

New data on hypogeous fungi from Greece with special reference to *Wakefieldia macrospora* (Hymenogastraceae, Agaricales) and *Geopora clausa* (Pyronemataceae, Pezizales)

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Abstract. This work provides new information about five interesting and uncommon hypogeous fungi from Greece – *Balsamia vulgaris*, *Geopora clausa*, *Hydnocystis piligera*, *Sclerogaster compactus* and *Wakefieldia macrospora*. Descriptions of the five species are included based upon Greek collections, accompanied by colour macro- and microphotographs, and molecular data of four of them. On the basis of molecular results, the genus *Wakefieldia* seems to be closely related to *Hebeloma* in the *Hymenogastraceae*, while *Geopora clausa* appears to be related to *Geopora* in the *Pyronemataceae*.

Key words: *Ascomycetes*, *Basidiomycetes*, *Boletales*, *Gastrales*, ITS – LSU

Introduction

Although the first records of hypogeous fungi from Greece date back to the middle of 19th century (Landerer 1858), the knowledge on this diverse ecological group in this country is still relatively scarce (Maire & Politis 1940; Zervakis *et al.* 1998, 1999; Diamandis & Perlerou 2008; Konstantinidis 2009). It is therefore the first author started collecting hypogeous fungi in 2008, citing rare or unknown species for Greece, (Agnello & Kaounas 2010, 2011). Five uncommon and interesting species are described and illustrated below.

Materials and methods

Hypogeous fungi were collected and identified by the first author, unless otherwise stated. Collections were made in 2008–2011 manually without the aid of dogs. The specimens cited in this paper are preserved and available for consult or revision in the private collection of V. Kaounas, abbreviated as

“VK” in the text below, in the Herbarium of the Universidad de Alcalá (AH), in the Herbarium of the Institute of Evolution, University of Haifa (HAI), and in the private collections of A. Montecchi, G. Konstantinidis and Miguel Ángel Ribes (noted as “AM”, “GK”, and “MAR” respectively).

The study of the specimens was conducted both in fresh and dried state. Microscopic study was performed under Nikon Eclipse e100 and Bresser Biolux AL light microscopes. Microscopic slides were mostly prepared in tap water. Congo red was also used as a mounting medium, especially when it was necessary to stain the hyphal walls or the spore ornamentation. Measurements were taken from several slides and 30 spores were measured from each species. The values are given below in the following form: (min–) mean±standard deviation (–max), excluding the ornamentation, where present.

The primary sources used for identification are Hawker (1954), Burdsall (1968), Pegler *et al.* (1993), Astier (1998), Montecchi & Sarasini (2000), Gori (2005) and Agnello (2011), but further essential references are listed under the description of each species.

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Molecular methods followed those described in Moreno *et al.* (2011). Phylogenetic analysis consisted in a maximum parsimony search in PAUP* 4.0b10 and a Bayesian analysis in MrBayes 3.1. Only values above 70% BP and 90 PP were considered significant. Sequences are stored in public databases under the codes stated in Table 1.

Survey of taxa

Balsamia vulgaris Vittad., Monogr. Tuberac.: 30 (1831)

Figs 1, 6–8

Ascomata hypogeous or semi-hypogeous, tuberiform, sometimes lobed, 1–3 cm in diam, hazel or light brown when young, orange-tinted when mature; surface covered with darker spherical, angular, pyramidal, or irregular verrucose warts of less than 0.5 mm across. **Peridium** thin, not separated from the gleba, with pseudoparenchymatous structure consisting of polygonal or rounded yellowish elements up to 30 µm in diam. **Gleba** pale white to pale yellow, with numerous small irregular elongated chambers and darker veins; odour at first sweet, then becoming stronger and somewhat unpleasant. **Asci** 8-spored, broadly clavate to ellipsoid or fusiform, stalked, up to 100 × 40 µm. **Ascospores** (22.5–) 27.0 ± 2.6 (–31) × (9–) 11.6 ± 1.3 (–14) µm, ratio (1.9–) 2.4 ± 0.2 (–2.7) (*n* = 30), ellipsoid to ellipsoid-cylindrical with rounded apices, hyaline, smooth, usually 3-guttulate with one central and two smaller polar guttules, thin-walled (wall < 1 µm thick), randomly arranged in asci. **Paraphyses** cylindrical, up to 5 µm wide.

Habitat – relatively widespread species that generally occurs in deciduous forests at different altitudes, often under moss in meadows and glades at the edges of woodlands, in autumn and winter.

Specimens examined. GREECE, Attika: Katsimidi, under *Cistus creticus* L. and *Quercus ilex* L., ca 650 m, 14 Dec 2008 (VK 604); Schinias, under *Quercus coccifera* L., ca 5 m, 22 Dec 2009 (VK 1290); Parnitha, under *Quercus ithaburensis* subsp. *macrolepis* (Kotschy) Hedge & Yalt., ca 500 m, 16 Nov 2010 (VK 1785); Rafina, under *Quercus coccifera* and *Pinus halepensis* Mill., ca 40 m, 9 Jan 2011 (VK 1916).

Recently reported from Greece by Diamandis & Perlerou (2008).

Geopora clausa (Tul. & C. Tul.) Burds., Mycologia 60: 507 (1968) **Figs 2, 9–11, 21**

Ascomata 0.5–2 (–3) cm in diam, hypogeous or semi-hypogeous, somewhat globose, usually more or less lobed or wrinkled, ochraceous or rusty-brown, with thin mycelial tufts seen sometimes at the base; surface covered with dark brown granules; odour strong, fruity. **Peridium** pseudoparenchymatous, composed of inflated or rounded elements of about 20 µm diam. **Gleba** whitish, consisting of a single chamber, often considerably wrinkled and forming a labyrinthoid structure. **Asci** cylindrical, 160–250 × 15–20 µm. **Ascospores** (22–) 23.7 ± 1.0 (–26) × (16–) 17.2 ± 0.7 (–18.5)

µm, ratio (1.3–) 1.4 ± 0.1 (–1.5) (*n* = 30), ellipsoid or ovoid, uniseriate in the asci, smooth, hyaline, guttulate, usually with a single large central guttule. **Paraphyses** cylindrical, septate, 3–6 µm wide at the top.

Habitat – occurs from autumn to spring as hypogeous or sometimes as semi-hypogeous, in sandy soils, especially in coastal pine forests and scrubland in Mediterranean ecosystems.

Specimens examined. GREECE, Attika: Schinias, under *Cistus creticus* and *Pinus halepensis*, ca 5 m, 12 Mar 2008, det. G. Konstantinidis & V. Kaounas (VK 313); *idem*, 21 Apr 2008 (VK 379); *idem*, 24 Dec 2008 (VK 630); *idem*, 27 Feb 2009 (VK 752); *idem*, 9 Dec 2009 (VK 1263); *idem*, under *Pinus pinea* L., ca 5 m, 2 Feb 2011 (VK 2029); *idem*, 14 Feb 2011 (VK 2061); *idem*, 11 Mar 2011 (VK 2101); Rafina, under *Pinus halepensis* and *Cistus monspeliensis* L. in sandy soil, ca 20 m, 5 Feb 2011 (VK 2039); *idem*, 9 Feb 2011 (VK 2046). ITALY, Oristano: Orosei, sandy soil under *Juniperus* sp. and *Cistus* sp., det. A. Montecchi, 17 Feb 1984 (AM 136, AH 39177); SPAIN, Cáceres, Cuestas de Jaraiz de la Vega, 19 Feb 2011, det. C. Gelpi (AH 39181).

Additional specimens examined.

Geopora cooperi Harkn.: GREECE, Attika: Parnitha, under *Abies cephalonica* Loudon and *Pinus nigra* J.F. Arnold in argillaceous soil, ca 1200 m, 16 Nov 2010, det. V. Kaounas (VK 1783); MOROCCO, Chefchaouen: Rif mountains, under *Abies pinsapo* Boiss. (AH 39089, AH 39106); SPAIN, Guadalajara: Tamajón, under *Q. ilex* and *Juniperus thurifera* L., 24 Nov 1982, det. R. Galán, (AH 9065); unknown origin (AH 9846).

Geopora foliacea (Schaeff.) S. Ahmad: SPAIN, Guadalajara (AH 38936, 38937).

There is one earlier reference for the occurrence of this species in Greece (Diamandis & Perlerou 2008). Molecular data of this species show that it is closely related to the main clade of the genus *Geopora* (Tamm *et al.* 2010), and unrelated to *Hydnocystis* (also see Fig. 21). This confirms the earlier combination made by Burdsall (1968). It should be noticed that the main clade of the genus *Geopora* does not include its type species, *G. cooperi* (Tamm *et al.* 2010), which seems to be more related to the genus *Picoa* (Sbissi *et al.* 2011). This could suggest the resurrection of the genus *Sepultaria*, and the respective transfer of *G. clausa*. Two different clades of *G. clausa* are revealed after molecular inference. One of them (VK2101, VK2039, VK2046 and AH39177) seems to match a sequence in public databases coming from an unidentified ectomycorrhizal fungus from southern France, and is somewhat related to several sequences of *Geopora* cf. *cooperi* from southern Spain. The second one is composed of sample AH39181, and matches the only sequence of *G. clausa* stored in GenBank (JF908766), obtained from an Italian specimen. None of these groups match the other Mediterranean species of *Hydnocystis*, *H. piligera* and *H. beccarii* Mattir. Spore dimensions seem to be over the range reported by Tulasne & Tulasne (1851; 16–19 µm), but still below those of Mattirolò's *H. beccarii* (24–27 µm).



Figs 1–5. Ascomata and basidiomata of hypogeous fungi. 1. Ascomata of *Balsamia vulgaris* (VK 1290). 2. Ascomata of *Geopora clausa* (VK 2029). 3. Ascomata of *Hydnocystis piligera* (VK 664). 4. Basidiomata of *Sclerogaster compactus* (VK 2040). 5. Basidiomata of *Wakefieldia macrospora* (VK 2118)

Table 1. Specimens used for DNA analysis of ITS/28S nLSU

Taxon	Herbarium	Origin	ITS/28S nLSU
<i>Geopora cooperi</i>	VK1783	Attika, Greece	JN812045
<i>Geopora cooperi</i>	AH9065	Madrid, Spain	JN812044
<i>Geopora cooperi</i>	AH9846	Spain	JN812041
<i>Geopora cooperi</i>	AH39089	Chefchaouen, Morocco	JN812042
<i>Geopora cooperi</i>	AH39106	Chefchaouen, Morocco	JN812043
<i>Geopora foliacea</i>	AH38936	Guadalajara, Spain	JN812047
<i>Geopora foliacea</i>	AH39351	Guadalajara, Spain	JN812046
<i>Geopora foliacea</i>	AH38937	Guadalajara, Spain	JN812048
<i>Geopora clausa</i>	AH39181	Cáceres, Spain	JN812053
<i>Geopora clausa</i>	VK2039	Attika, Greece	JN812049
<i>Geopora clausa</i>	VK2046	Attika, Greece	JN812049
<i>Geopora clausa</i>	VK2101	Attika, Greece	JN812051
<i>Geopora clausa</i>	AH39177	Sardinia, Italy	JN812052
<i>Hydnocystis piligera</i>	AH39302	Baleares, Spain	JN048888
<i>Hydnocystis piligera</i>	AH39303	Baleares, Spain	JN048886
<i>Hydnocystis piligera</i>	AH39304	Attika, Greece	JN048889
<i>Hydnocystis piligera</i>	AH39305	Nicosia, Cyprus	JN048887
<i>Hydnocystis piligera</i>	AH39306	Samaria, Israel	JN048890
<i>Hydnocystis piligera</i>	AH39178	Sardinia, Italy	JN812040
<i>Sclerogaster compactus</i>	VK2040	Attika, Greece	JN812054
<i>Wakefieldia macrospora</i>	VK1379	Attika, Greece	JN812039

Hydnocystis piligera Tul., in Tulasne & C. Tulasne, Giorn. Bot. Ital. 2(1): 60 (1845) **Figs 3, 12–14, 21**

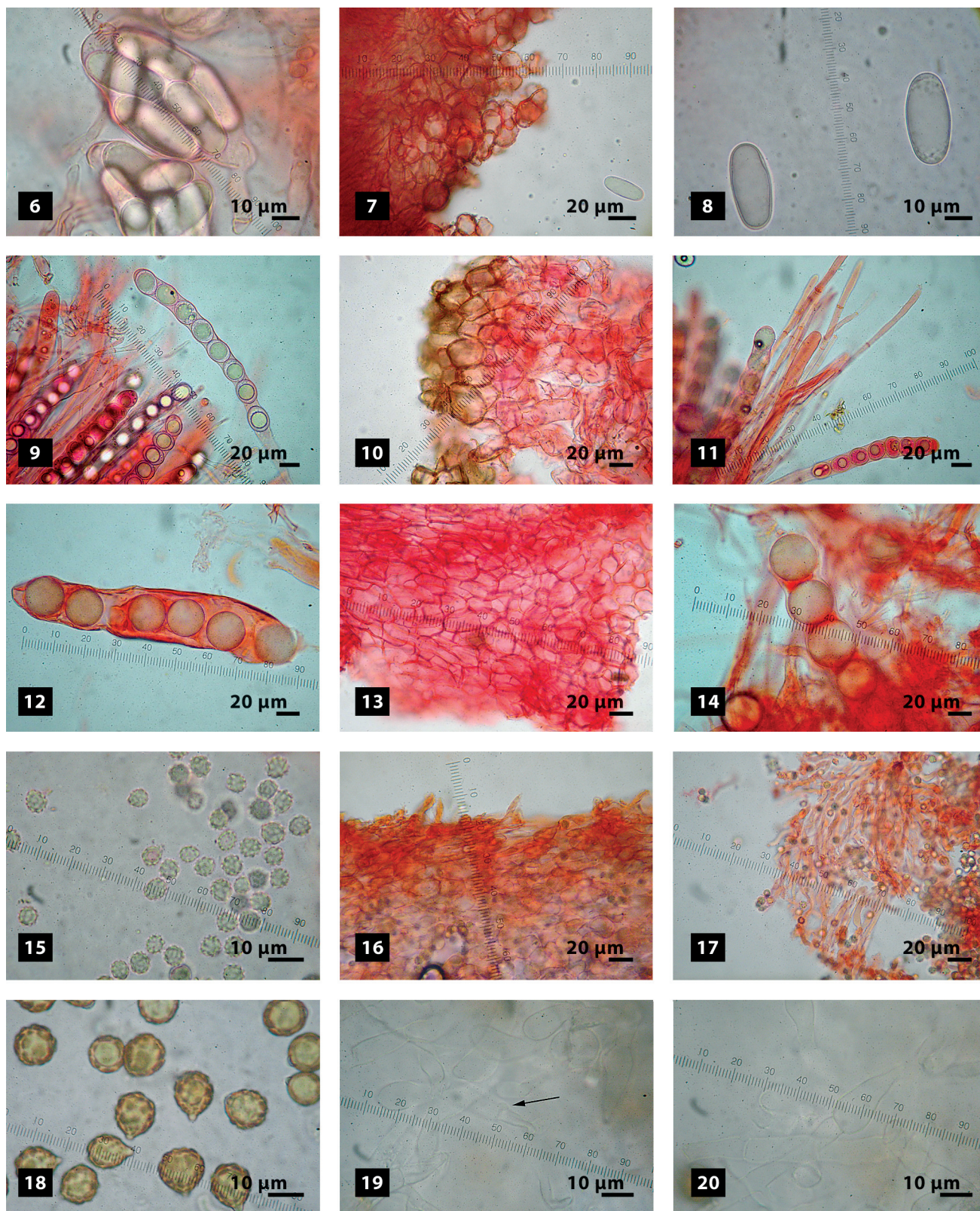
Ascomata 0.5–3.5 cm in diam, hypogeous, semi-hypogeous or sometimes epigeous, subglobose, slightly lobed, pale yellow, yellowish ochraceous to flesh coloured, hairy-pubescent. **Peridium** consisting of outer layer composed of up to 500 µm long wavy hairs, raising from inner pseudoparenchymatous layer of rounded or polygonal elements. **Gleba** thin, cottony-like, lining the chamber; odour fruity. **Asci** cylindrical, 8-spored, up to 300 × 50 µm. **Ascospores** (27–) 30.0±1.4 (–32) µm in diam ($n = 30$), spherical, hyaline, thin-walled, lacking guttules, uniseriate in asci. **Paraphyses** filamentous, septate, considerably longer than asci, up to 5 µm wide at the top.

Habitat – occurs as hypogeous or semi-hypogeous in sandy soils in scrubland in Mediterranean ecosystems, usually associated with species such as *Cupressus*, *Pinus*, *Pistacia*, *Cistus*, etc.; in Greece possibly associate of *Eucalyptus* sp.

Specimens examined. CYPRUS, Agia Paraskevi, under *Olea europaea*, leg. G. Konstantinidis, 14 Nov 2009 (GK 4337, AH 39305). GREECE, Attika: Nea Makri, under *Eucalyptus* sp.

and *Olea europaea* L., ca 50 m, 19 Jan 2009 (VK 664); *idem*, 1 Feb 2010 (VK 1357). ISRAEL, Samaria, Reihan forest, clayish soil under *Pinus* sp., leg. Y. Ur, 19 Feb 2007 (HAI-D-035, AH 39306). ITALY, Oristano: Su Cologone, under *Eucalyptus* sp., det. A. Montecchi, 28 Oct 1984 (AM 134, AH 39178). SPAIN, Islas Baleares, Mallorca, Formentor, Torrent des Estanyol, semihypogeous under *Quercus ilex* with *Chamaerops humilis* L., 8 Dec 2009 (MAR 081209-49, AH 39302); ISLAS BALEARES, Mallorca, Alcudia, Son Serra de Marina, semihypogeous in a moss area under *Juniperus oxycedrus* L., fixed dunes, 6 Dec 2009 (MAR 061209-05, AH 39303).

This is the first finding of this uncommon species in Greece. It is similar to *Geopora clausa*, but is easily distinguished on the account of its spherical (not ellipsoid to ovoid) ascospores. The Greek collections fit very well the descriptions in Burdsall (1968), Montecchi & Sarasini (2000), Gori (2005) and Agnello (2011). 28S nLSU data in Alvarado *et al.* (2011) showed that this species is related to *Stephensia bombycina* (Vittad.) Tul. & C. Tul. and unrelated to *Geopora*. In the present study, ITS data confirmed its status as an independent monospecific genus (Fig. 21).



Figs 6–20. Microscopic features of hypogeous fungi. 6–8. *Balsamia vulgaris* (VK 1290, in Congo red): 6. Asci with ascospores; 7. Peridium; 8. Ascospores; 9–11. *Geopora clausa* (VK 2029, in Congo red): 9. Asci with ascospores; 10. Peridium; 11. Asci and paraphyses; 12–14. *Hydnocystis piligera* (VK 664, in Congo red): 12. Asci with ascospores; 13. Peridium; 14. Ascospores and paraphyses; 15–17. *Sclerogaster compactus* (VK 2040, in Congo red): 15. Basidiospores; 16. Two-layered peridium; 17. Hyphae of the outer layer of the peridium; 18–20. *Wakefieldia macrospora* (VK 2118, in water): 18. Basidiospores; 19. Peridium (clamp-connexion marked by an arrow); 20. Peridial hyphae

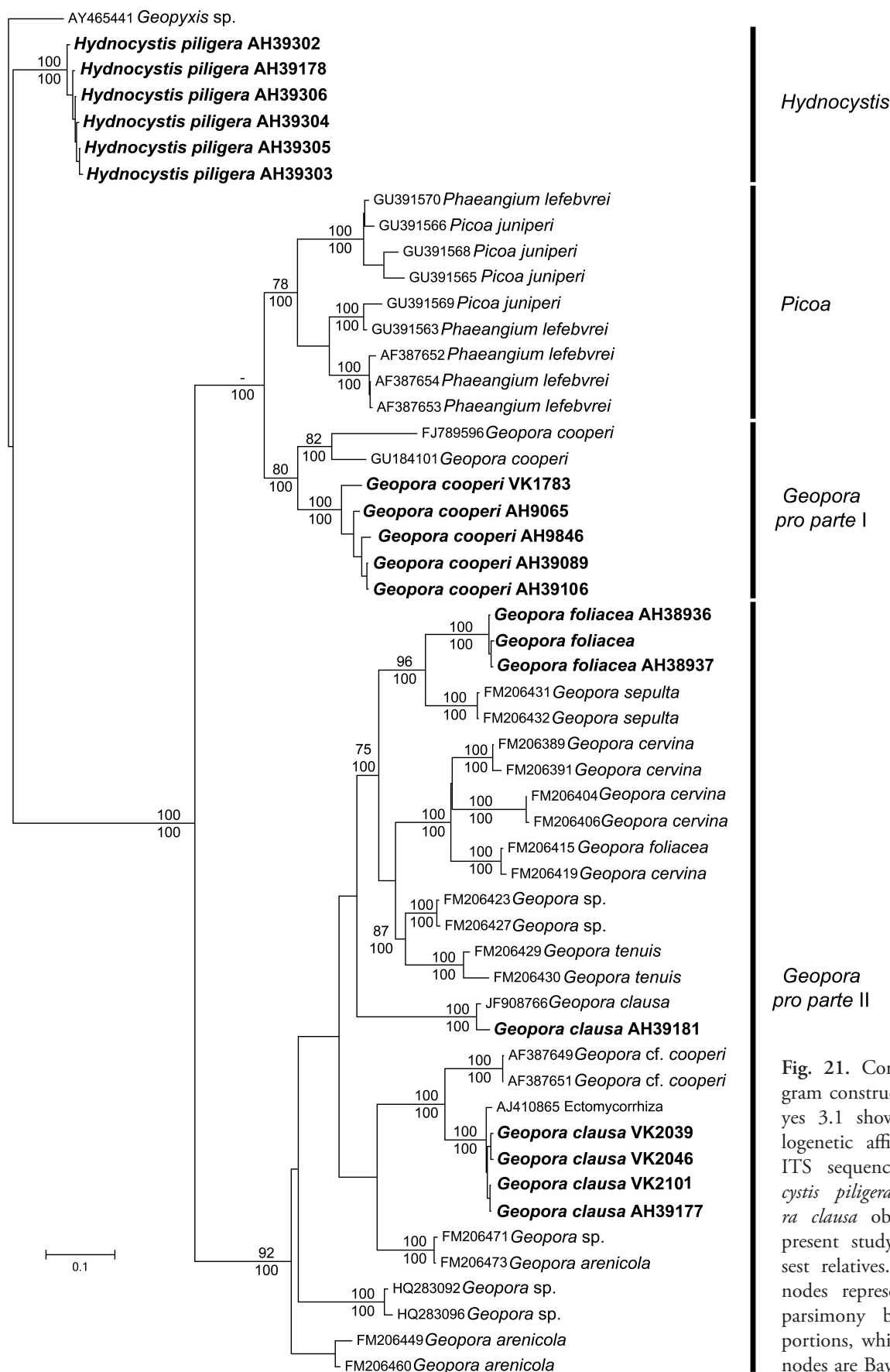


Fig. 21. Consensus phylogenetic tree constructed in Mr.Bayes 3.1 showing the phylogenetic affiliation of the ITS sequences of *Hydnocystis piligera* and *Geopora clausa* obtained in the present study and its closest relatives. Values above nodes represent maximum parsimony bootstrap proportions, while those below nodes are Bayesian posterior probabilities.

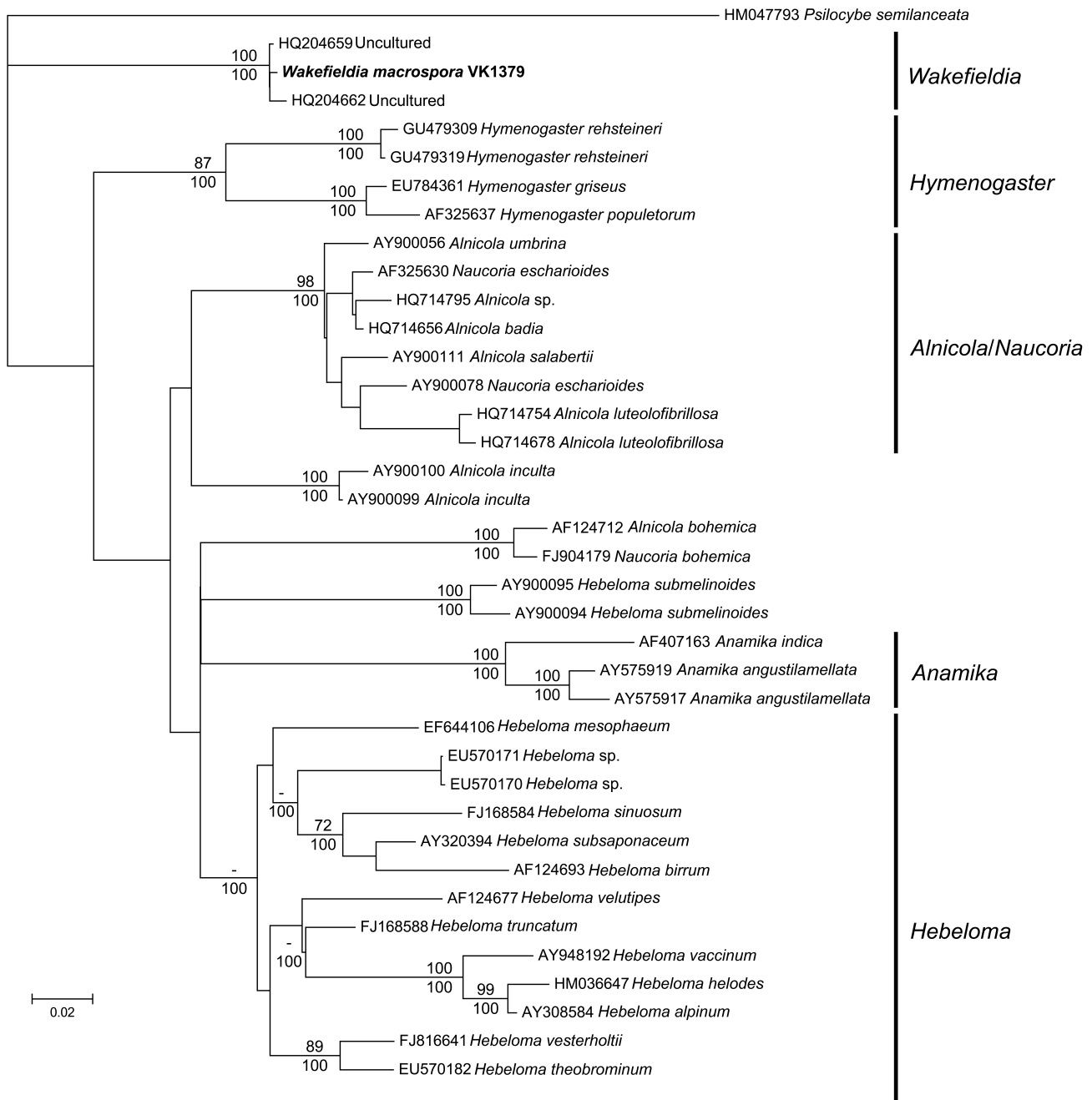


Fig. 22. Consensus phylogram constructed in Mr.Bayes 3.1 showing the phylogenetic affiliation of the ITS sequence of *Wakefieldia macrospora* obtained in the present study and its closest relatives. Values above nodes represent maximum parsimony bootstrap proportions, while those below nodes are Bayesian posterior probabilities.

Sclerogaster compactus (Tul. & C. Tul.) Sacc., Syll. fung. 11: 170 (1895) Figs 4, 15–17

Basidiomata gasterocarpic, 0.5–1 (–2) cm in diam, subglobose, smooth, somewhat elastic, initially whitish or yellowish, later dirty yellow. **Peridium** not separable from the gleba, consisting of two layers, the outer filamentous, composed of intewoven hyphae, the inner pseudoparenchymatous, of nearly spherical elements of 10–20 µm in diam. **Gleba** compact, composed of very small compartments (lens required), initially yellowish white to yellow or orange-yellow

later; columella absent or rudimentary. **Basidia** not seen. **Basidiospores** yellowish or greenish, spherical or sometimes subspherical, (5–) 6.2±0.7 (–7.5) µm ($n = 30$), verrucose, with ca 0.5 µm high cyanophilous warts, and with well seen sterigmatal remnants.

Habitat – occurs underground, often in large numbers, beneath decaying leaves or moss in broadleaf, mixed or coniferous forests, from autumn to spring, although Greek collections are made in the winter and spring.

Specimens examined. GREECE, Attika: Schinias, under *Pinus pinea*, ca 5 m, 21 Apr 2008, det. G. Konstantinidis & V. Kaounas (VK 378); Rafina, under *Pinus halepensis* and *Cistus monspeliensis*, ca 20 m, 7 Jan 2010, (VK 1335); *idem*, 9 May 2011, (VK 2040).

Sclerogaster compactus is somewhat similar to *S. gastrosporioides* Pilát & Svrček, but is easily separated by its distinctly smaller spores and the two-layered structure of the peridium. The Greek collections correspond well to the authoritative descriptions in Dodge & Zeller (1934), Hawker (1954), Pegler *et al.* (1993), Krieglsteiner (2000), Montecchi & Sarasini (2000), and Gori (2005). This is a rarely recorded species cited here for the first time from Greece (Zervakis *et al.* 1998; Diamandis & Perlerou 2008). As it comes out from the available literature it has not been found yet in any of the neighboring countries of the peninsula (see e. g. Jurc *et al.* 2005; Sesli & Denchev 2008; Denchev & Assyov 2010). 28S nLSU molecular results link those samples to other previous records of *S. compactus* from Europe (Hosaka & Castellano 2008) in the *Geastrales* (*Phallomycetidae*).

Wakefieldia macrospora (Hawker) Hawker, Phil. Trans. Roy. Soc. London, Ser. B, 237: 521 (1954) Figs 5, 18–20, 22

Basidiomata gasterocarpic, hypogeous, 0.5–2 cm in diam, lobed, subglobose to irregular, smooth, with small tufts of easily detachable mycelial strands at the base, initially white with yellowish tones, later ochraceous. **Peridium** in fresh state 0.2–0.3 mm wide, not easily separable from the gleba; hyphae with clamp-connexions. **Gleba** at first whitish grey, later greyish rose, grayish brown or brown, with blackish spots when dry, with minute chambers separated by tramal plates, without columella or sterile tissue, in maturity with peculiar potato-like smell. **Basidia** 36–43 × 9–10 µm, cylindrical, two-spored with blunt sterigmata, disintegrating at maturity. **Basidiospores** (12.5–) 14.4±1.1 (–17) µm in diam (*n* = 30), spherical, with a distinct 1–4 µm long hilar appendage, initially pear-shaped, almost smooth and covered by thin disrupting inamyloid perisporium, at maturity subglobose and with ornamentation of low and broad warts.

Habitat – occurs underground, usually in groups, in broadleaf forest (mostly beech and oak) on calcareous soils.

Specimens examined. GREECE: Portaria, Magnesia, under *Quercus frainetto* Ten., ca 750 m, 15 Apr 2008, det. G. Konstantinidis & V. Kaounas (VK 375); Katsimidi, Attica, under *Quercus ilex*, ca 650 m, 10 Jan 2010, (VK 1338); *idem*, 11 Feb 2010, (VK 1379); *idem*, 20 Feb 2010, (VK 1402); *idem*, 30 Mar 2011 (VK 2118).

The Greek specimens of *W. macrospora* agree well with the original description (Hawker 1951, 1954) and the later ones (Pegler & Young 1979; Martin *et al.* 1993; Pegler *et al.* 1993; Montecchi & Sarasini 2000; Gori 2005), although the basidiospores of the Greek specimens seem to be slightly smaller, but nonetheless being in the known range of variability.

Wakefieldia macrospora is the only European species of this small genus previously thought to be closely related to boletes

(Corner & Hawker 1953; Watling 2008). Macroscopically this fungus strongly resembles some species of *Hymenogaster*, but is easily recognized through microscopic examination, which reveals basidiospores characteristically ornamented with prominent conical hilar appendages (Fig. 18). Two poorly known taxa need to be considered in regard to *W. macrospora* – *Sclerogaster porquerollensis* Donnadini & G. Rioussset and *S. rhizopogon* Donnadini & G. Rioussset (Donadini 1979). Both of them have somewhat similarly coloured basidiomata (more or less resembling that of *W. macrospora*), spores similar in shape, size and ornamentation, and filamentous peridium. *Sclerogaster porquerollensis* can be distinguished on account of its generally one-spored basidia, although 2-, 3-, and 4-spored basidia have been also observed by the authors. The characteristic features of the remaining species, *S. rhizopogon*, are considered, by the authors, to be its white to ochraceous peridium and its 2-spored basidia. Both species are regarded as synonyms of *W. macrospora* by Vidal (1997) and were not considered in later works (Pegler *et al.* 1993; Montecchi & Sarasini 2000). Caution should be exercised to separate those two entities during identification, if indeed distinct from *W. macrospora*. On the basis of the present results, *Wakefieldia* should be considered an independent genus within the family *Hymenogastraceae* (*Agaricales*), with a close relationship with the genera *Hebeloma*, *Anamika*, *Hymenogaster*, and *Alnicolal Naucoria* (Fig. 22). The only ITS sequence obtained in this work seems to match another two stored in GenBank coming from environmental samples under *Quercus ilex*-dominated forest ecosystems in the Mediterranean basin.

This is apparently a very rare species so far known from Belgium, Czech Republic, Germany, Italy, Spain, Switzerland, and the United Kingdom (Hawker 1951, 1954; De Vries 1988; Martin *et al.* 1993; Pegler *et al.* 1993; Ludwig & Schnittler 1996; Montecchi & Sarasini 2000; Gori 2005; Riva 2009; Ortega *et al.* 2010). This is the first finding of this noteworthy species in Greece and apparently also in the Balkan Peninsula, as it comes out from the literature available (see also Diamandis & Perlerou 2008; Sesli & Denchev 2008; Denchev & Assyov 2010). Watling (2008) proposed that this fungus could be mycorrhizal with beech, as it is suggested by the specimens coming from the United Kingdom (Hawker 1951) where it was first collected and described. However, the four Greek collections suggest also a probable association with oaks, in accordance with Martin *et al.* (1993), Pegler *et al.* (1993), and Riva (2005) who proposed a wider range of hosts.

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