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Research Article

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

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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* (Wallr.) Sacc., *G. pseudobalsleyi* Agnello, Bratek & Cabero, *G. pseudoverrucosa* Bratek, Konstant. & Van Vooren, and *G. 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 (rDNA) dizileri kullanılarak moleküler filogenetik analizler yapılmıştır. Çalışmalar, yeni Türk koleksiyonlarını *Genea fragrans* (Wallr.) Sacc., *G. pseudobalsleyi* Agnello, Bratek & Cabero, *G. pseudoverrucosa* Bratek, Konstant. & Van Vooren ve *G. vagans* Mattir 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.

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 *Genea 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).

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 expands the documented diversity of *Genea* in Türkiye by documenting four additional species reported from Edirne and Kırklareli provinces: *G. fragrans* (Wallr.) Sacc., *G. pseudobalsleyi* Agnello, Bratek & J. Cabero, *G. pseudoverrucosa* Bratek, Konstant. & Van Vooren, and *G. vagans* Mattir. Each species displays distinct morphological and molecular characteristics.

Genea fragrans, initially described as *Hydnocaryon fragrans* (Wallroth 1833) and later renamed by Paoletti (Saccardo 1889), is characterized by subglobose ascospores adorned with block-like or pyramidal warts (Bertolini 2014). *Genea pseudobalsleyi* is notable for its hypogeous, black, warted ascomata and inner chamber epithelial lining. *Genea pseudoverrucosa* is distinguished by its black, folded ascomata with a labyrinthine inner chamber and ascospores featuring truncated warts (Alvarado *et al*. 2014). *Genea vagans* displays small, rounded, black, warted ascomata with ellipsoidal ascospores exhibiting prominent, fused conical warts (Ceruti 1960, Ribes *et al*. 2016).

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 Pınarhisar districts of Kırklareli, employing trained Lagotto Romagnolo truffle dogs as part of the collection process (Fig. 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. High-resolution imaging was performed using a Nikon D810 camera fitted with an AF-S NIKKOR 105mm 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).

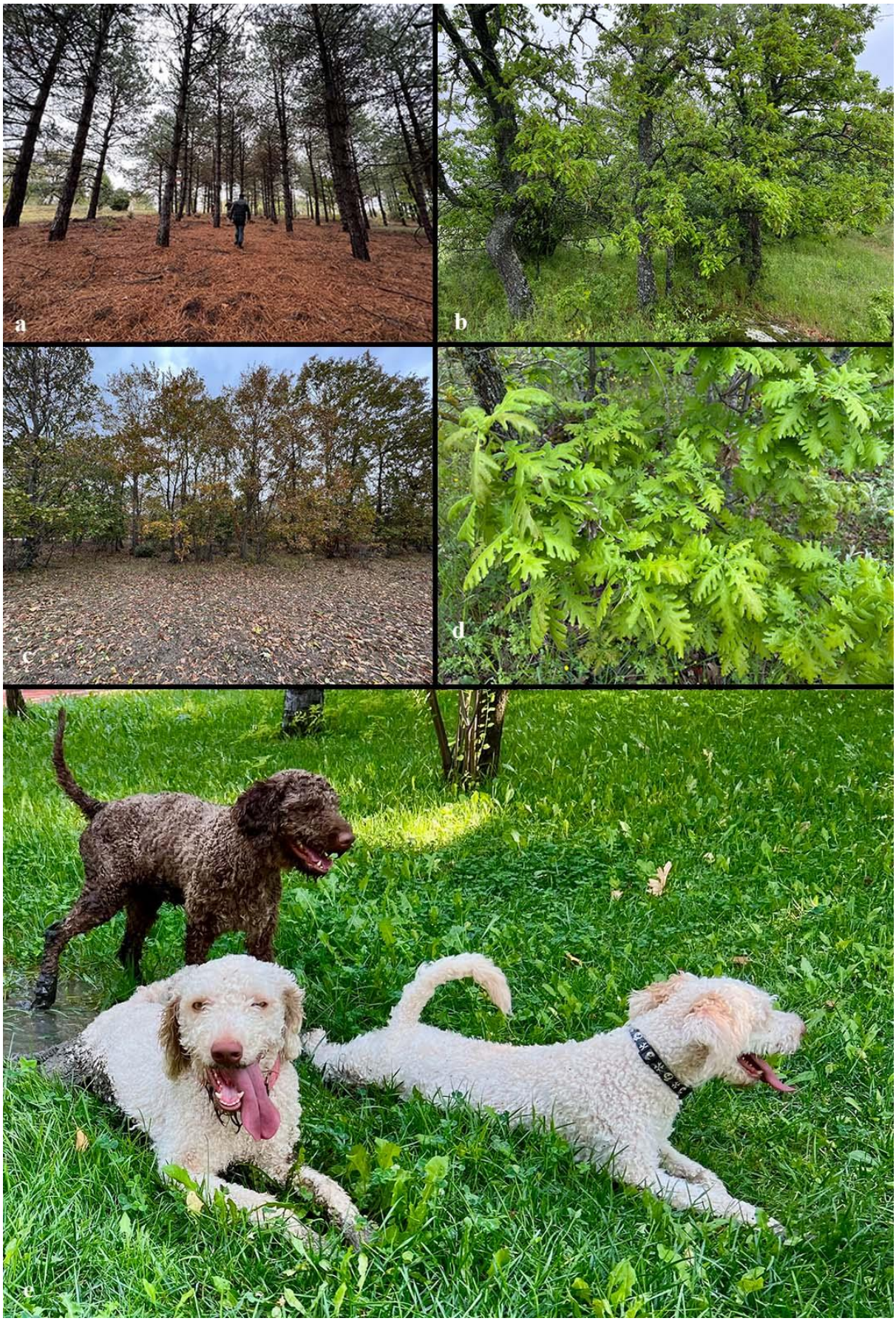

Fig. 1. **a-d.** Collection areas, **e.** truffle dogs (Lagotto Romagnolo).

Molecular Study

Determination of (ITS) rDNA Sequences

The nuclear ribosomal internal transcribed spacer (nrITS) rDNA region was amplified from genomic DNA isolated from *Genea* specimens using the polymerase chain reaction (PCR) method. This amplification strictly adhered to established and well-validated methodologies outlined in previous studies (Akata *et al*. 2023a,b, 2024a,b). 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-d), 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 Internal Transcribed Spacer (ITS) sequencing.

Taxonomy

Phylum ASCOMYCOTA (Berk) Caval.-Sm.

Ordo Pezizales J. Schöt.

Family *Pezizaceae* Dumort.

Genus *Genea* Vittad.

Genea fragrans (Wallr.) Sacc. (1889), (Figs 2, 6a,b)

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 µm 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 µm 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 µm, formed by brownish to dark brown angular cells measuring 20-45 µm wide. **Asci** 240-300 × 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) × (27)28-36(38) µm, (mean: 38 × 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 × 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), (Figs 3, 6c, d).

Material examined: Türkiye- Kırklareli, Pınarhisar, under oak, 480 m, 41°44′ N, 27°34′ ′E, 5 Oct. 2022, ANK Akata TT 127; *ibid.*, 312m, 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.

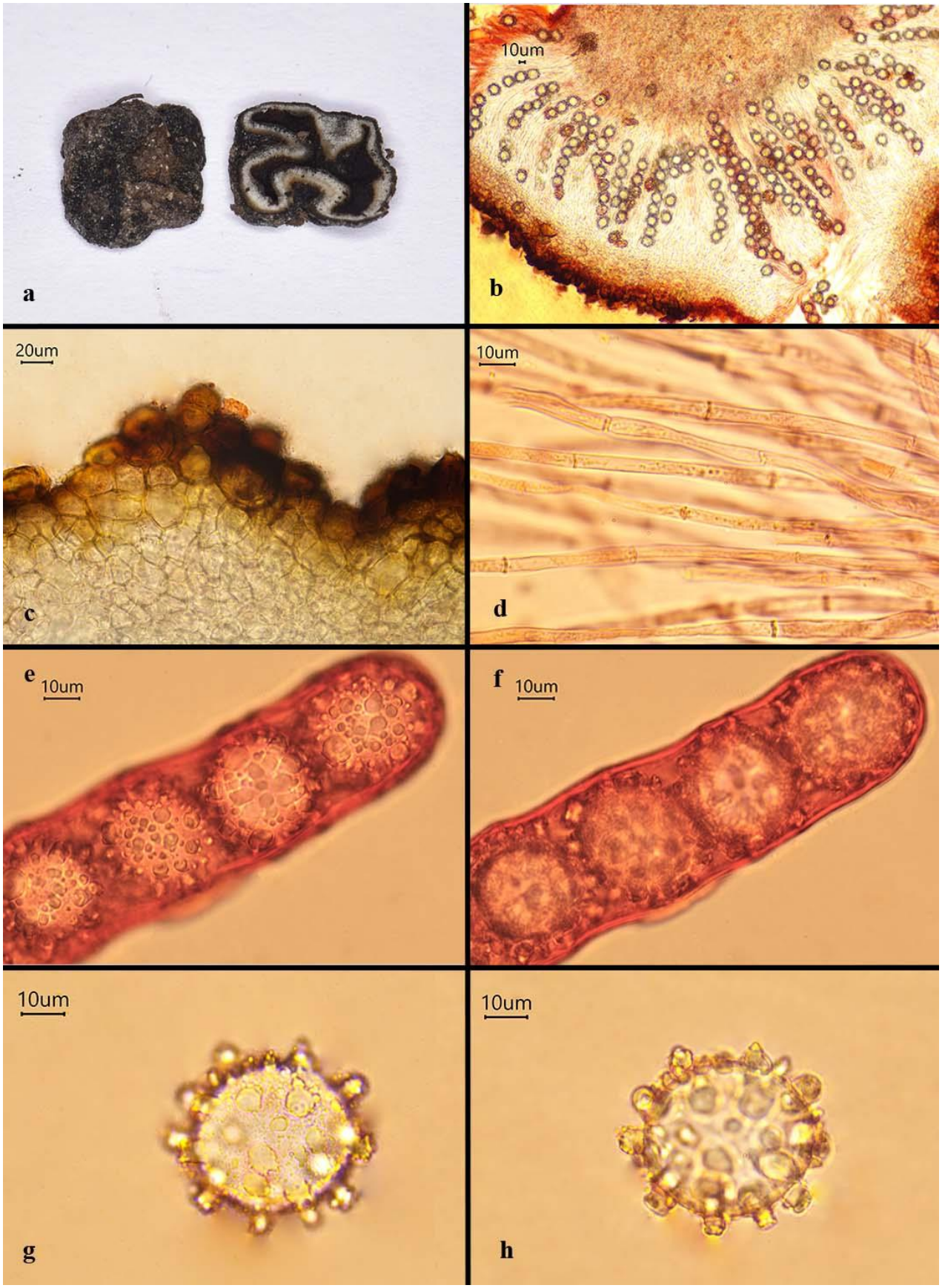

Fig. 2. *Genea fragrans*: **a.** Ascomata, **b.** microscopic cross-section of ascomata, **c.** peridium, **d.** septa of paraphyses, **e, f.** spores contained within the ascus, **g, h.** single ascospore.

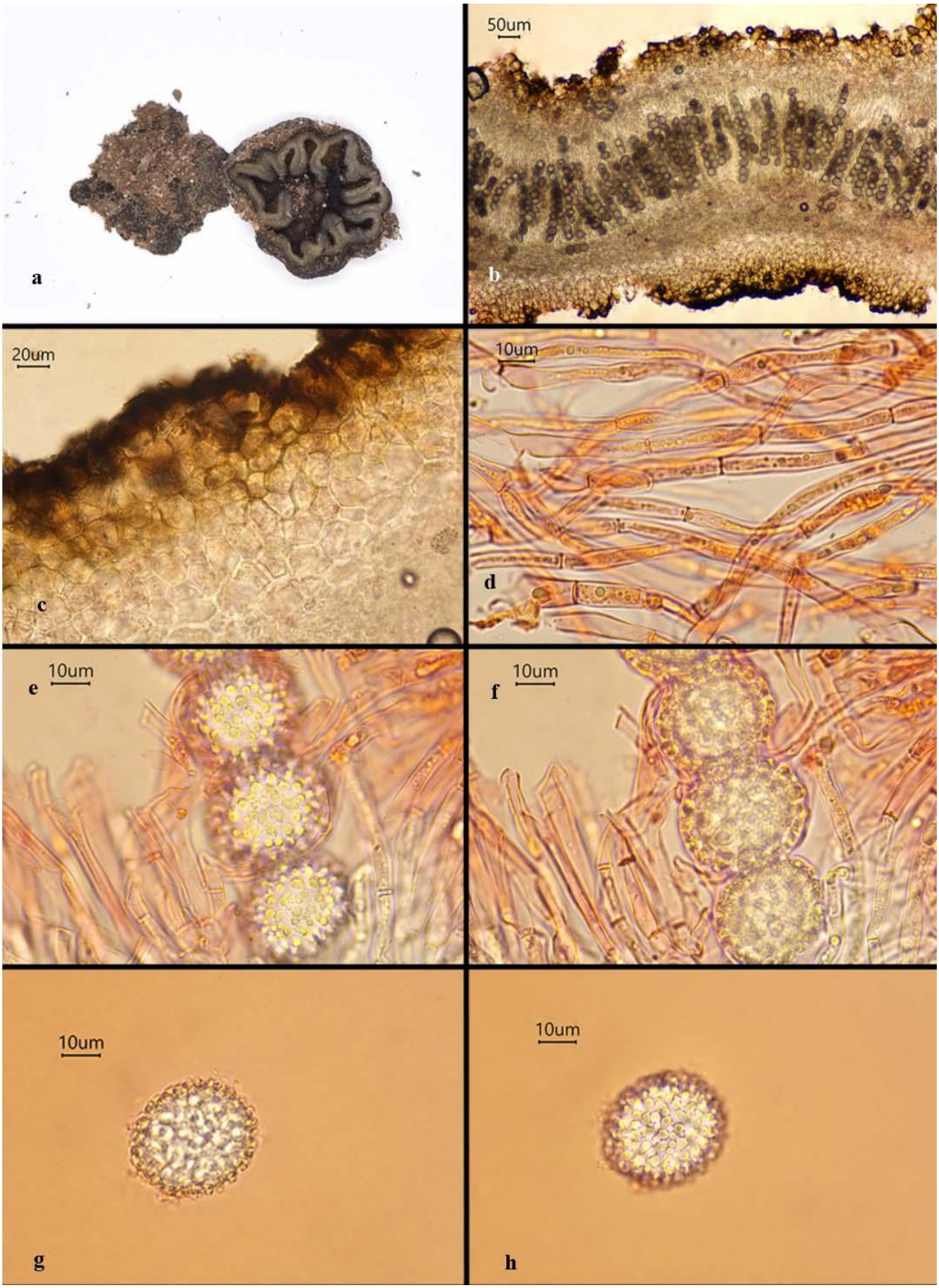

Fig. 3. *Genea pseudobalsleyi*: **a.** Ascomata, **b.** microscopic cross-section of ascomata, **c.** peridium, **d.** septa of paraphyses, **e, f.** spores contained within the ascus, **g, h.** single ascospore.

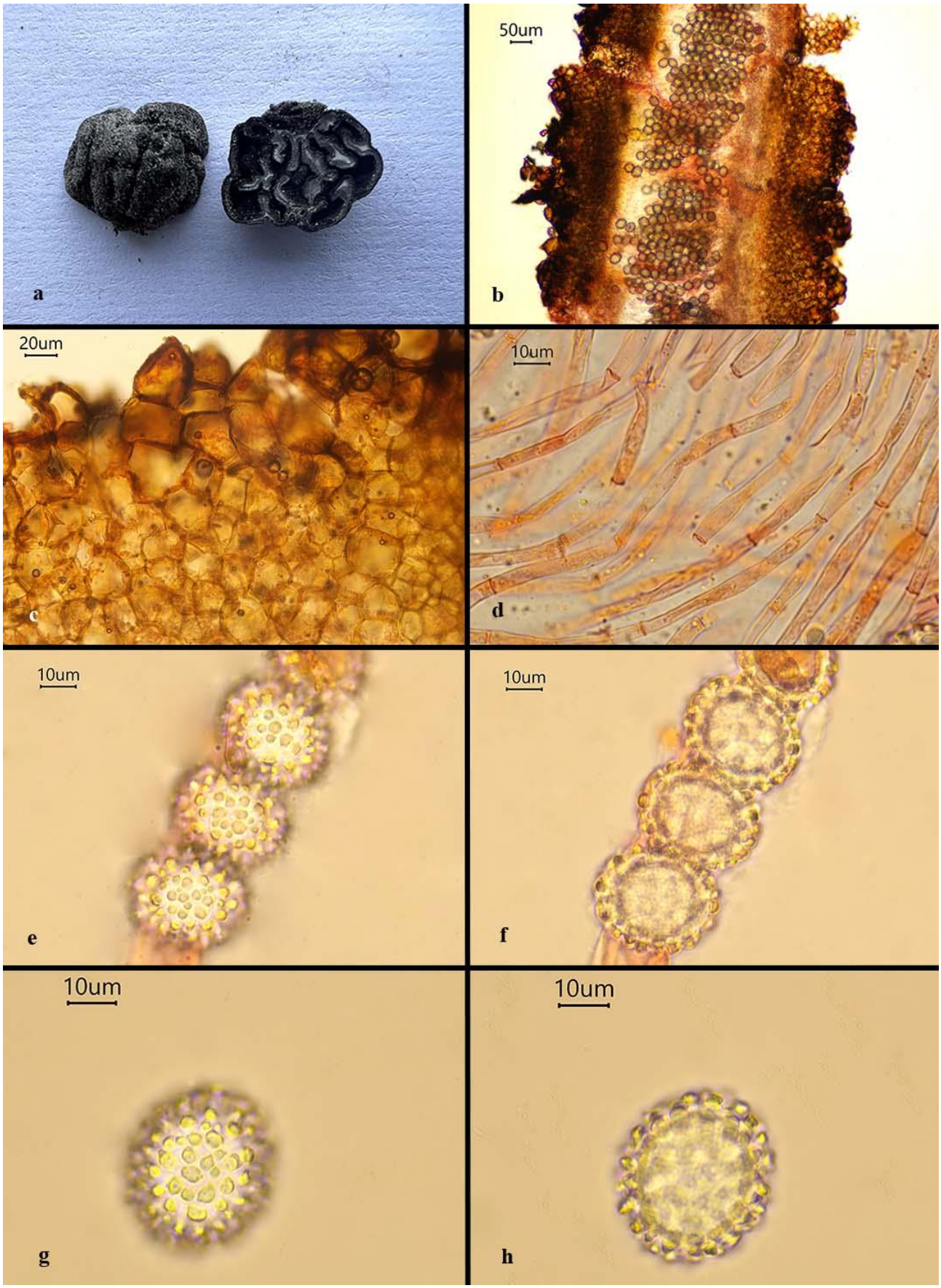

Fig. 4. *Genea pseudoverrucosa*: **a.** Ascomata, **b.** microscopic cross-section of ascomata, **c.** peridium, **d.** septa of paraphyses, **e, f.** spores contained within the ascus, **g, h.** single ascospore.

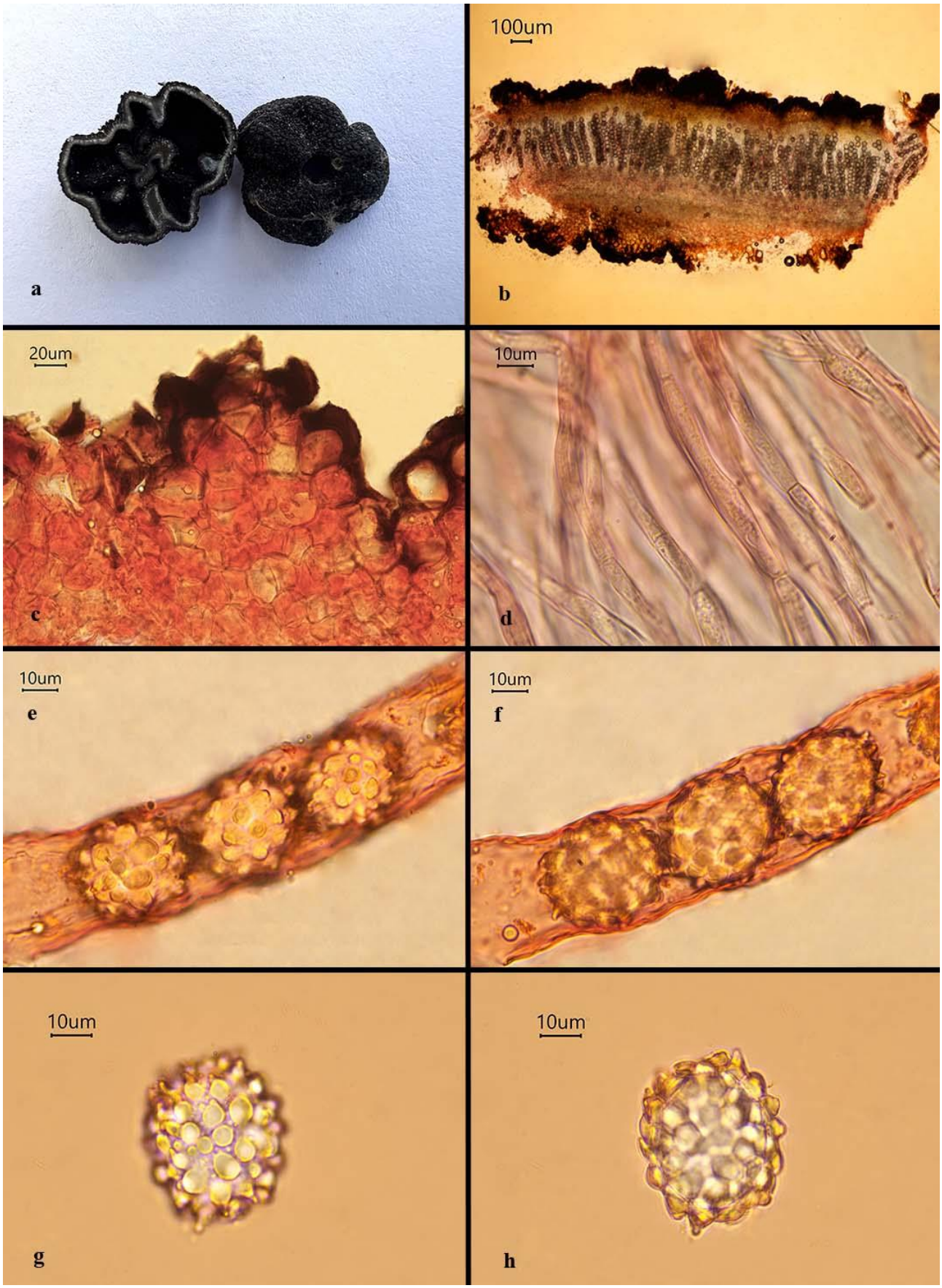

Fig. 5. *Genea vagans:* **a.** Ascomata, **b.** microscopic cross-section of ascomata, **c.** peridium, **d.** septa of paraphyses, **e, f.** spores contained within the ascus, **g, h.** single ascospore.

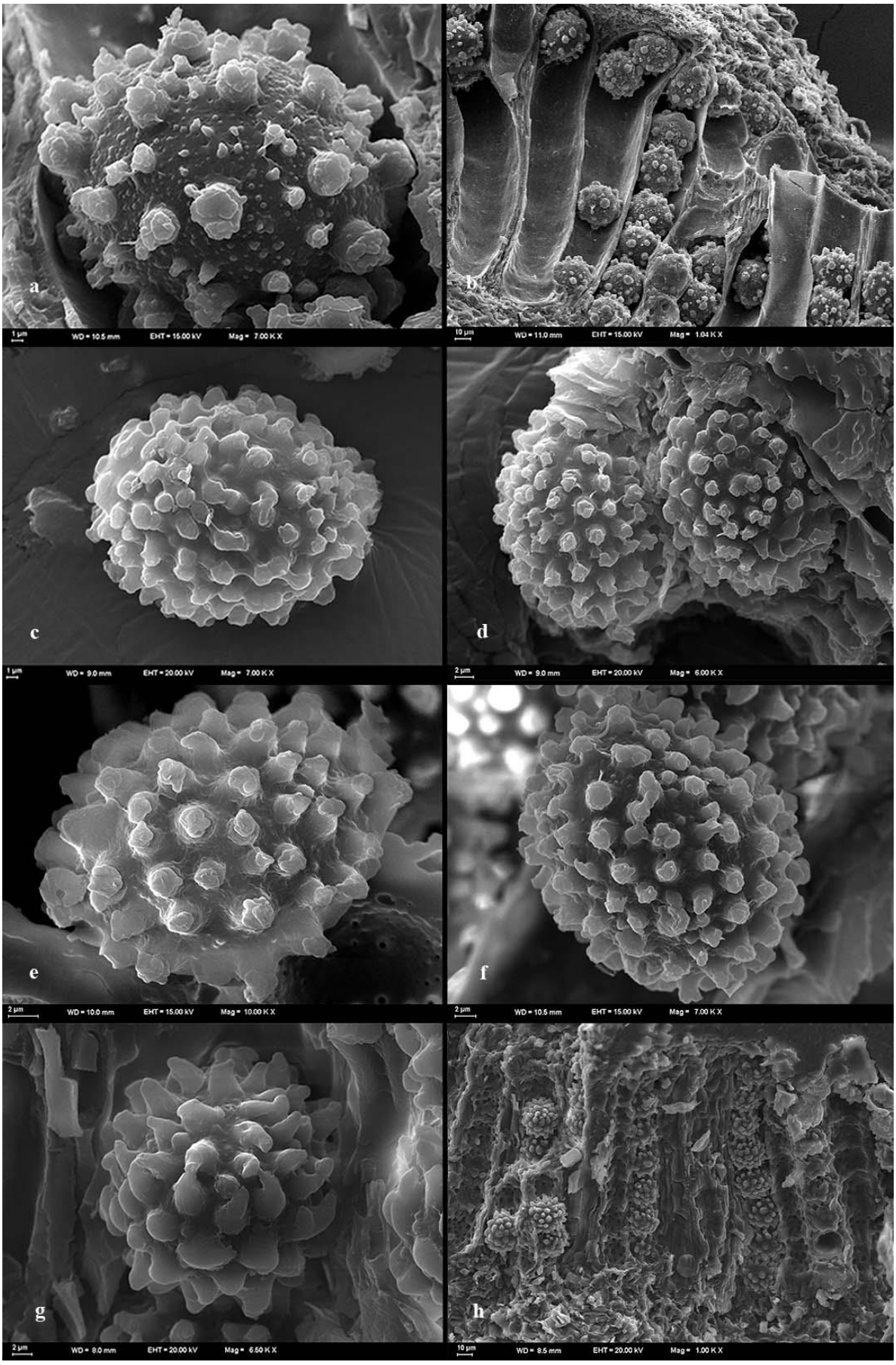

Fig. 6. SEM micrographs: **a, b.** *G. fragrans*, **c, d.** *G. pseudobalsleyi*, **e, f.** *G. pseudoverrucosa*, **g, h.** *G. vagans*.

Asci 180-240 × 35-40 µm, 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) × 23-26 µm, (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 × 2-2.5 µm.

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), (Fig. 4, Fig. 6e,f).

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 × 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), (Figs 5, 6g, h).

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 µm thick, composed 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 × 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) × (25)27-30(31) µm, (mean: 35 × 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 ×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).

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 (Fig. 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 *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.

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

Species	Specimen Voucher/Isolate/Strain	nrITS GenBank Accession Number	Geographical origin	Reference
Genea 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
Genea 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
Genea 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
Genea 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
Genea 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
Genea 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
Genea 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
Genea 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

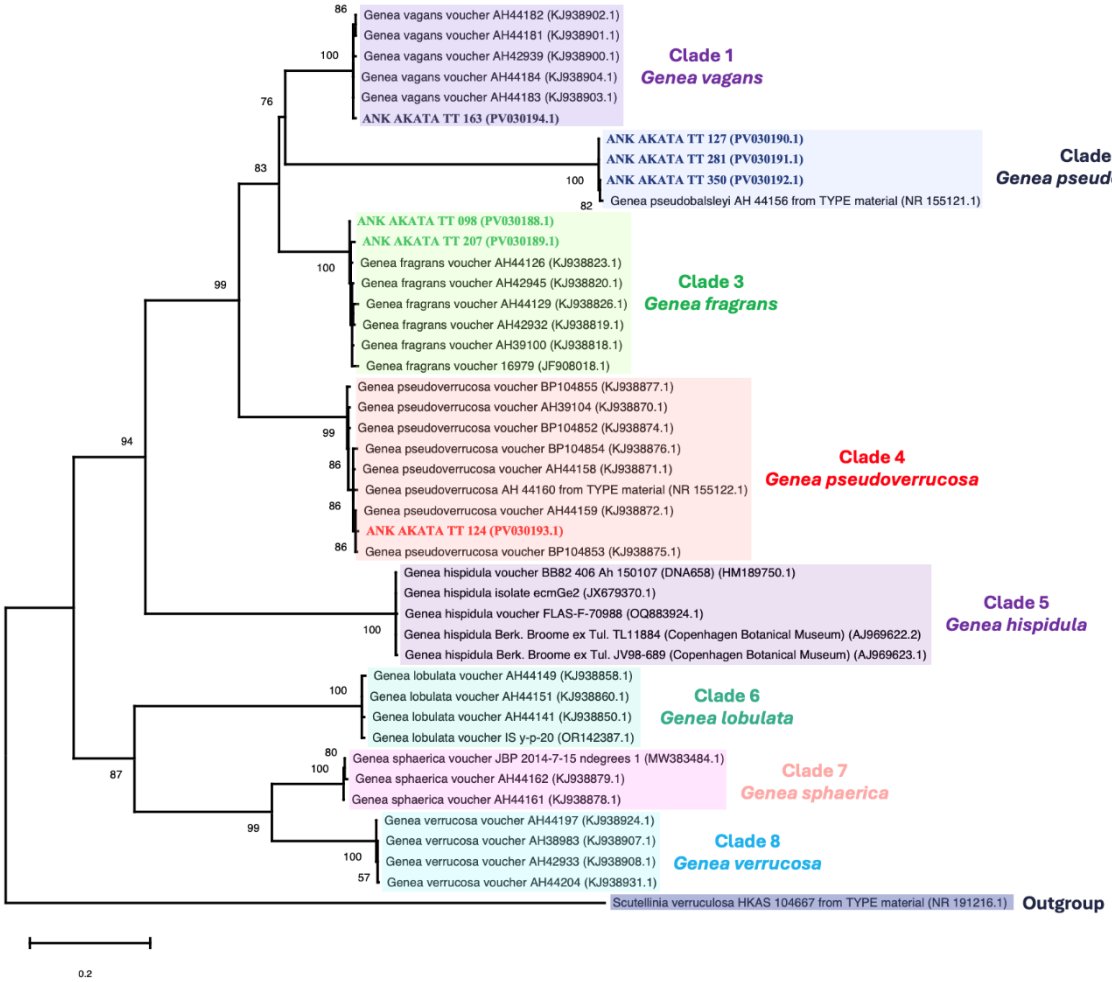

Fig. 7. Phylogram of maximum likelihood (ML) of a set of 44 *Genea* sequences based on the nrITS rDNA, rooted with *Scutellinia verruculosa* (outgroup). Nodes with ≥ 50% ML bootstrap support are annotated with their support values. Terminals that represent sequences obtained during this study are in 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.

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 × 19-22 µm and exhibit conical warts approximately measuring 2 × 1.5-4.5 µm, 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 × 35 µm. Over time, the conical spore warts of *G. verrucosa* may develop into aculeate forms but remain less prominent than the ornamentation 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 × 19.5-24 µm, and by its ornamentation, which consists of truncate-conical warts that are occasionally nearly cubic, reaching 3.8-5.5 µm 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 × 18-25.5 µm, and ornamentation consisting of conical warts with digitate apices, up to 2.3-5.3 µm 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 × 18-26 µm, but it is distinguishable by its 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 (36-40×24-28 µm) 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 × 18-26 µm, and unique ornamentation characterized by truncated or rounded warts measuring 2.1-6.5 × 2-6 µm (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 × 15.5-26 µm, but it is distinguished by its distinct ornamentation, with warts reaching 3-6 µm 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 × 27-28 µm, and adorned with prominent conical warts that frequently coalesce at their bases. Lawrynowicz (1988) reported nearly identical dimensions, with ascospores measuring 31-38 × 27-28 µm. However, Vidal (1997) and Montecchi & Sarasini (2000) documented significantly smaller ascospore sizes, ranging from 18-22 µm, 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 31.2-38.4 × 27.1-30.2 µm. Alvarado *et al*. (2016) further corroborated these findings, reporting ascospore sizes of 32-41 × 27-37 µm based on authentic material from Mattirolo and additional specimens. In our study, ascospore dimensions of 31-38 × 27-30 µm 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 × 18-20 µm 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 × 17-20 µm, 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 brush-like 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 identifying species. Genetic markers, such as rRNA gene regions (nrITS, nrSSU, and nrLSU) 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 (Table 1) and their related isolates of *Genea* (Table 1, Fig. 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 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.

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