans.* (a) ascomata; (b) microscopic cross-section of ascomata; (c) peridium; (d) septa of paraphyses; (e, f) spores contained within the ascus; (g, h) single ascospore.

Genea species. Phylogenetic analyses confirmed the close relationship between our specimens and their associated *Genea* species, with high bootstrap branch support rates, thus validating their identity.

Discussion

Genea verrucosa, frequently compared with *G. fragrans*, is a darkly pigmented species characterized by significantly smaller ascospores and unique spore ornamentation (Bertolini, 2014). The ascospores of *G. verrucosa* measure $21-26\times19-22~\mu m$ and exhibit conical warts approximately measuring $2\times1.5-4.5~\mu m$, which are smaller and less prominent than the larger and more distinct ornamentation observed in *G. fragrans* (Türkoğlu & Castellano, 2014; Alvarado et al., 2016). Despite similarities in macroscopic appearance, the ascospores and asci of *G. verrucosa* are generally smaller, with asci not exceeding $250\times35~\mu m$. Over time, the conical spore warts of *G. verrucosa* may develop into aculeate forms but remain less prominent than the ornamentation

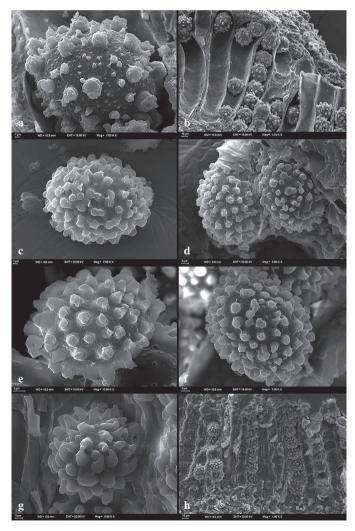


Figure 6. Scanning electron microscope micrographs. (a, b) *Genea fragrans*; (c, d) *Genea pseudobalsleyi*; (e, f) *Genea pseudoverrucosa*; (g, h) *Genea vagans*.

of *G. fragrans*. The ecological preferences of *G. verrucosa* further distinguish it, because it primarily associates with oak trees and is widely distributed across Europe, particularly in the Mediterranean region (Hollós, 1911; Diamandis & Perlerou, 2008; Alvarado et al., 2014; Bertolini, 2014).

Other species within the genus also display significant morphological and ecological distinctions: G. brunneocarpa G. Moreno, Cabero & Kaounas shares some similarities with G. fragrans but differs in ascospore size, measuring $28-31.5 \times 19.5-24 \, \mu m$, and by its ornamentation, which consists of truncate-conical warts that are occasionally nearly cubic, reaching $3.8-5.5 \, \mu m$ high. The brownish peridium and simpler internal chamber structure of G. brunneocarpa further set it apart. Unlike G. fragrans, this species is chiefly associated with holm oak and Aleppo pine,

thriving on calcareous soils and fruiting between February and April. Its distribution is limited to Mediterranean regions, with records from Greece and Spain (Alvarado et al., 2014).

Similarly, *G. compressa* Merényi, Cabero & G. Moreno is a closely related species that can be distinguished by its smaller ascospores, measuring $23.5–30.5\times18–25.5~\mu m$, and ornamentation consisting of conical warts with digitate apices, up to $2.3–5.3~\mu m$ high. It is commonly associated with oak species and found in mixed habitats alongside common hornbeam or Atlas cedar, with a distribution spanning Hungary, Morocco, and Spain (Kaounas et al., 2016).

Another closely related species, *G. fageticola* Konstantin., Cabero & Faust. García shares overlapping spore dimensions with *G. fragrans*, $28-36.5 \times 18-26 \mu m$, but it is distinguishable by its

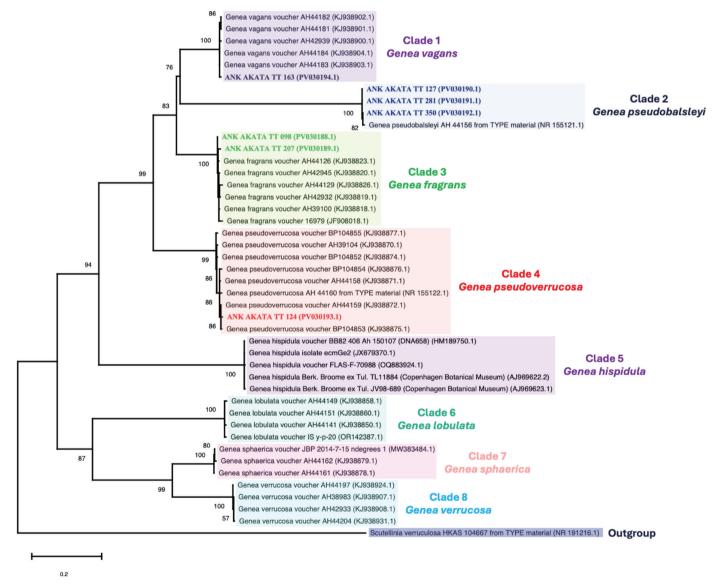


Figure 7. Phylogram of ML of a set of 44 *Genea* sequences based on the nrITS rDNA, rooted with *Scutellinia verruculosa* (outgroup). Nodes with $\geq 50\%$ ML bootstrap support are annotated with their support values. Terminals that represent sequences obtained during this study are in bold. Each sequence is accompanied by its respective GenBank accession number, and a scale bar in the lower left corner indicates a genetic distance of 0.2. ML = maximum likelihood; nrITS = nuclear ribosomal internal transcribed spacer.

Table 1. GenBank accession numbers and collection sites of Genea specimens examined.

Species	Specimen voucher/isolate/ strain	nrITS GenBank Accession Number	Geographical origin	Reference
G. fragrans	ANK Akata TT 098	PV030188	Türkiye, Kırklareli, Pınarhisar	Current study
	ANK Akata TT 207	PV030189	Türkiye, Kırklareli, Pınarhisar	Current study
	AH44129	KJ938826	Spain, Zamora, Peleagonzalo	Alvarado et al., 2016
	AH42932	KJ938819	Spain, Madrid, Torrelaguna	Alvarado et al., 2016
	AH42945	KJ938820	Morocco, Chefchaouen	Alvarado et al., 2016
	AH39100	KJ938818	Morocco, Chefchaouen	Alvarado et al., 2016
	AH44126	KJ938823	Greece, Pigi Kilkis	Alvarado et al., 2016
	16979	JF908018	Italy	Osmundson et al., 2013
G. pseudobalsleyi	ANK Akata TT 127	PV030190	Türkiye, Kırklareli, Pınarhisar	Current study
	ANK Akata TT 281	PV030191	Türkiye, Kırklareli, Pınarhisar	Current study
	ANK Akata TT 350	PV030192	Türkiye, Edirne, Uzunköprü	Current study
	AH44156	NR_155121	Italy, Brindisi, Bosco Compare	Alvarado et al., 2016
G. vagans	ANK Akata TT 163	PV030194	Türkiye, Kırklareli, Demirköy	Current study
	AH44182	KJ938902	Spain, Zamora, Quintana de Sanabria	Alvarado et al., 2016
	AH44183	KJ938903	Spain, Zamora, Quintana de Sanabria	Alvarado et al., 2016
	AH44184	KJ938904	Spain, Girona, Campelles	Alvarado et al., 2016
	AH44181	KJ938901	Spain, Asturias, Pola de Somiedo	Alvarado et al., 2016
	AH42939	KJ938900	Spain, Guadalajara, El Ordial	Alvarado et al., 2016
G. pseudoverrucosa	ANK Akata TT 124	PV030193	Türkiye, Kırklareli, Pınarhisar	Current study
	AH44158	KJ938871	-	Alvarado et al., 2016
	AH44159	KJ938872	-	Alvarado et al., 2016
	AH44160	NR_155122	-	Alvarado et al., 2016
	AH39104	KJ938870	-	Alvarado et al., 2016
	BP104852	KJ938874	Hungary, Heves county, Bükk mountains, Szilvásvárad	Alvarado et al., 2016
	BP104853	KJ938875	Hungary, Pest county, Budapest	Alvarado et al., 2016
	BP104854	KJ938876	Hungary, Győr-Moson-Sopron, Fertőrákos	Alvarado et al., 2016
	BP104855	KJ938877	Romania, Harghita, Cristuru Secuiesc	Alvarado et al., 2016
G. verrucosa	AH42933	KJ938908	Spain, Guadalajara, Algora	Alvarado et al., 2016
	AH44204	KJ938931	Spain, La Rioja, Torrecilla en Cameros	Alvarado et al., 2016
	AH38983	KJ938907	Spain, Guadalajara, Valdearenas	Alvarado et al., 2016
	AH44197	KJ938924	Spain, Zamora, Peleagonzalo, Monte San Miguel	Alvarado et al., 2016
G. hispidula	FLAS-F-70988	OQ883924	USA: VT, Rutland Co.	Unpublished
	Berk. & Broome ex Tul. TL11884 (Copenhagen Botanical Museum)	AJ969622	Denmark: Broby Vesterskov, South Zealand	Tedersoo et al., 2006
	Berk. & Broome ex Tul. JV98-689 (Copenhagen Botanical Museum)	AJ969623	United Kingdom: Shropshire, Dudmaston Estate	Tedersoo et al., 2006
	BB82_406_Ah_150107 (DNA658)	HM189750	-	Unpublished
	ecmGe2	JX679370	Czech Republic	Unpublished

Table 1. Continued.

Species	Specimen voucher/isolate/ strain	nrITS GenBank Accession Number	Geographical origin	Reference
G. lobulata	AH44141	KJ938850	Cyprus	Alvarado et al., 2016
	AH44149	KJ938858	Greece, Attica, Parnitha	Alvarado et al., 2016
	AH44151	KJ938860	Greece, Attica, Parnitha	Alvarado et al., 2016
	IS_y-p-20	OR142387	Israel	Unpublished
G. sphaerica	AH44161	KJ938878	Germany, Grockstädt	Alvarado et al., 2016
	JBP 2014-7-15-1	MW383484	France: Sexey aux Forges Meurthe-et- Moselle	Unpublished
	AH44162	KJ938879	Germany, Leinefelde	Alvarado et al., 2016
Scutellinia verruculosa	HKAS:104667	NR_191216	China, Sichuan	Zeng et al., 2022

ANK = Ankara University; nrITS = nuclear ribosomal internal transcribed spacer.

spherical ascomata, the absence of labyrinthine hymenium folds, and the presence of small polygonal warts on its peridium instead of minute papillae. Additionally, *G. fageticola* has a brownish epithecium and a basal tuft of reddish or brownish hyphae, both absent in *G. fragrans*. This species, reported from Greece and Spain, associates with European beech and occasionally with sessile oak, emerging during late summer and winter (Alvarado et al., 2014; Kaounas et al., 2016).

Genea pseudobalsleyi exhibits notable morphological similarities with G. balsleyi M.E. Sm., primarily due to its black peridium surface, ascospore dimensions (24–30 × 20–25 μm), and ornamentation patterns (Alvarado et al., 2014). Nevertheless, it is distinguished by unique structural features, such as prominent projections on the peridium wall that create intricate, labyrinthine, chambered cavities absent in G. balsleyi (Smith, 2007). Geographic distribution further differentiates these species, as G. balsleyi is restricted to North America and typically associated with oak, while G. pseudobalsleyi is exclusively recorded in Europe (Smith, 2007; Alvarado et al., 2014). Additionally, G. balsleyi is characterized by a bilayered peridium structure, a feature not found in G. pseudobalsleyi (Alvarado et al., 2014).

In contrast, the rare American species *G. macrosiphon* Gilkey, while showing macroscopic resemblance to *G. pseudobalsleyi*, is distinct due to its significantly larger ascospore dimensions (36–40 \times 24–28 μ m) and highly inflated pseudoparenchymatous peridium cells (Gilkey, 1939; Alvarado et al., 2014).

Distinctive morphological features of *G. pseudobalsleyi* set it apart from closely related species. Compared to *G. verrucosa*, *G. pseudobalsleyi* is characterized by densely packed and truncated ascospore ornamentation, in stark contrast to the thinner, sharper, and more scattered ornamentation observed in *G. verrucosa* (Alvarado et al., 2014; Bertolini, 2014; Türkoğlu & Castellano, 2014). Furthermore, although *G. compressa* shares macroscopic similarities and identical ascospore dimensions, 23.5–30.5 × 18–25.5 μm, with *G. pseudobalsleyi*, it is readily distinguishable by its

unique conical spore ornamentation. *Genea compressa* primarily grows in autumn under various host plants, including oak, and is distributed across regions such as Spain and Hungary (Alvarado et al., 2014).

Additional distinctions are evident in other closely related species. For instance, *G. fageticola* displays notably larger ascospores, measuring 28–36.5 \times 18–26 μ m, and unique ornamentation characterized by truncated or rounded warts measuring 2.1–6.5 \times 2–6 μ m (Alvarado et al., 2014). In contrast, *G. cephalonica* Kaounas, Agnello & P. Alvarado, which is exclusively associated with Greek fir (*Abies cephalonica* Loudon) in Greece, features slightly smaller ascospores, 24–35 \times 15.5–26 μ m, but it is distinguished by its distinct ornamentation, with warts reaching 3–6 μ m in height (Kaounas et al., 2016).

The macroscopic features of *G. pseudoverrucosa* resemble *G. fragrans* but are often misidentified as *G. verrucosa* due to similarities in ascospore dimensions. Its spore ornamentation, characterized by truncate warts, is similar to that of *G. fragrans*; however, the warts in *G. pseudoverrucosa* are lower, denser, and more uniform. In contrast, *G. fragrans* has more prominent and scattered warts, often interspersed with smaller ones. *G. pseudoverrucosa* also shares similarities with *G. brunneocarpa*, yet the latter displays more irregularly scattered warts, necessitating ecological and macroscopic observations to separate them. Similarly, *G. pseudobalsleyi* features a black, warted peridium and comparable ascospores but it is distinguished by its thinner warts, 1.5–2 µm wide. The North American species *G. balsleyi* exhibits a bilayered peridium, a hollow inner cavity, and conical spore warts (Gilkey, 1939; Alvarado et al., 2014).

The original Italian collections of *G. vagans*, first described by Mattirolo (1900a), were subsequently detailed and illustrated by Ceruti (1960), who characterized the species as producing small, rounded ascomata with a black verrucose peridium. The ascospores were ellipsoidal, measuring $35-38 \times 27-28 \mu m$, and adorned with prominent conical warts that frequently coalesce at their bases.

Lawrynowicz (1988) reported nearly identical dimensions, with ascospores measuring $31\text{--}38 \times 27\text{--}28~\mu m$. However, Vidal (1997) and Montecchi and Sarasini (2000) documented significantly smaller ascospore sizes, ranging from $18\text{--}22~\mu m$, highlighting variability in reported measurements. A later study by Ribes et al. (2016) aligned more closely with Ceruti (1960) and Lawrynowicz (1988), recording ascospore dimensions of $31.2\text{--}38.4 \times 27.1\text{--}30.2~\mu m$. Alvarado et al. (2016) further corroborated these findings, reporting ascospore sizes of $32\text{--}41 \times 27\text{--}37~\mu m$ based on authentic material from Mattirolo and additional specimens. In our study, ascospore dimensions of $31\text{--}38 \times 27\text{--}30~\mu m$ were observed, consistent with the findings of Lawrynowicz (1988) and Ribes et al. (2016), reinforcing the morphological variability within this species.

Genea vagans has often been misidentified due to its resemblance to other species, such as G. anthracina Heblack & Stewart, an American species. While both species share similar macroscopic features, including small, black fruiting bodies with a single basal cavity, G. anthracina is distinguishable by its smaller ascospores, which measure $22-26 \times 18-20 \mu m$ and are ornamented with subglobose, irregular, and occasionally truncated warts (Stewart & Heblack, 1979). Confusion also arises with G. pinicola V. Kaounas, J. Cabero & F. García, a species that transitions from an initial yellowish hue to a yellowish-brown (Alvarado et al., 2014). Although typically associated with pine, collections of G. pinicola have also been documented under oak. This species has ascospores measuring $26-29 \times 17-20 \mu m$, with ornamentation made of small conical warts, 1-3 µm in height (Alvarado et al., 2014; Ribes et al., 2016). Externally, G. vagans also resembles G. sphaerica Tul. & C. Tul., sharing similarities in shape and colour (Vacek, 1951; Hawker, 1954). However, detailed microscopic analysis reveals key differences between the two species: G. sphaerica is characterized by broadly elliptical to sub-spherical ascospores, measuring 20–25 × 18–20 μm, densely ornamented with fine, truncated, or brushlike warts 0.5–1.5 µm in height (Alvarado et al., 2014, 2016). Additionally, G. sphaerica possesses a basal cavity with numerous folds, a feature absent in G. vagans (Ribes et al., 2016).

The genetic diversity among fungal species significantly surpasses their morphological appearance, necessitating the integration of genetic data with traditional morphological methods for species identification. Genetic markers, such as rRNA gene regions (nrITS, nuclear ribosomal small subunit, and nuclear ribosomal large subunit) and protein-coding gene sequences, have been employed in molecular systematics for decades (Raja et al., 2017). Among these, the ITS region is extensively used in fungal molecular taxonomy, providing valuable insights (White et al., 1990). Additionally, advancements in high-throughput sequencing and bioinformatics now enable whole-genome comparisons and phylogenomic analyses, which may soon surpass traditional molecular phylogenetic studies based on a limited number of marker genes (Marian et al., 2024).

In this study, nuclear ITS rDNA sequences were used to identify the fungal specimens ANK Akata TT 098, ANK Akata TT 124, ANK Akata TT 127, ANK Akata TT 163, ANK Akata TT 207, ANK Akata TT 281, and ANK Akata TT 350. This analysis demonstrated a genetic similarity of over 99% between the specimens and their related isolates of *Genea* (Table 1, Figure 6).

This study reports the first occurrence of *G. fragrans*, *G. pseudobalsleyi*, *G. pseudoverrucosa*, and *G. vagans* in Türkiye. The research achieved precise taxonomic identification using a combined approach of detailed morphological analyses and molecular phylogenetic methods focused on nrITS sequences. As a result, the number of documented *Genea* species known in Türkiye has increased to nine.

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: All data are available within the study.

Footnotes

Authorship Contributions: Conceptualization: E.K., G.D., and I.A.; Design/methodology: E.K., G.D., and I.A.; Execution/investigation: E.K., G.D., and I.A.; Resources/materials: E.K. and I.A.; Data acquisition: E.K., G.D., Em.K., and I.A.; Data analysis/interpretation: E.Ş., Em.K., and I.A.; Writing – original draft: E.Ş. and I.A.; Writing – review & editing/critical revision: I.A.

Conflict of Interest: No conflict of interest was declared by the authors.

Funding: The study was supported by the Turkish Scientific and Technological Research Council (TÜBİTAK) with project number 121Z924.

References

Agnello, C., Kaounas, V., & Alvarado, P. (2016). Genea gorii, una nuova specie descritta dall'Italia meridionale. *Rivista di Micologia*, 59(3), 195–202.

Akata, İ., Şen, İ., Sevindik, M., & Kabaktepe, Ş. (2022). Truffle checklist of Turkey II with a new record. *Turkish Journal of Agriculture-Food Science and Technology*, 10(10), 1913–1920. https://doi.org/10.24925/turjaf.v10i10.1913-1920.5482

Akata, İ., Şen, İ., Şahin, E., Çöl, B., & Keskin, E. (2023a). Delastria, a new genus of hypogeous fungi record for the Turkish mycobiota. *Trakya University Journal of Natural Sciences*, 24(2), 85–90. https://doi.org/10.23902/trkjnat.1331537

Akata, İ., Kumru, E., Ediş, G., Özbey, B. G., & Şahin, E. (2023b). Three new records for Turkish Agaricales inhabiting Ankara University Beşevler 10th Year Campus area. *Kastamonu University Journal of Forestry Faculty*, 23(3), 250–263. https://doi.org/10.17475/kastorman.1394933

Akata, İ., Kumru, E., Şahin, E., Acar, İ., & Kaya, E. (2024a). Amanita vidua: A new record for Turkish Amanita section Phalloideae based on morphological and molecular data. *Trakya University Journal of Natural Sciences*, 25(1), 97–110. https://doi.org/10.23902/trkjnat.1446327

Akata, İ., Ediş, G., Kumru, E., Acar, İ., & Şahin, E. (2024b). Initial report of Inocybe costinitii in Türkiye with morphological and molecular data. *Kahramanmaraş Sütçü İmam Üniversitesi Tarım ve Doğa Dergisi*, 27(6), 1304–1312. https://doi.org/10.18016/ksutarimdoga.vi.1467628

Akata, İ., Ediş, G., Kumru, E., Acar, İ., & Şahin, E. (2024c). Taxonomic studies on *Rhodocybe asyae* specimens discovered in a new location. *Kahramanmaraş Sütçü İmam Üniversitesi Tarım ve Doğa Dergisi, 27*(Suppl 1), 124–132. https://doi.org/10.18016/ksutarimdoga.vi.1507554

- Akata, İ., Kumru, E., Ediş, G., Acar, İ., & Şahin, E. (2024d). Two newly reported Agaricales species from Türkiye with morphological and molecular data. Kastamonu University Journal of Forestry Faculty, 24(3), 260–280. https://doi.org/10.17475/kastorman.1599952
- Alvarado, P., Cabero, J., Moreno, G., Bratek, Z., Van Vooren, N., Kaounas, V., Konstantinidis, G., Agnello, C., Merényi, Z., & Smith, M. E. (2014). Species diversity of *Genea* (Ascomycota, Pezizales) in Europe. *Ascomycete.org*, *6*(3), 41–51. https://doi.org/10.25664/art-0098
- Alvarado, P., Cabero, J., Moreno, G., Bratek, Z., Van Vooren, N., Kaounas, V., Konstantinidis, G., Agnello, C., Merényi, Z., Smith, M. E., Vizzini, A., & Trappe, J. M. (2016). Phylogenetic overview of the genus *Genea* (Pezizales, Ascomycota) with an emphasis on European taxa. *Mycologia*, 108(2), 441–456. https://doi.org/10.3852/15-199
- Alvarado, P., Healy, R., Moreno, G., Cabero, J., Scholler, M., Schneider, A., Vizzini, A., Kaounas, V., Vidal, J. M., Hensel, G., Rubio, E., Mujic, A., & Smith, M. E. (2018). Phylogenetic studies in *Genabea, Myrmecocystis*, and related genera. *Mycologia*, *110*(2), 401–418. https://doi.org/10.1080/00275514.2018.1451140
- Alvarado, P., Pérez, J. B., van Vooren, N., Bernauer, T., Hensel, G., & Scholler, M. (2021). *Genea coronata* (Pyronemataceae, Pezizales), a cryptic new species in a highly polymorphic genus. *Sydowia*, 73, 1–12. https://doi.org/10.12905/0380.sydowia73-2020-0001
- Berber, O., Uzun, Y., & Kaya, A. (2019). *Genea lobulata*, a new hypogeous ascomycete record for Turkish mycobiota. *Süleyman Demirel Üniversitesi Fen Bilimleri Enstitüsü Dergisi*, 23(3), 922–924. https://doi.org/10.19113/sdufenbed.563863
- Berkeley, M. J., & Broome, C. E. (1846). Notices of British hypogaeous fungi. *Annals and Magazine of Natural History*, 18, 73–82. https://doi.org/10.1080/037454809496568
- Bertolini, V. (2014). Funghi ipogei: uno sguardo alle Genea. *Bollettino del Circolo Micologico G. Carini, 67*, 21–40.
- Bresadola, J. (1893). Mycetes australienses novi, ct emendanda ad Floram Mycologicam Australiae. *Hedwigia*, 32(3), 118–119.
- Bratek, Z., Merényi, Z., & Varga, T. (2013). Changes of hypogeous funga in the Carpathian-Pannonian region in the past centuries. *Acta Mycologica*, 48(1), 33–39. https://doi.org/10.5586/am.2013.005
- Bucholtz, F. (1901). Hypogaeen aus Russland. Hedwigia, 40, 304-322.
- Ceruti, A. (1960). *Iconographia mycologica. Supplementum II, Elaphomycetales et Tuberales.* Museo Tridentino di Scienze Naturali.
- Corda, A. C. I. (1854). Icones fungorum hucusque cognitorum (Vol. 6). F. Ehrlich.
- Cribb, J. W. (1960). Two new species of subterranean Ascomycetes from Queensland. *Papers from the Department of Botany, the University of Queensland,* 4, 35–37.
- Crous, P. W., Osieck, E. R., Jurjević, Ž., Boers, J., van Iperen, A. L., Starink-Willemse, M., ... & Groenewald, J. Z. (2021). Fungal Planet description sheets: 1284–1382. *Persoonia*, 47, 178–374. https://doi.org/10.3767/persoonia.2021.47.06
- Diamandis, S., & Perlerou, C. (2008). Recent records of hypogeous fungi in Greece. *Acta Mycologica*, 43(2), 139–142. https://doi.org/10.5586/am.2008.017
- Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32(5), 1792–1797. https://doi.org/10.1093/nar/gkh340
- Gilkey, H. M. (1939). *Tuberales of North America*. Oregon State Monographs. Studies in Botany, 1, 1–63.
- Guevara-Guerrero, G., Stielow, B., Tamm, H., Cázares-Gonzalez, E., & Göker, M. (2012). *Genea mexicana*, sp. nov., and *Geopora tolucana*, sp. nov.,

- new hypogeous Pyronemataceae from Mexico, and the taxonomy of Geopora reevaluated. *Mycological Progress*, 11,711–724. https://doi.org/10.1007/s11557-011-0781-y
- Harkness, H. W. (1899). California hypogaeous fungi. *Proceedings of the California Academy of Sciences*, 1(8), 241–264.
- Hawker, L. E. (1954). British hypogeous fungi. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 237, 429–546. https://doi.org/10.1098/rstb.1954.0002
- Hollós, L. (1911). Magyarország földalatti gombái, szarvasgombafélei: Fungi hypogaei Hungariae. K. M. Termeszettudomanyi Tarsulat.
- Imai, S. (1933). On two new species of Tuberaceae. *Proceedings of the Imperial Academy of Japan*, 9, 182–184.
- Kajevska, I., Rusevska, K., & Karadelev, M. (2013). The Family Pyronemataceae (Pezizales, Ascomycota) in the Republic of Macedonia. *Macedonian Journal of Ecology and Environment*, 15(1), 11–22. https://doi.org/10.59194/MJEE13151011k
- Kaounas, V., Agnello, C., & Alvarado, P. (2016). *Genea cephalonicae* sp. nov. Ascomycota, Pezizales, a new hypogeous species from Greece. *Ascomycete.org*, 8(3), 105–110. https://doi.org/10.25664/art-0179
- Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution*, *35*, 1547–1549. https://doi.org/10.1093/molbev/msy096
- Læssøe, T., & Hansen, K. (2007). Truffle trouble: What happened to the Tuberales? *Mycological Research*, 111(9), 1075–1099. https://doi.org/10.1016/j.mycres.2007.08.004
- Landi, M., Salerni, E., Ambrosio, E., D'Aguanno, M., Nucci, A., Saveri, C., Perini, C., & Angiolini, C. (2015). Concordance between vascular plant and macrofungal community composition in broadleaf deciduous forests in central Italy. *iForest Biogeosciences and Forestry*, 8(3), 279–286. https://doi.org/10.3832/ifor1199-008
- Lawrynowicz, M. (1988). *Grzyby (Mycota) XVIII (Ascomycetes, Elaphomycetales, Tuberales)*. Polska Akademia Nauk.
- Marian, I. M., Valdes, I. D., Hayes, R. D., La Butti, K., Duffy, K., Chovatia, M., ... & Ohm, R. A. (2024). High phenotypic and genotypic plasticity among strains of the mushroom-forming fungus *Schizophyllum commune*. *Fungal Genetics and Biology*, *173*, 103913. https://doi.org/10.1016/j.fgb.2024.103913
- Mattirolo, O. (1900a). Elenco dei "fungi hypogaei" raccolti nelle Foreste di Vallombrosa negli anni 1899–1900. *Malpighia*, 14, 1–24.
- Mattirolo, O. (1900b). Gli ipogei di Sardegna e di Sicilia. Malpighia, 14, 39–110.
- Montecchi, A., & Sarasini, M. (2000). Funghi ipogei d'Europa. Associazione Micologia Bresadola.
- Moreno-Arroyo, B., Gómez, J., & Calonge, F. D. (1998). *Genea subbaetica*, sp. nov., encontrada en España. *Boletín de la Sociedad Micológica de Madrid*, 23, 85–89
- Osmundson, T. W., Robert, V. A., Schoch, C. L., Baker, L. J., Smith, A., Robich, G., Mizzan, L., & Garbelotto, M. M. (2013). Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLOS ONE*, 8(4), e62419. https://doi.org/10.1371/journal.pone.0062419
- Paz, A., Chautrand, P., & Lavoise, C. (2016). *Genea amici* una especie nueva encontrada en Córcega. *Yesca*, 28, 139–150.
- Paz, A., Chautrand, P., & Lavoise, C. (2019). *Genea darii* une nouvelle espèce du sud de l'Europe. *Bulletin de la Fédération des Associations Mycologiques Méditerranéennes*, 55, 3–14.

- Perez, J. B. (2024). Catalogue d'Ascomycètes hypogés de la région Auvergne-Rhône-Alpes. Bulletin Mycologique et Botanique Dauphiné-Savoie, 253, 37–49.
- Pfister, D. H. (1984). *Genea-Jafneadelphus*-a Tuberalean-Pezizalean connection. *Mycologia*, 76, 170–172. https://doi.org/10.1080/00275514.1984.12023823
- Raja, H. A., Miller, A. N., Pearce, C. J., & Oberlies, N. H. (2017). Fungal identification using molecular tools: a primer for the natural products research community. *Journal of Natural Products*, 80(3), 756–770. https://doi.org/10.1021/acs.jnatprod.6b01085
- Ribes, M. A., Hernanz, J., Tello, S., Campos, J. C., Paz, A., Sánchez, G., Pancorbo, F., & Serrano, F. (2016). Contribución al conocimiento de la biodiversidad fúngica del Parque Nacional de Ordesa y Monte Perdido I. *Pirineos, 171*, e021. https://doi.org/10.3989/Pirineos.2016.171005
- Riva, A. (2009). Wakefieldia macrospora e *Genea fragrans*, due funghi ipogei nuovi per il Ticino. *Schweizerische Zeitschrift für Pilzkunde*, 87, 119–121.
- Saccardo, P. A. (1889). Sylloge Fungorum hucusque cognitorum (Vol. 8). Patavii.
- Saitta, A., Gargano, M. L., Morara, M., Ilice, M., & Venturella, G. (2008). The hypogeous fungi from Sicily (southern Italy): New additions. *Mycologia Balcanica*, *5*, 147–152.
- Savić, D., Kajevska, I., & Milosavljević, N. (2018). Checklist of Pezizomycetes from Serbia. *Bulletin of the Natural History Museum*, 11, 21–61. https://doi.org/10.5937/bnhmb1811021S
- Smith, M. E. (2007). NATS truffle and truffle-like fungi 15: *Genea balsleyi* sp. nov. (Pyronemataceae), a new hypogeous ascomycete from New Jersey. *Mycotaxon*, 99, 239–244.
- Smith, M. E., Trappe, J. M., & Rizzo, D. M. (2006). *Genea, Genabea*, and *Gilkeya* gen. nov.: Ascomata and ectomycorrhiza formation in a *Quercus* woodland. *Mycologia*, 98(5), 699–716. https://doi.org/10.1080/15572536.2006.11832642
- Stewart, E. L., & Heblack, R. K. (1979). Hypogeous fungi of Minnesota: *Genea anthracina* sp. nov. *Mycotaxon*, *9*, 451–458.
- Tedersoo, L., Hansen, K., Perry, B. A., & Kjøller, R. (2006). Molecular and morphological diversity of pezizalean ectomycorrhiza. *New Phytologist*, *170*(3), 581–596. https://doi.org/10.1111/j.1469-8137.2006.01678.x
- Trappe, J. M. (1979). The order, families, and genera of hypogeous Ascomycotina (truffles and their relatives). *Mycotaxon*, *9*, 297–340.
- Trappe, J. M., & Guzmán, G. (1971). Notes on some hypogeous fungi from Mexico. *Mycologia*, 63(2), 317–332. https://doi.org/10.1080/00275514.1971.12 019112

- Tulasne, L. R., & Tulasne, C. (1851). Fungi hypogaei: histoire et monographie des champignons hypogés. F. Klincksieck.
- Türkoğlu, A., & Castellano, M. A. (2014). New records of some ascomycete truffle fungi from Turkey. *Turkish Journal of Botany*, 38(2), 406–416. https://doi.org/10.3906/bot-1303-24
- Uzun, Y., & Kaya, A. (2019). New additions to Turkish Pezizales from the Eastern Black Sea Region. *Turkish Journal of Botany*, 43, 262–270. https://doi.org/10.3906/bot-1802-34
- Vacek, V. (1951). Zemnička kulovitá-Genea sphaerica Tul. Česká Mykologie, 5(1-2), 3-5.
- Velenovský, J. (1922). České Houby (Vols. 4-5). České Botanické Společnosti.
- Venturella, G., Pecorella, E., Saitta, A., Zambonelli, A., & Morara, M. (2006). Ecology and distribution of hypogeous fungi from Sicily (southern Italy). *Cryptogamie, Mycologie*, *27*(3), 201–217.
- Vidal, J. M. (1997). Algunos hongos hipogeos nuevos o poco citados de Cataluña (Zygomycotina, Ascomycotina y Basidiomycotina). *Revista Catalana de Micologia*, 20, 25–62.
- Vittadini, C. (1831). Monographia Tuberacearum. Milano, Italia.
- Wallroth, K. F. W. (1833). Flora cryptogamica Germaniae (Vol. 2). Nuremberg, Germany.
- White, T. J., Bruns, T., Lee, S., & Taylor, J. W. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In M. A. Innis & D. H. Gelfand (Eds.), *PCR Protocols: A Guide to Methods and Applications* (pp. 315–322). Academic Press.
- Zeng, M., Gentekaki, E., Zeng, X. Y., Hyde, K. D., Zhao, Q., & Tian, Q. (2022). Evolutionary relationships and allied species of Pyronemataceae, with segregation of the novel family Pyropyxidaceae. *Mycosphere*, *13*(2), 207–280. https://doi.org/10.5943/mycosphere/si/1f/7
- Zhang, B. C. (1991). Taxonomic status of *Genabea*, with two new species of *Genea* (Pezizales). *Mycological Research*, 95(8), 986–994. https://doi.org/10.1016/S0953-7562(09)80096-8
- Zotti, M., Vizzini, A., Di Piazza, S., Pavarino, M., & Mariotti, M. G. (2010). Hypogeous fungi in Liguria (Italy): Distribution and ecology. *Cryptogamie, Mycologie*, 31(1), 47–57.