TAXONOMIC REVISION OF THE *APHAENOGASTER SUBTERRANEA* SPECIES GROUP (HYMENOPTERA: FORMICIDAE)

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Abstract.— Based on the recent developments by studies on the *Aphaenogaster subterranea* group and new molecular data, we provide a revision that summarizes the knowledge on the diversity and distribution of its members. We describe two species new to science: *A. asterioni* Borowiec, Menchetti, Salata, Vila & Zięcina **sp. nov.** and *A. tristis* Borowiec, Menchetti, Salata, Vila & Zięcina **sp. nov.** *Aphaenogaster lesbica* Forel, 1913 **syn. nov.** is proposed as a junior synonym of *A. subterranea* (Latreille, 1798); *A. kurdica* Ruzsky, 1905 is excluded from the *subterranea* species group, and the following species are redescribed: *A. epirotes* (Emery, 1895), *A. holtzi* (Emery, 1898), and *A. subcostata* Viehmeyer, 1922. A key to workers of all species belonging to the *subterranea* species group is proposed. Lectotypes are designated for: *A. ichnusa* Santschi, 1925, *A. holtzi* (Emery, 1898), and *A. subcostata* Viehmeyer, 1922.

Key words.— Myrmicinae, new species, taxonomy, Balkans

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Introduction

Aphaenogaster Mayr, 1853 is a large and diverse ant genus comprising 204 extant species, 12 extant subspecies, and 12 fossil species (Bolton 2023). The distribution range of its species is primarily enclosed within the Holarctic subtropical regions and the subequatorial and equatorial zones constituting the Indomalayan and Australasian realms. Conversely, fewer species are present in the northern Neotropics (Central America and the Caribbean), the Nearctic realm, and the temperate regions of Australasia (Schifani *et al*. 2022).

The most recent phylogenomic evidence strongly indicates that the current definition of the genus is polyphyletic. The species in Asia, Australia, Madagascar, and Central America subequatorial and equatorial regions are proposed to be reassigned to a distinct genus, tentatively named the "*Deromyrma* clade" (the name pays homage to the former subgenus *Deromyrma* Forel, 1913, now recognized as a junior synonym of *Aphaenogaster*). Thus, the 'true' *Aphaenogaster* genus, exclusive to the Holarctic region, is believed to have originated in the Palearctic and is a sister genus to the seed-harvesting genus *Messor* Forel, 1890 (Branstetter *et al*. 2022).

The first infrageneric division of members of *Aphaenogaster* was proposed by Emery (1915), who established four subgenera based on morphological traits. However, the subsequent authors abandoned the subgeneric division (e.g., Bolton 1982, 1995). Later, Schulz (1994) proposed a preliminary division of some West-Palearctic taxa that was afterward used as a base for further species-group divisions and reclassifications (e.g., Boer 2013, Salata and Borowiec 2018, Alicata and Schifani 2019, Salata *et al*. 2021, Schifani *et al*. 2021). Finally, Schifani *et al*. (2022) proved that all formerly recognized subgenera and species groups were non-monophyletic and proposed a new classification based on phylogeny and morphological characters.

The *Aphaenogaster subterranea* species group was originally proposed by Schultz (1994) and included twelve species. Later, the group has undergone numerous changes. Salata and Borowiec (2018) and Bračko *et al*. (2019) transferred or described taxa new for the group, while Alicata and Schifani (2019) distinguished a new species group comprising taxa formerly assigned to the *A. subterranea* species group. The final reorganization of the *subterranea* species group was proposed by Schifani *et al*. (2022), who listed the following morphological characters as defining for the investigated group: medium-sized species, large parts of the body shiny but always at least the front part of the head dull and covered with shallow wrinkles; the posterior edge of the head overruns the antennae; median funiculus segments about as long as wide (but not more than 1/2 times as long); yellowish-red to dark brown body; head rectangular rounded; metanotal groove present, deep and narrow; pronotum and mesonotum form regular convexity, mesonotum not raised above the surface of pronotum; propodeal spines short, not longer than half length of the first segment of antennal funiculus; mesosoma short. The authors listed the following eight species as members of the *subterranea* group: *A. ichnusa* Santschi, 1925, *A. maculifrons* Kiran & Aktaç, 2008, *A. kurdica* Ruzsky, 1905, *A. subterranea* (Latreille, 1798), *A. epirotes* (Emery, 1895), *A. subcostata* Viehmeyer, 1922, *A. holtzi* (Emery, 1898), and *A. lesbica* Forel, 1913 and suggested that this group is distributed across Southern Europe, Anatolia, and Transcaucasia.

Some species of the *subterranea* group were recently redescribed and their distribution data was updated. These studies were focused on the Western-Mediterranean taxa and included redescriptions of *A. subterranea* and *A. ichnusa* (Galkowski *et al*. 2019) and analyses of the morphology of their sexual castes and distribution ranges (Schifani *et al*. 2023). On the other hand, the diversity of the *subterranea* species group from Eastern-Mediterranean is poorly studied, despite some sources suggesting that the Balkans may harbor some undescribed species belonging to the group (Schifani *et al*. 2022).

In this work, we summarize the knowledge of the diversity of the *subterranea* species group by providing more insight into its species richness in the Eastern Mediterranean. We describe two species new to science from Greece: *A. asterioni* Borowiec, Menchetti, Salata, Vila & Zięcina sp. nov. and *A. tristis* Borowiec, Menchetti, Salata, Vila & Zięcina sp. nov. Furthermore, *Aphaenogaster lesbica* Forel, 1913 is proposed as a junior synonym of *A. subterranea* (Latreille, 1798), and *A. kurdica* Ruzsky, 1905 is excluded from the species group. We also redescribe *A. epirotes* (Emery, 1895), *A. subcostata* Viehmeyer, 1922, and *A. holtzi* (Emery, 1898) and introduce a key to all species belonging to the *subterranea* species group.

Material and methods

Our recognition of species follows the biological species concept and species boundaries are based on comparative morphology and known geographic distributions of investigated taxa. Where sympatric populations exhibit consistently different phenotypes, they are considered different species. Molecular analyses based on mitochondrial DNA sequences from cytochrome oxidase I (COI) gene fragments were carried out to test the monophyly and assess divergence of putative species previously delimited by morphological analyses. The species group division follows Schifani *et al*. (2022). The surface sculpturing glossary follows Harris (1979).

Photographs were taken using a Nikon SMZ 1500 stereomicroscope, Nikon D5200 camera, and Helicon Focus software. All given label data of type specimens are in the original spelling, presented in square brackets; a vertical bar (|) separates data on different rows, and double vertical bars (||) separate labels. Images of type specimens are available online on AntWeb (www.AntWeb.org) and are accessible using the unique identifying specimen codes provided in the description sections.

The pilosity inclination degree follows that used by Wilson (1955). Appressed (0–5°) hairs run parallel or nearly parallel to the body surface, decumbent hairs stand 5–20°, subdecumbent 20–60°, suberect 60–80°, and erect 80–90° from the surface (as per Fig. 3 Wilson 1955). The biology sections, if not stated otherwise, provide data collected during fieldwork.

Examined specimens are housed in the following collections:

BFUS – Biological Faculty, University of Sofia, Bulgaria;
GBC – Gregor Bračko collection;
MHNG – Musée d'Histoire Naturelle Genève, Geneva, Switzerland;
MMC – Mattia Menchetti collection;
MNHW – Museum of Natural History, University of Wroclaw, Wroclaw, Poland;
NHMB – Naturhistorisches Museum, Basel, Switzerland;
NHMC – Natural History Museum of Crete, Iraklion, Greece;
ZMHB – Museum für Naturkunde an der Humboldt-Universität zu Berlin, Berlin, Germany.

Molecular analysis

A total of 95 specimens were selected for genetic analysis. Different amounts of tissue were used for DNA extractions based on the preservation of the specimens (from a leg to the entire specimen). The genetic data (DNA-barcoding, mitochondrial gene cytochrome c oxidase I, COI, 658 bp) was generated at two institutes: at the Centre for Biodiversity Genomics, University of Guelph, Canada, using the primers LepF1 and LepR1 (deWaard *et al*. 2008) and at the Institut de Biologia Evolutiva (IBE), Barcelona, Spain, following the protocol by Schär *et al*. (2020) with the primers LCO1490/HC02198 (Folmer *et al*. 1994). At IBE, PCR products were visualized by gel electrophoresis and sent to Macrogen Europe for Sanger sequencing. Raw sequences were edited and aligned in Geneious Prime 2020.2.4 (Kearse *et al*. 2012). Chromatograms were inspected for the presence of double peaks and sequences for the presence of stop codons.

We added 52 sequences retrieved from GenBank for the species: *A. epirotes,* three sequences from Schifani *et al*. (2022) (accession numbers OM896861-OM896863); *A. holtzi*, two sequences from Schifani *et al*. (2022) (a.n. OM896864, OM896865); *A. ichnusa*, two sequences from Gómez *et al*. (2018) (a.n. MF926338, MF926343), 16 sequences from Galkowski *et al*. (2019) (a.n. MH138330, MH138333-MH138335, MH138337, MH138339, MH138340, MH138343, MH138345, MH138348, MH630454, MH630457-MH630459, MH630462, MH630463), four sequences from Schär *et al*. (2020) (a.n. MT606277-MT606280), two sequences from Schifani *et al*. (2022) (a.n. OM896858, OM896859); *A. maculifrons*, one sequence from Schifani *et al*. (2022) (OM896857); *A. subterranea*, one sequence from Gómez *et al*. (2018) (a.n. MF926350), 17 sequences from Galkowski *et al*. (2019) (a.n. MH138331, MH138332, MH138336, MH138338, MH138341, MH138342, MH138344, MH138346, MH138347, MH138349, MH138350, MH630453, MH630455, MH630456, MH630460, MH630461, MH630464), four sequences from Schifani *et al*. (2022) (a.n. OM896853-OM896856). All the newly generated sequences were submitted to GenBank (accession numbers PP476387-PP476481, Table 1).

A maximum likelihood tree was produced using IQ-TREE 2 (Minh *et al*. 2020) and ModelFinder (Kalyaanamoorthy *et al*. 2017) with the full dataset of 149 COI sequences, including two species used as outgroups (*A. charesi* Salata & Borowiec, 2016, a.n. OM896834, and *A. peloponnesiaca* Salata *et al*., 2021, a.n. OM896837, both from Schifani *et al*. (2022)). Maps showing the genetic structure, Principal Component Analyses (PCoA) and haplotype networks were produced for each species for which more than two sequences were available (i.e. *A. epirotes*, *A. ichnusa*, *A. subterranea* and *A. tristis* sp. nov.) using the script available from Dapporto *et al*. (2022). One sample of *A. subterranea* (a.n. MMH630461) known to be introgressed from *A. ichnusa* (Galkowski *et al*. 2019) was removed from these analyses to facilitate the interpretation of the results.

Morphometric character recording

In the present study, 17 continuous morphometric traits were recorded in 158 worker individuals from 63 collecting sites in the Mediterranean. Measurements were taken with a Nikon SMZ18 stereomicroscope equipped with an ocular micrometer at a magnification of ×25 to ×100 and The Imaging Source DFK 33UX250 camera with NIS Elements D version: 5.1 program to record measures. Body size dimensions are expressed in mm. All measurements and indices are presented as arithmetic means with standard deviation and ranges are shown as minimum and maximum values in parentheses. All measurements were made by DZ. Measurements and indexes (mainly after Csősz & Fisher 2016).

CL: Maximum length of the head capsule in median line. The head must be carefully tilted to the position with the true maximum; excavations of hind vertex and / or clypeus, if any, reduce CL.

CW: Maximum width of the head capsule in full-face view without the compound eyes. Measured posterior of the eyes.

FRS: Frontal carina distance. Distance of the frontal carinae immediately caudal of the posterior intersection points between the frontal carinae and the torular lamellae. If these dorsal lamellae do not laterally surpass the frontal carinae, the deepest point of scape corner pits may be taken as a reference line. These pits take up the inner corner of the scape base when the scape is fully directed caudally and produce a dark triangular shadow in the lateral frontal lobes immediately posterior to the dorsal lamellae of the scape joint capsule.

EL: Maximum diameter of the compound eye.

MD: Malar distance. Minimum distance from the anterior margin of the compound eye to where the mandible articulates with the head capsule.

SL: Maximum straight line scape length excluding the articular condyle.

ML: Mesosoma length from caudalmost point of the propodeal lobe to the transition point between anterior pronotal slope and anterior propodeal shield (preferentially measured in lateral view; if the transition point is not well defined, use dorsal view and take the centre of the dark-shaded borderline between pronotal slope and pronotal shield as an anterior reference point).

SPST: Distance between the centre of propodeal stigma and spine tip. The stigma centre refers to the midpoint defined by the outer cuticular ring but not to the centre of the real stigma opening that may be positioned eccentrically.

MPST: Maximum distance from the centre of the propodeal spiracle to the posteroventral corner of the ventrolateral margin of the metapleuron.

PEH: Maximum petiole height. The chord of the ventral petiolar profile at node level is the reference line perpendicular to which the maximum height of the petiole is measured.

PEL: Petiole length. Horizontal distance between the petiolar spiracle and the most caudo-dorsal point of the petiole.

PPH: Maximum height of the postpetiole in lateral view measured perpendicularly to a line defined by the linear section of the segment border between dorsal and ventral petiolar sclerite.

PPL: Postpetiole length. The horizontal distance from the tip of the frontolateral node corner to the caudalmost point of the petiole.

HTL: Hind tibia length. With full width and length of hind tibia positioned in visual plane, measured from the most distal point near the extensor profile to the proximal constriction point of flexor profile.

MW: Maximum mesosoma width. This is the pronotal width in workers.

PEW: Maximum width of petiole.

PPW: Maximum width of postpetiole.

CS: Cephalic size. The arithmetic mean of CL and CW.

Abbreviations:

w – worker.

Results and discussion

Synopsis of the members of the *Aphaenogaster subterranea* species-group

Aphaenogaster asterioni Borowiec, Menchetti, Salata, Vila & Zięcina **sp. nov.**
Aphaenogaster epirotes (Emery, 1895).
Aphaenogaster holtzi (Emery, 1898).
Aphaenogaster ichnusa Santschi, 1925.
Aphaenogaster maculifrons Kiran & Aktaç, 2008.
Aphaenogaster subterranea (Latreille, 1798).
=*Aphaenogaster lesbica* Forel, 1913 **syn. nov.**
Aphaenogaster subcostata Viehmeyer, 1922.
Aphaenogaster tristis Borowiec, Menchetti, Salata, Vila & Zięcina **sp. nov.**

Comment. The enigmatic taxon *Aphaenogaster kurdica* Ruzsky, 1905 was described by Ruzsky from Armenia as a subspecies of *A. subterranea*. Its description and author's remarks suggested that *A. kurdica* morphologically was the most similar to *A. holtzi*. However, a few years after the description, Emery (1908) considered *A. kurdica* as a subspecies of *A. smythiesii*. Based on the redescription provided in Emery's work, *A. kurdica* has a mesonotum distinctly surmounting pronotum, and thus its morphology does not match the criteria defining taxa currently considered as the *subterranea* species group. Thus, based on the gathered evidence, we decided to exclude this species from the *Aphaenogaster subterranea* group sensu Schifani *et al*. (2022). Also, in our opinion, the photographs available on AntWeb.org (CFH000010, photo by Donat Agosti) represent a specimen of *A. subterranea*, which has a confirmed presence in this region. The taxonomic status and species group affiliation of *A. kurdica* remain unclear and will be resolved once the type specimens are available for investigation.

Schifani *et al*. (2022) listed two other taxa that might belong to the *subterranea* species group: *A. burri* (Donisthorpe, 1950) and *A. depressa* Bolton, 1995. *Aphaenogaster burri* is known only from a sexual form and we could not verify its species group affiliation. However, our study of the photographs of the type specimen of *A. depressa* (AntWeb.org, CASENT0900460) revealed that the species does not belong to the investigated species group.

Key to species of the *Aphaenogaster subterranea* species-group

(workers only)

1. Vertex and sides posterolateral from eyes smooth or imbricate (Figs 2, 4, 15, 17, 19, 21, 32, 33, 35, 37, 39) **2**
–. Vertex and sides posterolateral from eyes distinctly sculptured, sometimes the sculpture is weaker than the rest of the head but never smooth or imbricate (Figs 6, 8, 9, 12, 23, 25, 27, 30, 41, 43, 44, 47, 49) . . . **5**
2. Head and mesosoma predominantly smooth and shiny (only lateral frons with very few fine and interrupted costulae), occipital margin of the head with numerous long and erect setae (Figs 14–17). Body uniformly yellow. Türkiye and Iran . . . . . ***A. holtzi***
–. At least central frons and most often also lateral sides of pronotum with visible and dense sculpture, occipital margin of head with sparser, decumbent to suberect setae (Figs 18–21, 31–39). Body often partly to mostly brown **3**
3. Head, in frontal view, subtrapezoidal; lateral frons with thick and sparse costulae with smooth to microrugulae interspaces (Figs 1–4). Cretan endemic . . . . . ***A. asterioni***
–. Head, in frontal view, suboval; lateral frons with thick to thin and dense rugulae. Europe, Asia Minor and Caucasian countries **4**
4. Pronotum almost entirely smooth and most often lacking longitudinal costulae on its lateral sides; propodeal spines small, most often reduced to a denticle (CS/SPST: 6.39 ± 0.43) (Figs 18, 19). Only western Europe . . . . . ***A. ichnusa***
–. Pronotum with more developed sculpture (dorsal surface smooth to indistinctly imbricate and lateral sides with dense and thick to thin longitudinal costulae); propodeal spines more developed, most often narrower and longer (CS/SPST: 5.41 ± 0.45) (Figs 31, 32, 36, 37). Widespread in Europe, Asia Minor and Caucasian countries . . . . . ***A. subterranea***
5. Head, in frontal view, subrectangular; at least frons with dense and thick costulae with smooth to rugulose interspaces (Figs 24, 25, 42, 43, 48, 49) **6**
–. Head, in frontal view, suboval; whole head with thick and sparse rugocostae (Figs 8, 9, 29, 30) **7**
6. Sides of pronotum in dorsal view regularly rounded, also in anterolateral corners. Frontovertex with well marked dark spot. Frons with dense and thick costulae with rugulose interspaces; vertex and sides posterolateral from eyes with slightly reduced sculpture, indistinctly rugulose and shiny (Figs 22–25). Western Türkiye . . . . . ***A. maculifrons***
–. Sides of pronotum in dorsal view not regularly rounded, with well marked anterolateral corners armed with setose tubercles. Frons distinctly rugose with additional interrupted and dense costulae; vertex and sides posterolateral from eyes equally sculptured and only occasionally with weaker, but still distinct, sculpture (Figs 40–49). West, Central and South Greece . . . . . ***A. tristis***
7. First segment of funiculus short, approximately two times as long as wide, not flattened laterally, gradually widened from base to apex. Body reddish brown to black, mesosoma not or only slightly paler than head; head with thick and sparse rugocostae with rugulose interspaces; pronotum with thick and sparse rugae to rugocostae with smooth and shiny interspaces (sometimes lateral sides of pronotum with additional longitudinal costae) (Figs 5–11). Balkan Peninsula, Ionian Islands, Cyclades and northern Aegean region south to Lesbos . . . . ***A. epirotes***
–. First segment of funiculus elongate, approximately 3.5 times as long as wide and strongly flattened laterally. Body yellowish to bright brown, mesosoma always paler coloured than head; head with thick and sparse rugocostae with smooth to indistinctly imbricate interspaces; pronotum with thin and sparse rugae to rugocostae, interspaces smooth and shiny (Figs 26–30). Dodecanese, southern Aegean Islands north to Samos and western Türkiye . . . . . ***A. subcostata***

Species accounts

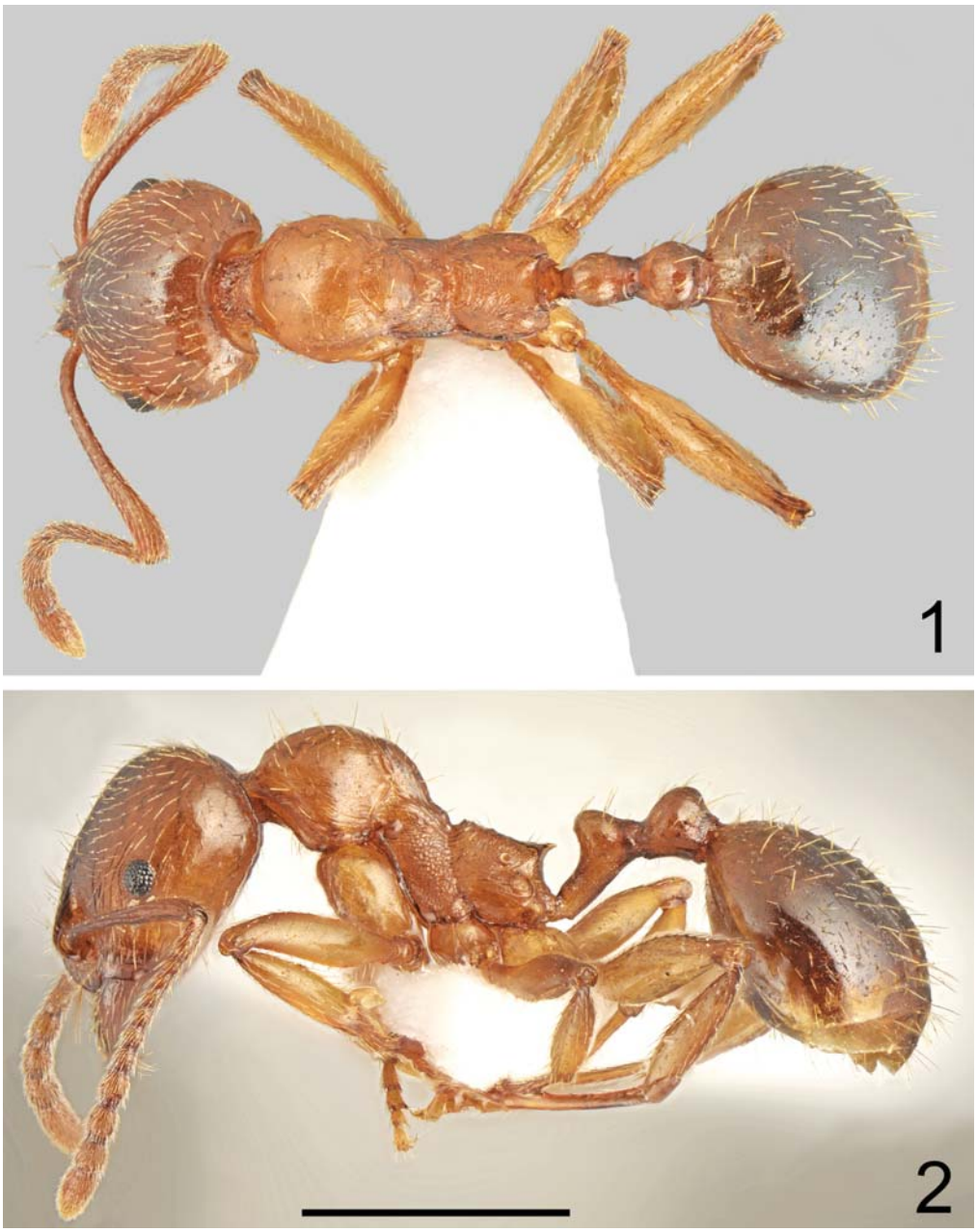
Aphaenogaster asterioni Borowiec, Menchetti, Salata, Vila & Zięcina sp. nov.
(Figs 1–4)

Type material. Holotype (w.): Collection L. Borowiec | Formicidae | LBC-GR01422 || GREECE, Crete, Rethymno | Orthes Gorge, 318 m | 35,3336 N / 24,6848 E | 28 IV 2014. S. Salata (MNHW). Paratypes (35w.): same colony, the same data as the holotype (MNHW, NHMC, MHNG).

Other material. See Table 2.

Etymology. Named after Asterion, the birth name of a mythological creature later known as Minotaur.

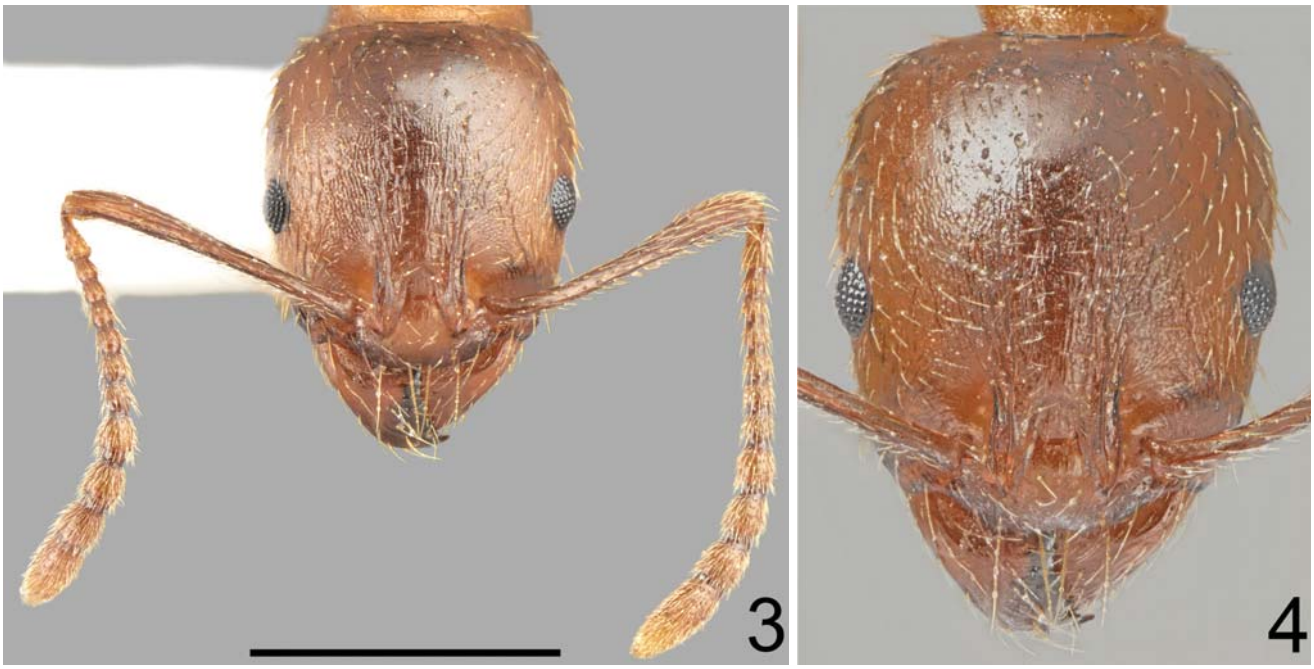
Comparative diagnosis. *Aphaenogaster asterioni* belongs to the complex of species with partly smooth and shiny head. The complex comprises additionally *A. subterranea*, *A. ichnusa*, and *A. holtzi*. *Aphaenogaster asterioni* differs from all the remaining three species in subtrapezoid head shape. Additionally, the '*lesbica*' morph of *A. subterranea* is darker (uniformly brown to dark brown) while *A. asterioni* has yellow to rusty yellow body with sometimes slightly obscure spots on the head and the sides of the pronotum are paler coloured than mesosoma. The typical morph of *A. subterranea* differs in longer and less obliquely mesopleuron than in *A. asterioni*; thus, the mesosoma in lateral view looks less plump and less humpier. *Aphaenogaster asterioni* differs



Figures 1, 2. *Aphaenogaster asterioni* sp. nov., worker: (1) dorsal, (2) lateral (scale bar = 1 mm, photographed by L. Borowiec).

additionally from both morphs in weaker and sparser sculpture on lateral frons and more developed humeral tubercles Also, both species are separated geographically, *A. asterioni* is endemic to Crete while both morphs of *A. subterranea* are widespread in the Balkans and Europe but not recorded from Crete. *Aphaenogaster ichnusa* differs in stronger and denser sculpture on lateral frons and less developed humeral tubercles. Both species are separated geographically, *A. ichnusa* is known only from western Europe while *A. asterioni* is endemic to Crete. *Aphaenogaster holtzi* well differs in mostly uniform yellow body, head and mesosoma predominantly smooth and shiny (only lateral frons with very few fine and interrupted costulae), and in occipital margin of the head with numerous long and erect setae.

Description. Worker. Measurements (Table 3). **Colouration.** Head, mesosoma, petiole, and postpetiole yellowish brown to brown, sometimes mesosoma brighter than head; frons darker brown; gaster dark



Figures 3, 4. *Aphaenogaster asterioni* sp. nov., worker: (3) head and antennae, (4) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

brown (Figs 1–4). **Head.** Subtrapezoidal; lateral sides widening posteriorly, posterior margin straight (Fig. 3). Anterior margin of clypeus distinctly convex, medial notch present. Eyes small and suboval. Antennal scape short, in lateral view slightly curved, gradually widening posteriorly, funiculus long, club indistinct and 4-segmented (Fig. 3). Scape with short and sparse costae, shiny, covered with thin, dense, decumbent to suberect setae. Mandibles rounded with thick and sparse striae, shiny. Clypeus shiny and smooth. Frontal carinae short, slightly extending beyond frontal lobes. Antennal fossa deep and with sparse and indistinct rugocostulae. Frontal lobes narrow, rugulose (Fig. 4). Medial frons with dense and thin rugocostulae; frons laterally and genae with thicker but sparser short and interrupted costulae and smooth to indistinctly microrugulae interspaces; vertex and sides posterolateral from eyes smooth or imbricate, shiny. Whole head with subdecumbent to erect, pale, short and thick setae (Figs 3–4). **Mesosoma.** Humeral tubercle poorly developed; promesonotum well above level of propodeum; metanotal groove present. Propodeal spines present, short and triangular (Fig. 2). Dorsal promesonotum predominantly smooth or imbricate, sometimes with indistinct rugulae; lateral sides of pronotum imbricate and sometimes with additional indistinct and dense costulae; propodeum and lateral mesonotum distinctly rugocostate. Entire mesosoma with erect, pale, moderately long and thick setae (Figs 1–2). **Petiole.** Elongate with long peduncle, node rounded, whole surface smooth and shiny. Dorsal surface with sparse, long, erect setae (Figs 1–2). **Postpetiole.** In lateral view rounded, smooth and shiny. Dorsal surface with sparse, long, erect setae (Figs 1–2). **Gaster.** Smooth and shiny, with erect, thin, pale setae (Figs 1–2).

Biology. The several nests were located under flat stones placed very close to the watercourse banks overgrown by deciduous trees and blackberry bushes. Foraging workers were collected in the leaf litter, on tree trunks close to the soil and on the wet wall of a water reservoir that served as a watering station for goats.

Distribution. Greece, Cretan endemic.

Aphaenogaster epirotes (Emery, 1895) (Figs 5–13)

Stenamma (*Aphaenogaster*) *epirotes* Emery, 1895: 72 (w.). Albania (Avlona = recent Vlorë).

Other material. Table 2.

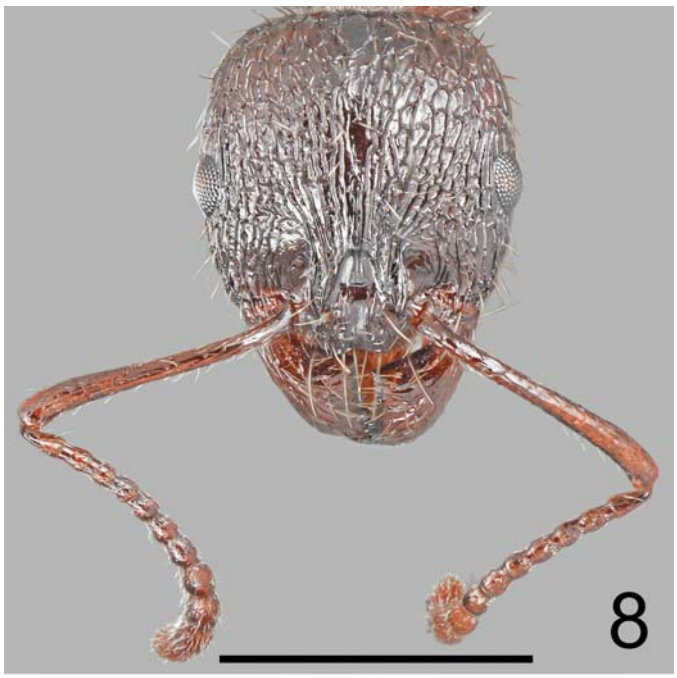
Comparative diagnosis. *Aphaenogaster epirotes* and *A. subcostata* are the only species in the group with whole head with thick and sparse rugocostae. *Aphaenogaster subcostata* differs in first segment of funiculus elongate, 3.5–3.6 × as long as wide and strongly flattened laterally, and in yellowish to bright brown body with mesosoma always paler coloured than head. Both species are separated geographically, *A. epirotes* is common in the Balkans, Ionian Islands,

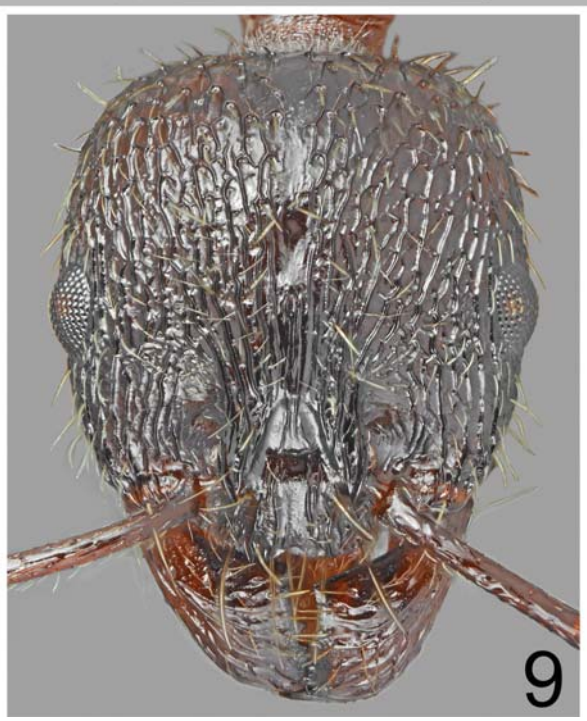
Figures 5–7. *Aphaenogaster epirotes* (Emery), worker of northern populations: (5) dorsal, (6) lateral, (7) basal segments of antennal funicle (scale bar = 1 mm, photographed by L. Borowiec).

Cyclades and northern Aegean Islands south to Lesbos, while *A. subcostata* is rare species known only from Dodecanese, southern Aegean Islands north to Samos and from western Türkiye.

Redescription. Worker. Measurements (See Table 3). **Colouration.** Whole body uniformly coloured from reddish brown to black with legs, antennae and mandibles always slightly brighter (Figs 5–11). **Head.** Suboval; lateral sides rounded, posterior margin straight (Figs 8, 12). Anterior margin of clypeus distinctly convex, medial notch present. Eyes moderate and suboval. Antennal scape short, in lateral view slightly curved, gradually widening posteriorly, funiculus long, club indistinct and 4-segmented (Figs 8, 12). Scape with short and dense costae, shiny, covered with thin, dense, decumbent to suberect setae. Mandibles

rounded with thick and sparse striae, shiny. Clypeus predominantly smooth with sparse and short costulae. Frontal carinae short, slightly extending beyond frontal lobes. Antennal fossa deep, with thick and sparse rugocostae and smooth interspaces. Frontal lobes narrow, smooth (Figs 8, 12). Whole surface of head with thick and sparse rugocostae with rugulose interspaces; central frons with smooth interspaces; sometimes vertex with slightly weaker sculpture. Whole head with subdecumbent to erect, pale, short and thick setae (Figs 9–13). **Mesosoma.** Humeral tubercle weakly developed; promesonotum well above level of



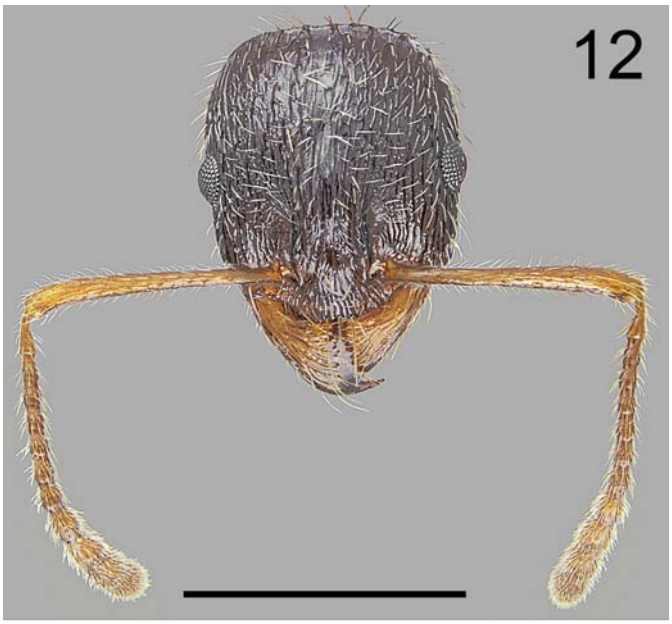


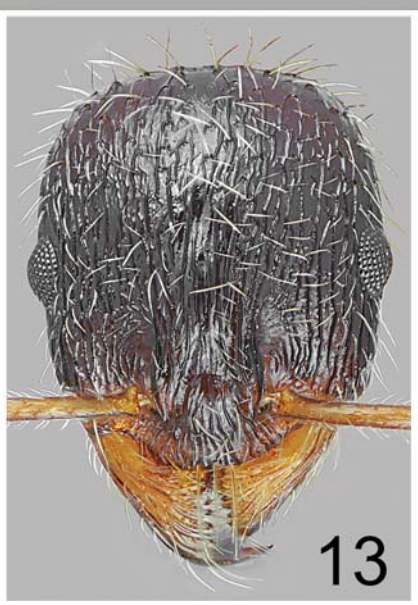
Figures 8, 9. *Aphaenogaster epirotes* (Emery), worker of northern populations: (8) head and antennae, (9) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

Figures 10, 11. *Aphaenogaster epirotes* (Emery), worker of southern populations: (10) dorsal, (11) lateral (scale bar = 1 mm, photographed by L. Borowiec).

propodeum; metanotal groove present. Propodeal spines present, short and triangular (Figs 6, 11). Whole mesosoma with thick and sparse rugae to rugocostae, interspaces smooth and shiny; pronotum always with sparser and weaker sculpture and sometimes with additional longitudinal costae on lateral sides. Entire mesosoma with erect, pale, moderately long and thick setae (Figs 5, 6, 10, 11). **Petiole.** Elongate with long peduncle, node rounded, whole surface indistinctly rugose to partially smooth; shiny. Dorsal surface with sparse, long, erect setae (Figs 5, 6, 10, 11). **Postpetiole.** In lateral view rounded, indistinctly rugose to partially smooth; shiny. Dorsal surface with sparse, long, erect setae (Figs 5, 6, 10, 11). **Gaster.** Smooth and shiny, with erect, thin, pale setae (Figs 5, 6, 10, 11).

Biology. *Aphaenogaster epirotes* prefers shadow habitats. Most records are from deciduous forests, especially from shaded valleys close to streams or from oak forests. Only a few records are from pine forests. Noted also from old olive plantations, mountain pastures, alpine zones with limestone rocks, parks with deciduous trees, shrubs along roadsides, and burned forests, occasionally in shrubs inside cypress





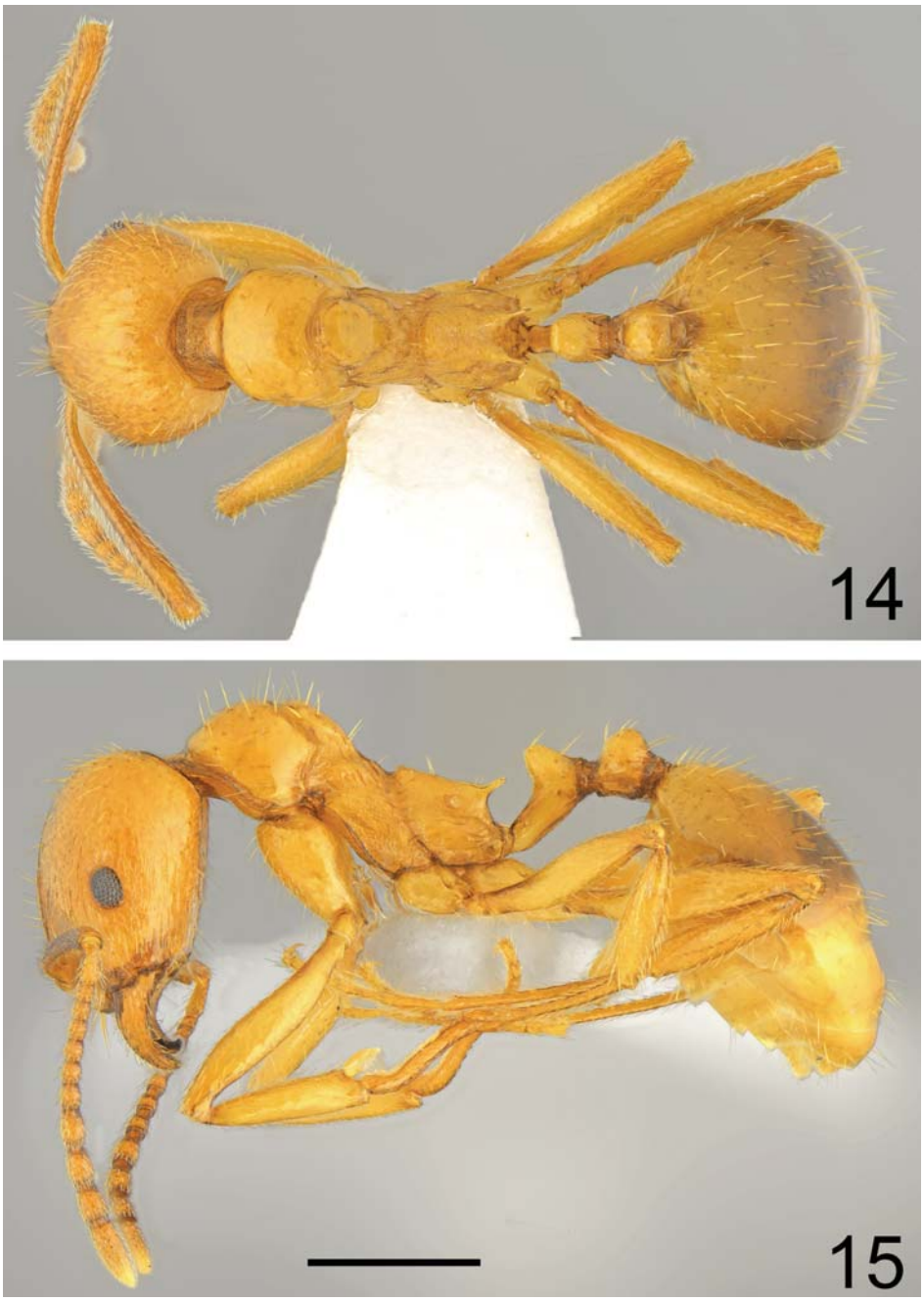
Figures 12, 13. *Aphaenogaster epirotes* (Emery), worker of southern populations: (12) head and antennae, (13) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

forest and xerothermophile oak forest, xerothermous karst grasslands. Workers are active outside their nests, mainly on cloudy days and in the evenings, probably also at night. The species was observed on large stones, directly on the soil, or penetrating large herbs in shady forests. Nests under stones or simply in the soil, colonies are small to moderate, and the greatest number of workers observed in the colonies did not exceed 60 individuals. Lowland and highland species, most nests were located in areas between 4 to 500 m, the highest locality came from a deciduous forest at an altitude 1054 m a.s.l.

Distribution. All confirmed records indicate that the species has a distribution range restricted to the Balkan Peninsula and the Aegean region. Record from Israel (Voshnak & Ionescu-Hirsch 2009) needs verification.

Aphaenogaster holtzi (Emery, 1898)
(Figs 14–17)

Stenamma (*Aphaenogaster*) *subterraneum* subsp. *holtzi* Emery, 1898: 139 (w.) Lectotype [designated here], worker, Mersina [Mersin], Türkiye (coll. Holtz) (MSNG) [Syntype worker images examined, AntWeb, CASENT0904178, photos by Will Ericson, available on https://www.AntWeb.org].

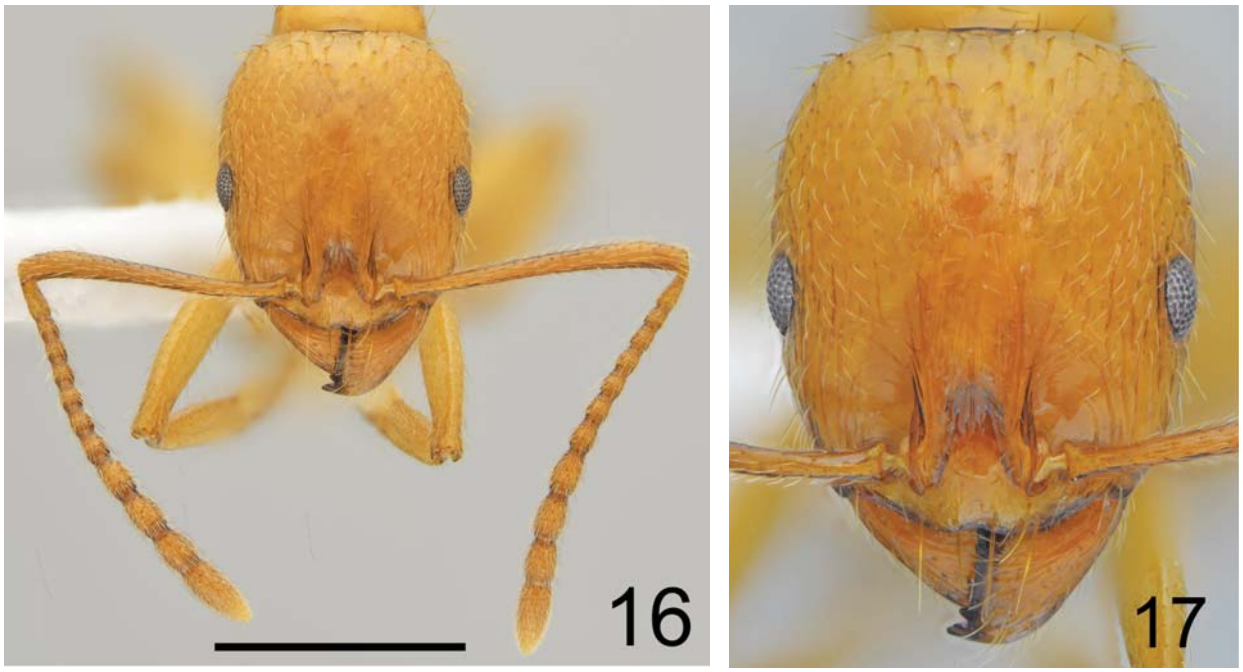


Figures 14, 15. *Aphaenogaster holtzi* (Emery), worker: (14) dorsal, (15) lateral (scale bar = 1 mm, photographed by L. Borowiec).

Other material. Table 2.

Comparative diagnosis. Due to the head being at least partly smooth and shiny *Aphaenogaster holtzi* is similar to *A. asterioni*, *A. ichnusa,* and *A. subterranea* but it differs from congeners in predominantly smooth and shiny head and mesosoma, presence of numerous erect setae on the occipital margin of the head, and uniformly pale yellow body.

Redescription. Worker. Measurements (See Table 3). **Colouration.** Whole body uniformly coloured, pale yellow (Figs 14–17). **Head.** Suboval; lateral sides rounded, posterior margin straight (Fig. 16). Anterior margin of clypeus distinctly convex, medial notch present. Eyes moderate and suboval. Antennal scape short, in lateral view slightly curved, gradually widening posteriorly, funiculus long, club indistinct and 4-segmented



Figures 16, 17. *Aphaenogaster holtzi* (Emery), worker: (16) head and antennae, (17) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

(Fig. 16). Scape with short and dense costae, shiny, covered with thin, dense, decumbent to erect setae. Mandibles rounded with fine and sparse striae, shiny. Clypeus smooth, sometimes with a few sparse and indistinct costulae. Frontal carinae short, slightly extending beyond frontal lobes. Antennal fossa deep, with thin, indistinct and sparse rugocostae and smooth interspaces. Frontal lobes narrow, smooth (Fig. 17). Whole surface of head predominantly smooth; only lateral frons with some indistinct, sparse and interrupted rugocostae. Whole head with subdecumbent to erect, pale, short and thick setae (Figs 16, 17). **Mesosoma.** Humeral tubercle not developed; promesonotum well above level of propodeum; metanotal groove present. Propodeal spines present, short and triangular (Fig. 15). Pronotum smooth and shiny; mesonotum and propodeum with very thin and sparse rugocostae. Entire mesosoma with erect, pale, long and thick setae (Figs 14, 15). **Petiole.** Elongate with long peduncle, node rounded, whole surface smooth; shiny. Dorsal surface with sparse, moderately long, erect setae (Figs 14, 15). **Postpetiole.** In lateral view rounded, smooth and shiny. Dorsal surface with sparse, moderately long, erect setae (Figs 14, 15). **Gaster.** Smooth and shiny, with erect, thin, pale setae (Figs 14, 15).

Biology. Almost unknown, in Türkiye it was collected in mountains at altitudes 1250 and 1600 m.

Distribution. Türkiye (Kiran & Karaman 2020) and Iran (Moradloo *et al*. 2015).

Aphaenogaster ichnusa Santschi, 1925
(Figs 18–21)

Aphaenogaster (*Attomyrma*) *subterranea* var. *ichnusa* Santschi, 1925: 341 (w.). Lectotype [designated here], worker, Sorgono, Sardinia, Italy (coll. Krausse) (NHMB) [Lectotype worker images examined, AntWeb, CASENT0913132, photos by Z. Leberman, available on https://www.AntWeb.org].

Other material. Table 2.

Comparative diagnosis. A member of a complex of species with a head partly smooth and shiny. This complex comprises *A. asterioni*, *A. holtzi*, *A. ichnusa,* and *A. subterranea*. *Aphaenogaster ichnusa* is the most similar to *A. subterranea* and differs in almost entirely smooth pronotum, often lacking longitudinal costulae on its lateral sides and smaller propodeal spines that are often reduced to a denticle. *Aphaenogaster holtzi* differs in uniformly pale yellow body and the presence of numerous erect setae in the occipital part of the head. See also diagnosis for *A. asterioni*.

Description. See Galkowski *et al*. 2019: 423 (redescription, w.); Schifani *et al*. 2023: 145 (diagnosis, m.), 147 (diagnosis, q.).

Biology. *Aphaenogaster ichnusa* inhabits areas with a Mediterranean climate. Its colonies are often found nesting under rocks, and it is especially abundant in shady forest habitats with sufficient humidity and leaf litter (Schifani *et al*. 2023).

Distribution. Spain, France, and Italy (Schifani *et al*. 2023).

Figures 18, 19. *Aphaenogaster ichnusa* Santschi, worker: (18) dorsal, (19) lateral (scale bar = 1 mm, photographed by L. Borowiec).

Aphaenogaster maculifrons Kiran & Aktaç, 2008
(Figs 22–25)

Aphaenogaster (*Attomyrma*) *maculifrons* Kiran & Aktaç, 2008 in Kiran *et al*. 2008: 691, fig. 2 (w.q.) Paratype, worker, 1500 m, Akşehir, Konya Prov., Türkiye, 01.08.2002, 38°30'29" N/ 28°04'35" E (MNHW) [personally investigated].

Other material. Table 2.

Comparative diagnosis. Due to the whole head surface with distinct microsculpture and lacking smooth and shiny areas on the vertex and occipital area, *A. maculifrons* is the most similar to *A. tristis*. *Aphaenogaster tristis* differs in not regularly rounded sides of the pronotum, in dorsal view, with the presence of well-marked humeral tubercles with setae on their tips, and in distinctly rugose with additional interrupted and dense costulae frons. Both species are separated geographically; *A. maculifrons*

Figures 20, 21. *Aphaenogaster ichnusa* Santschi, worker: (20) head and antennae, (21) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

is known from western Türkiye, while *A. tristis* is known only from western, central, and southern Greece.

Description. See Kiran *et al*. 2008: 691.

Biology. In Konya province, this species was found in almost all forest groves overgrown with old *Pinus nigra* trees at altitudes from 1420 to 1770 m. Nests were under large stones and contained several thousand workers. In ancient Termessos of Antalya Province, a single nest was found under a large stone in an oak forest at 1018 m a.s.l. In Anatolia, this species was noted from mountain localities at an altitude between 1234 and 1689 m a.s.l. (Kiran & Karaman 2021).

Distribution. Türkiye: Anatolia (Kiran *et al*. 2008, Kiran & Karaman 2020, 2021).

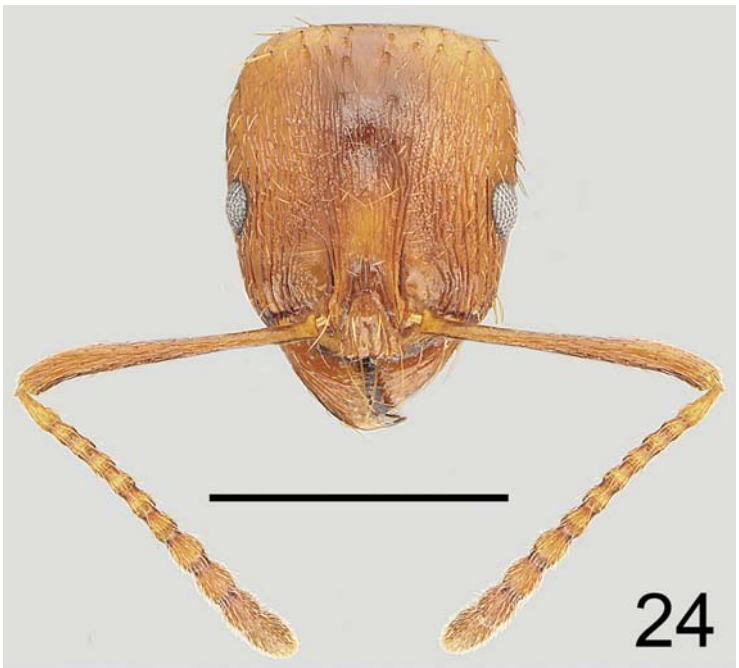
Figures 22, 23. *Aphaenogaster maculifrons* Kiran & Aktaç, worker: (22) dorsal, (23) lateral (scale bar = 1 mm, photographed by L. Borowiec).

Aphaenogaster subcostata Viehmeyer, 1922
(Figs 26–30)

Aphaenogaster (*Attomyrma*) *subcostata* Viehmeyer, 1922: 205 (w.) Lectotype [designated here], worker, Hadj Kiri [Hacikiri], Taurus, Türkiye (MHNG) [Lectotype worker images examined, AntWeb, CASENT0907698, photos by Z. Leberman, available on https://www.AntWeb.org]. Paratypes, 3 workers, the same data as lectotype (ZHMB) [Paralectotype workers images examined, AntWeb, FOCOL1220, FOCOL1221, FOCOL1222, photos by Christiana Klingenberg, available on https://www.AntWeb.org].

Other material. Table 2.

Comparative diagnosis. *Aphaenogaster subcostata* with *A. epirotes* form a complex of species characterized by the whole head with thick and sparse rugocostae forming longitudinal and partly reticulate sculpture. *Aphaenogaster epirotes* differs in the short and not flattened laterally first segment of funiculus that is approximately 2.2 × as long as wide, and in reddish brown to black body with mesosoma rarely



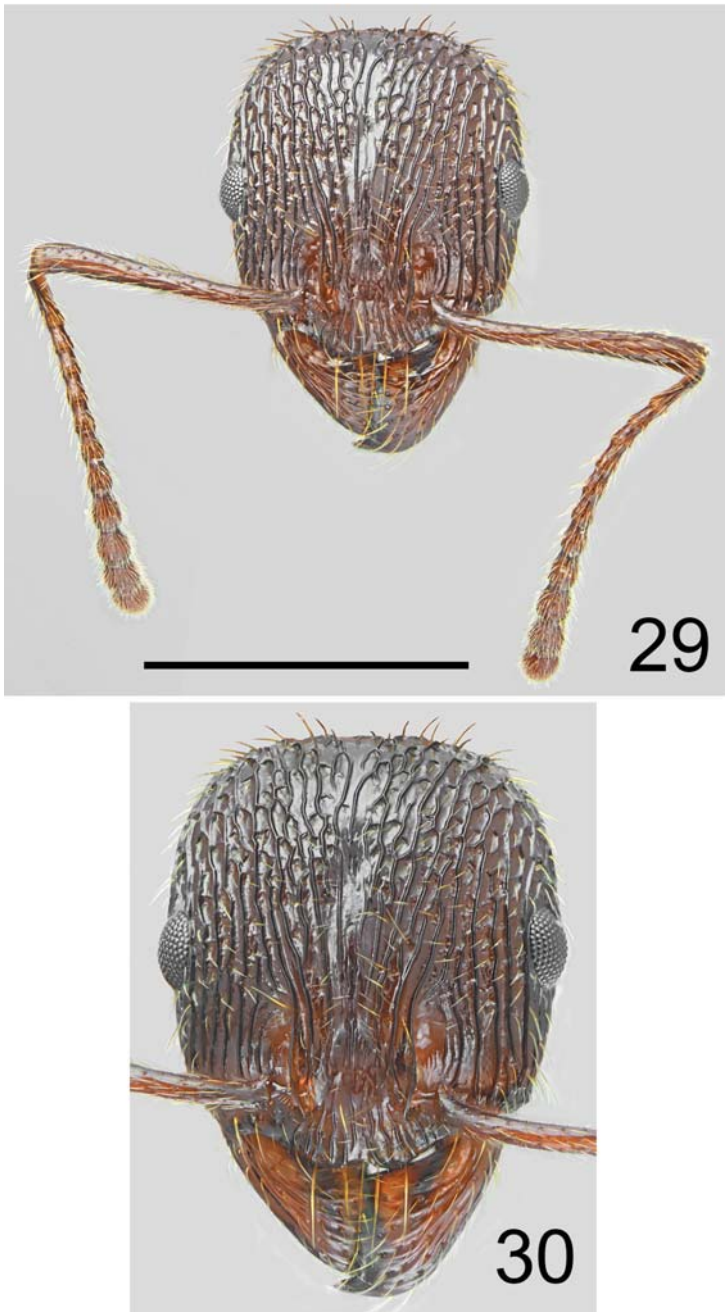
Figures 24, 25. *Aphaenogaster maculifrons* Kiran & Aktaç, worker: (24) head and antennae, (25) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

slightly paler than the head. Also, both species are separated geographically, *A. epirotes* is common in the Balkans, the Ionian Islands, Cyclades, and northern Aegean Islands south to Lesbos, while *A. subcostata* is a rare species known only from Dodecanese, the southern Aegean Islands north to Samos, and from western Türkiye.

***Redescription*.** Worker. Measurements (See Table 3). **Colouration.** Head, mesosoma, petiole, and postpetiole yellowish brown to bright brown; frons and gaster darker (Figs 26–30). **Head.** Suboval; lateral sides rounded, posterior margin convex (Fig. 29). Anterior margin of clypeus distinctly convex, medial notch present. Eyes moderate and suboval. Antennal scape short, in lateral view slightly curved, gradually widening posteriorly, funiculus long, club indistinct and 4-segmented (Fig. 29). Scape with short and dense costae, shiny, covered with thin, dense, decumbent to

Figures 26–28. *Aphaenogaster subcostata* Viehmeyer, worker: (26) dorsal, (27) lateral, (28) basal segments of antennal funicle (scale bar = 1 mm, photographed by L. Borowiec).

suberect setae. Mandibles rounded with thick and sparse striae, shiny. Clypeus with sparse and short costulae and smooth interspaces. Frontal carinae short, slightly extending beyond frontal lobes. Antennal fossa deep, with thick and sparse rugocostae and smooth interspaces. Frontal lobes narrow, smooth (Fig. 29). Whole surface of head with thick and sparse rugocostae with smooth to indistinctly imbricate interspaces. In northern populations rugocostae in occipital part of head often forms reticulate sculpture, in populations from southern Greece predominate longitudinal and zigzag costae, without or with rudiments of reticulate sculpture. Whole head with subdecumbent to erect, pale, short and thick setae (Figs 29, 30). **Mesosoma.** Humeral tubercle not developed; promesonotum well above level of propodeum; metanotal groove present.



Figures 29, 30. *Aphaenogaster subcostata* Viehmeyer, worker: (29) head and antennae, (30) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

Propodeal spines present, short and triangular (Fig. 27). Whole mesosoma with thin and sparse rugae to rugocostae, interspaces smooth and shiny; pronotum always with sparser and weaker sculpture. Entire mesosoma with erect, pale, moderately long and thick setae (Figs 26, 27). **Petiole.** Elongate with long peduncle, node rounded, whole surface indistinctly rugose to partially smooth; shiny. Dorsal surface with sparse, long, erect setae (Figs 26, 27). **Postpetiole.** In lateral view rounded, indistinctly rugose to partially smooth; shiny. Dorsal surface with sparse, long, erect setae (Figs 26, 27). **Gaster.** Smooth and shiny, with erect, thin, pale setae (Figs 26, 27).

Distribution. Greece: Samos (Borowiec & Salata 2018), Dodecanese and Türkiye (Kiran & Karaman 2020).

Figures 31–33. *Aphaenogaster subterranea* (Latreille), worker: (31) typical pale morph dorsal, (32) typical pale morph lateral, (33) typical dark morph lateral (scale bar = 1 mm, photographed by L. Borowiec).

Biology. Poorly known. *Aphaenogaster subcostata* was collected in Greece in the open oak forest close to Xerorrema stream (Samos, 15 m), in shady pine forests (Samos, Kastania vic., 350 m) and mountain pastures with shrubs (Samos, Pandroso, 670 m). It is also known from a seaside location at Nera islet. In Türkiye the species is known from its alpine locations in Taurus Mountains.

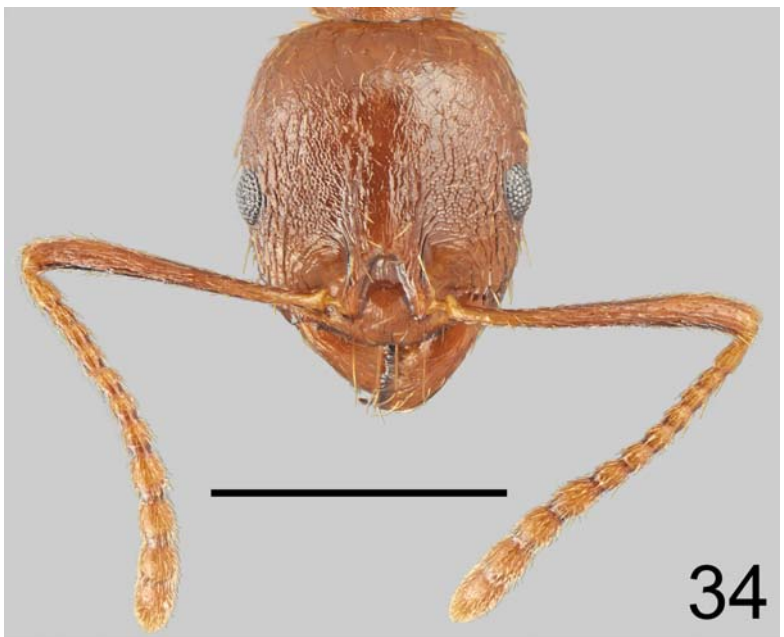
Aphaenogaster subterranea (Latreille, 1798) (Figs 31–39)

Formica subteranea Latreille, 1798: 49 (w.q.m.) Topotype, worker, Brive-la-Gaillarde, France (MNHW) [personally investigated].
= *Aphaenogaster pallida* var. *lesbica* Forel, 1913: 429 (w.) Holotype, worker, Lesbos, Greece (coll. U. Sahlberg) (MHNG) [Holotype worker images examined, AntWeb, CASENT0907690, photos by Will Ericson, available on], **syn. nov.**

Other material. Table 2.

Comparative diagnosis. A member of a complex of species with a head partly smooth and shiny. This complex comprises *A. asterioni*, *A. holtz*i, *A. ichnusa*, and *A. subterranea*. *Aphaenogaster subterranea* is most similar to *A. ichnusa* and differs in more developed sculpture on the pronotum (dorsal surface smooth to indistinctly imbricate and lateral sides with dense and thick to thin longitudinal costulae), and more developed propodeal spines that are most often narrower and longer. *Aphaenogaster holtzi* differs in uniformly pale yellow body and the presence of numerous erect setae in occipital part of the head. See also the diagnosis of *A. asterioni*.

Redescription. See Galkowski *et al*., 2019: 422 (w.); Schifani *et al*. 2023: 145 (diagnosis, m.), 147 (diagnosis, q.).



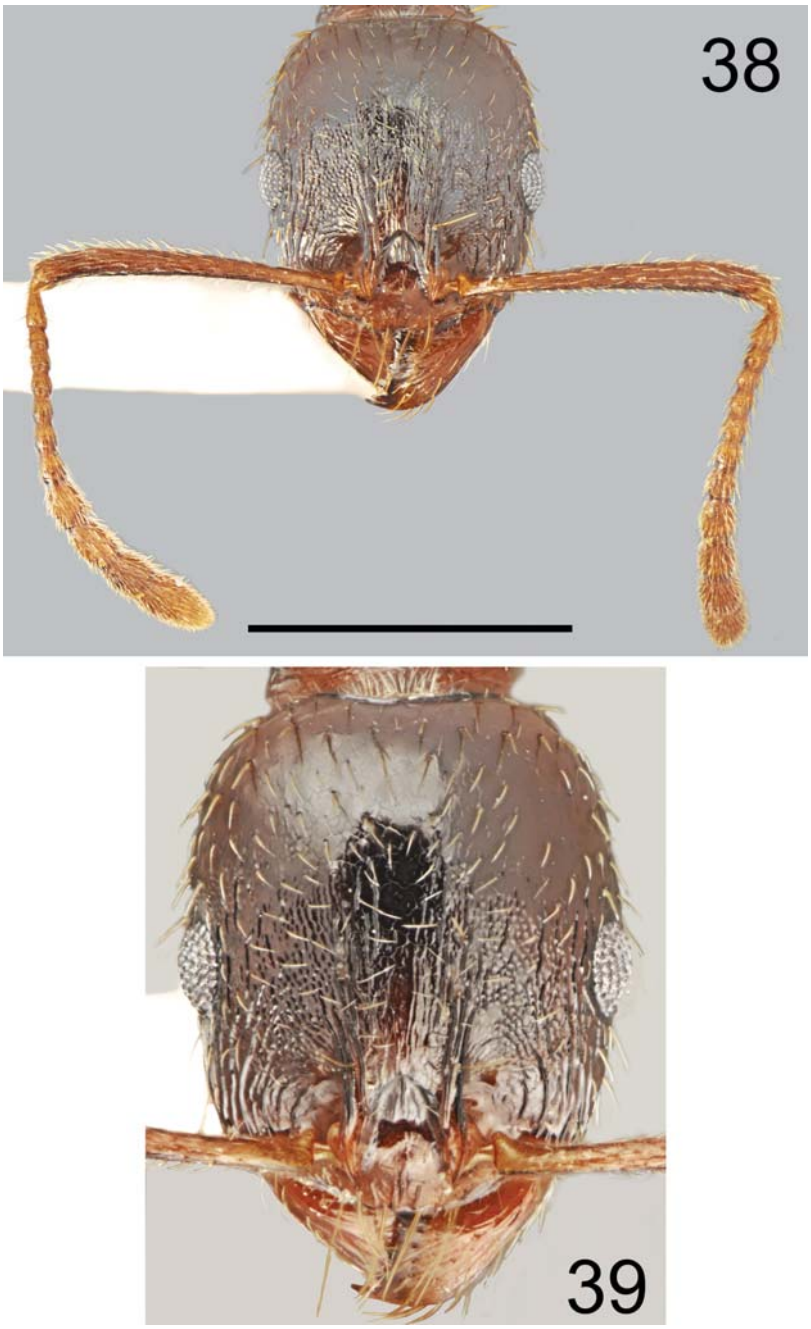
Figures 34, 35. *Aphaenogaster subterranea* (Latreille), worker of typical pale form: (34) head and antennae, (35) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

Figures 36, 37. *Aphaenogaster subterranea* (Latreille), worker of '*lesbica*' morph: (36) dorsal, (37) lateral (scale bar = 1 mm, photographed by L. Borowiec).

Biology. Common ubiquitous species. Prefers forest habitats, especially shadow and humid deciduous forests (oak, chestnut), stream valleys with plane trees, highly in mountains was observed in beech and fir forests. Less common in dry oak forests but frequently noted in habitats at proximity to the water sources (see note below). Occasionally observed in olive plantations and open habitats such as mountain pastures with shrubs and rocks. In such places nest were usually placed close to the bush's trunk or on the shady side of rock. Only a few observations are from village gardens, and only five records from pine forests. Nests most often are located under stones, colonies are large, often with more than 300 workers. This species was collected at various altitudes ranging from 3 to 1336 m a.s.l., but most records are from altitudes below 900 m a.s.l.

Distribution. Europe (except for the northern part), Türkiye, and Transcaucasian countries.

Note. *Aphaenogaster lesbica* was described by Forel (1913) as a subspecies of *A. pallida* and separated by more developed head sculpture and longer propodeal spines. Later, it was elevated to the species rank by Agosti and Collingwood (1987a) but still was considered a species morphologically similar to *A. pallida* (Agosti and Collingwood 1987b). The affiliation of *A. lesbica* with *A. pallida* was also confirmed by Schulz (1994) and Boer (2013) in their *Aphaenogaster*



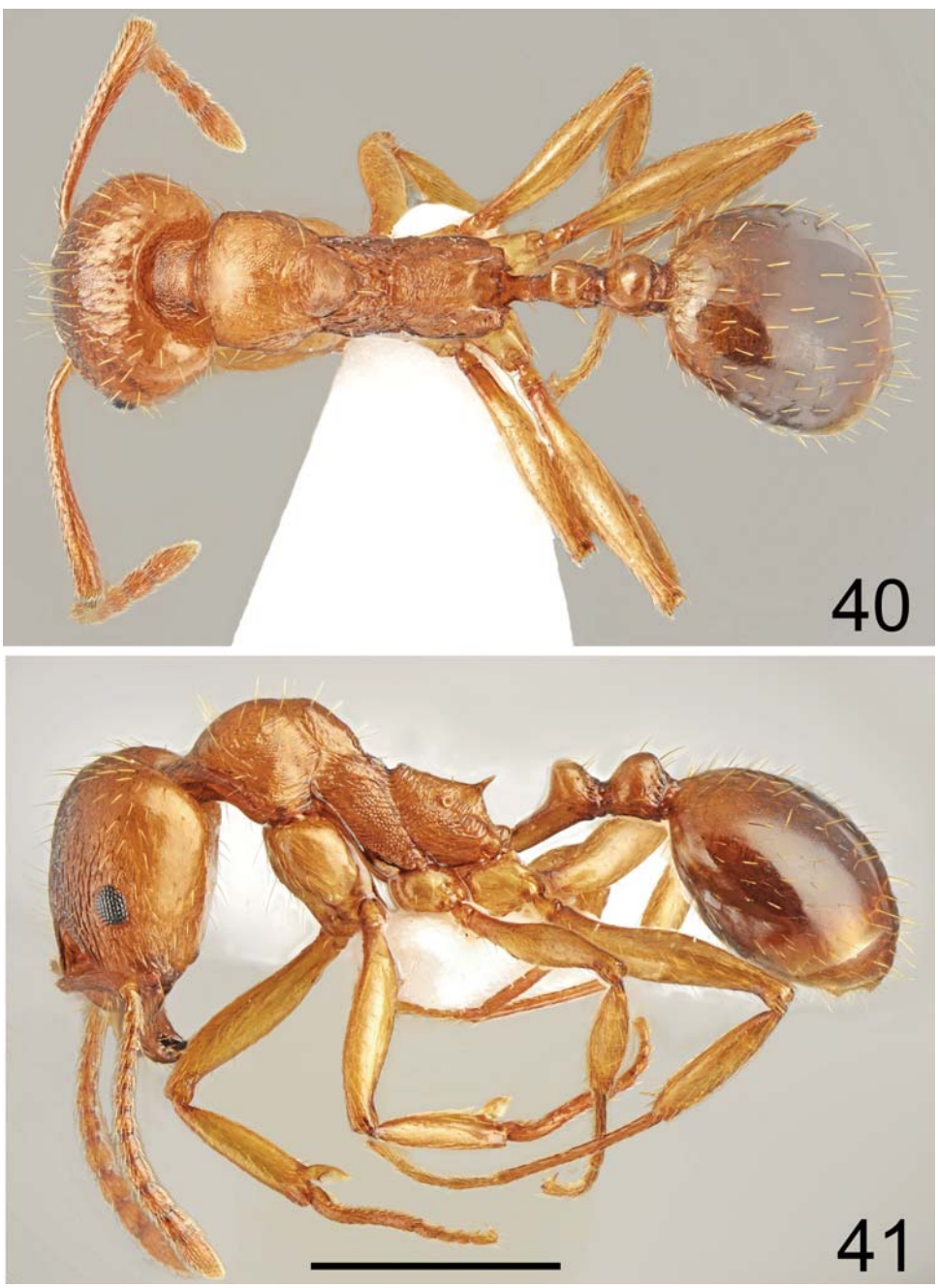
Figures 38, 39. *Aphaenogaster subterranea* (Latreille), worker of '*lesbica*' morph: (38) head and antennae, (39) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

species group divisions. Only recently, *A. lesbica* was assigned to the *subterranea* species group (Bračko *et al*. 2016, 2019, Schifani *et al*. 2023) based on an examination of holotype preserved in MHNG. Examination of large series from Lesbos (Greece), the terra typica for *Aphaenogaster pallida lesbica*, which have characteristics of the holotype of *A. lesbica,* showed that there are two different morphotypes within the *A. subterranea* complex in the Balkan Peninsula and that each of them has different habitat preferences. Overall, the morphotype described as *A. lesbica* is smaller, darker coloured, with less developed head sculpture and distinctly slimmer head. The '*lesbica*' morphotype appears to be associated with wet habitats and all its nests were observed close to streams and other water sources, On the other hand, the typical '*subterranea*' morphotype was observed in a wider range of habitats, both in wet areas and those

far from water sources. However, the nest samples of each morphotype show that there is a large overlap of the above-mentioned morphological traits and the genetic studies have not revealed significant distance allowing these two morphotypes to be recognized as separate species. Therefore, we propose to recognize *A. lesbica* as a younger synonym of *A. subterranea*.

Aphaenogaster tristis Borowiec, Menchetti, Salata, Vila & Zięcina, sp. nov.
(Figs 40–49)

Type material. Holotype (w.): Collection L. Borowiec | Formicidae | LBC-GR02140 || GREECE, Pel. Lakonia | 3.2 km NW Polidroso, 1000 m | 37.19874 N / 22.57603 E | 18 VI 2016, L. Borowiec (MNHW).



Figures 40, 41. *Aphaenogaster tristis* sp. nov., worker of typical morph from Peloponnese: (40) dorsal, (41) lateral (scale bar = 1 mm, photographed by L. Borowiec).

Figures 42, 43. *Aphaenogaster tristis* sp. nov., worker of typical morph from Peloponnese: (42) head and antennae, (43) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

Paratypes (16w.): the same data as the holotype (MNHW, NHMC); 16w.: Collection L. Borowiec | Formicidae | LBC-GR02158 || GREECE, Pel. Lakonia | 3.2 km NE Vemvakou, 1370 m | 37.25344 N / 22.59165 E | 18 VI 2016, L. Borowiec (MNHW, MHNG).

Other material. Table 2.

Etymology. Latin *tristis* means gloomy, sad, shadowy. Named after almost completely microreticulate head and mesosoma, which gives the species a subdued appearance, in contrast to the highly shiny species such as *A. subterranea* or *A. holtzi*.

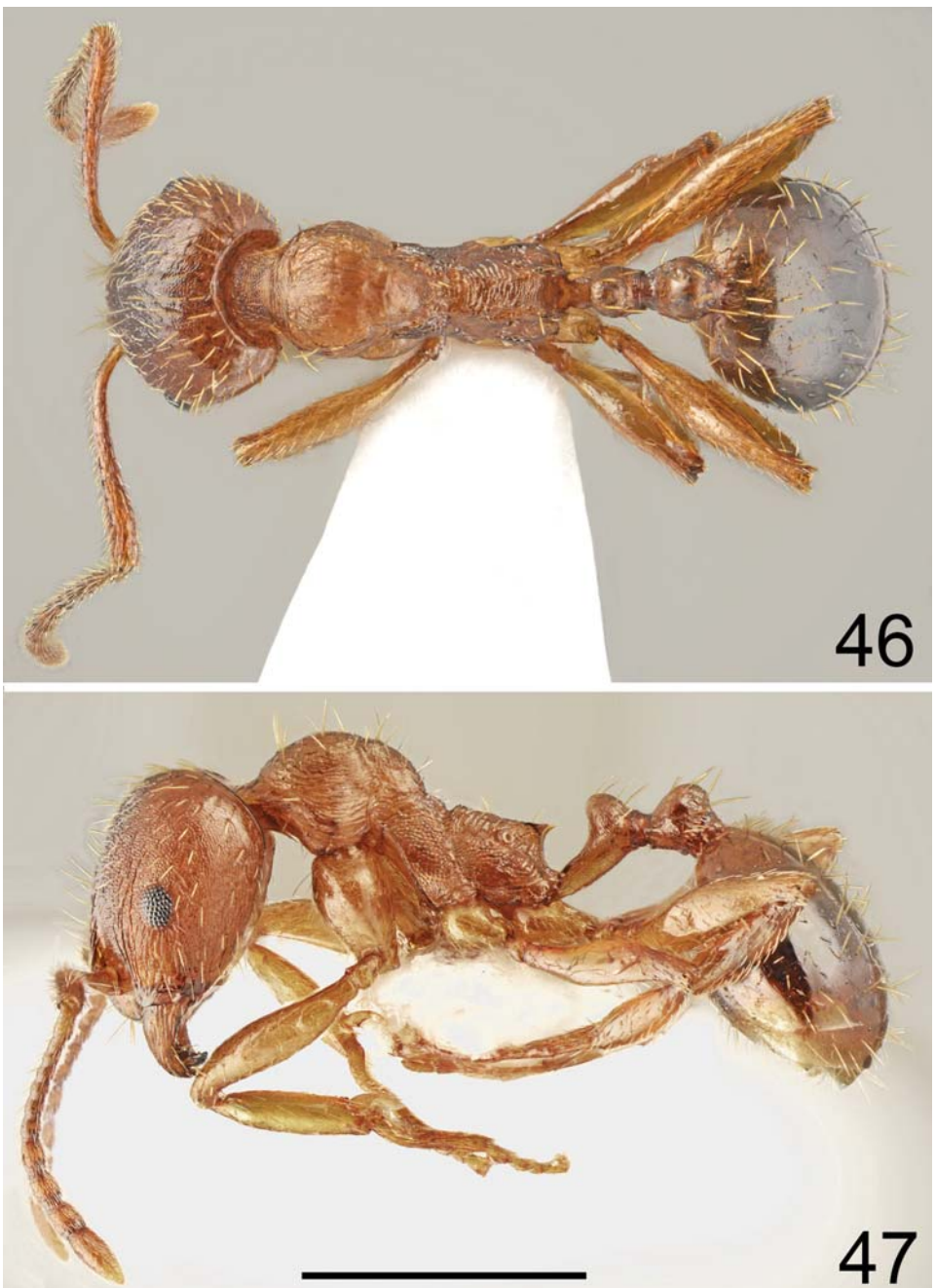
Comments. *Aphaenogaster tristis* and *A. maculifrons* form a complex of species characterized by head on the whole surface with distinct microsculpture, lacking smooth and shiny areas in the vertex and occipitum. *Aphaenogaster tristis* is the most similar

to *A. maculifrons* but differs in distinctly rugose frons with additional interrupted and dense costulae, and vertex and sides posterolateral from eyes equally sculptured and only occasionally with weaker, but still distinct, sculpture. Both species are separated geographically, *A. tristis* is known from western, central, and southern Greece, while *A. maculifrons* is known only from western Türkiye.

Description. Worker. Measurements (Table 3). **Colouration.** Head, mesosoma, petiole, and postpetiole yellowish brown to brown; frons and propodeum darker than the rest of the body; gaster dark brown to black with brighter yellowish spot at the basal part of the first tergite (Figs 40–49). **Head.** Subrectangular; lateral sides indistinctly rounded, posterior margin straight (Figs 42, 48). Anterior margin of clypeus distinctly

Figures 44, 45. *Aphaenogaster tristis* sp. nov., worker lateral: (44) morph from Cyclades, (45) morph from Cephalonia (scale bar = 1 mm, photographed by L. Borowiec).

convex, medial notch present. Eyes moderate and suboval. Antennal scape short, in lateral view slightly curved, gradually widening posteriorly, funiculus long, club indistinct and 4-segmented (Figs 42, 48). Scape with short and dense costae, shiny, covered with thin, dense, decumbent to suberect setae. Mandibles rounded with thick and sparse striae, shiny. Clypeus predominantly smooth with sparse and short costulae. Frontal carinae short, slightly extending beyond frontal lobes. Antennal fossa deep and with dense and distinct rugocostulae. Frontal lobes narrow, smooth (Figs 42, 48). Whole surface of head distinctly rugose; frons and gena with additional interrupted and dense costulae; vertex and sides posterolateral from eyes sometimes with weaker sculpture but never smooth and shiny. Whole head with subdecumbent to erect, pale, short and thick



Figures 46, 47. *Aphaenogaster tristis* sp. nov., worker of morph from Corfu: (46) dorsal, (47) lateral (scale bar = 1 mm, photographed by L. Borowiec).

setae (Figs 43, 49). **Mesosoma.** Humeral tubercle developed, usually with long and erect seta on their apex; promesonotum well above level of propodeum; metanotal groove present. Propodeal spines present, short and triangular (Figs 41, 44, 45, 47). Whole mesosome distinctly rugose; its lateral sites sometimes with additional longitudinal costulae; pronotal dorsum with weaker but still distinct sculpture. Entire mesosoma with erect, pale, moderately long and thick setae (Figs 40, 41, 44–47). **Petiole.** Elongate with long peduncle, node rounded, whole surface indistinctly rugose to partially smooth; shiny. Dorsal surface with sparse, long, erect setae (Figs 40, 41, 44–47). **Postpetiole.** In lateral view rounded, indistinctly rugose to partially smooth; shiny. Dorsal surface with sparse, long, erect setae (Figs 40, 41, 44–47). **Gaster.** Smooth and shiny, with erect, thin, pale setae (Figs 40, 41, 44–47).

Figures 48, 49. *Aphaenogaster tristis* sp. nov., worker of morph from Corfu: (48) head and antennae, (49) head sculpture (scale bar = 1 mm, photographed by L. Borowiec).

Distribution. Endemic to Greece (Cyclades, Ionian Islands, Peloponnese, Sterea Ellas (Euboea Island) and Thessaly.

Biology. *Aphaenogaster tristis* is mostly associated with coniferous forests (especially fir forests), and only once it was observed in a stream valley with plane trees and in mixed forest. Another single record comes from rocky alpine pastures close to fir forest. Most likely it is an alpine species, as most of its records are from shadow, mountain habitats from 500 to 1950 m a.s.l. Its nests were located under stones not necessarily near watercourses, often in stony parts of fir forests far from the water. Exceptionally, one nest from Corfu (Ionian Islands) was located under a stone in a shadow deciduous forest at an altitude of 179 m, and the population from Naxos, Cyclades inhabits humid and dark deciduous forest located in a small valley at an altitude 462–476 m. Also, one worker was observed on the rock wall in the gorge across the deciduous forest.

Note. The insular populations of *A. tristis* sometimes differ from the mainland ones, but we couldn't find any strong evidence supporting their distinctness. For example, the population from Naxos (Cyclades) has overall shorter propodeal spines, the population from Corfu (Ionian Island) has smaller body size, more subdecumbent to suberected pubescence of antennal scapus, and dorsum of pronotum partly with fain longitudinal rugae, some populations from Cephalonia (Ionian Islands) exhibit slightly weaker head sculpture but this character is variable within the colony and might be caused by some external factors. The observed differences also might be a manifestation of the ongoing divergence of this species.

DNA based analysis

All eight species here proposed, delimited based on qualitative, external morphological characteristics, are recovered as monophyletic and well supported in the COI tree. The only exception is a French *A. subterranea* specimen (a.n. MMH630461) which was stated to be introgressed from *A. ichnusa* (Galkowski *et al.* 2019), albeit this specimen has not been morphologically examined in this paper. The species *A. subcostata* was here sequenced for the first time and it is recovered as sister to *A. epirotes* (bootstrap support >95) (Fig. 50). The clade containing these two species and *A. holtzi* is not fully supported (bootstrap support 70–90), as is also the case for the clade containing *A. ichnusa* and *A. maculifrons,* and the sister relationship of *A. tristis* and *A. asterioni*. The specimens of *A. subterranea* resembling the *lesbica* morphotype are scattered within the clade of *A. subterranea*, sharing the same haplotype with *A. subterranea* s.l. in two out of three specimens.

Maps showing the genetic structure (Fig. 51) show similar patterns across the four species investigated, with several continental haplotypes structured spatially, although at different spatial scales: low diversity at a wide scale in *A. ichnusa*, and higher diversity for the rest, distributed at a smaller scale in the case of *A. epirotes* and *A. tristis*. A high haplotype endemicity is obtained in big islands (Corsica, Sardinia and Sicily) and also at smaller ones, both in the Western and Eastern Mediterranean. *Aphaenogaster epirotes* is well structured spatially (Fig. 51a) with a high intraspecific divergence (p. dist. = 3.4%) and two main haplogroups (Fig. 51b,c), one in Cephalonia and Zakynthos and the other spread across the rest of the sampled species range. *Aphaenogaster ichnusa* shows a high spatial structure with a moderate intraspecific divergence (p. dist. = 1.8%). This species has three main haplogroups, a continental one (which is also present in some smaller islands, i.e. Mallorca and Tuscan Archipelago), one endemic of Corsica and Sardinia, and a Southern Italian one (including some endemic haplotypes in the Aeolian Islands, a recent volcanic archipelago). *Aphaenogaster subterranea* has a high spatial structure and high intraspecific divergence (p. dist. = 3.7%). Four main haplogroups are found in this species which are present in West Europe, Eastern Europe, Southern Italy and Georgia. *Aphaenogaster tristis* sp. nov. is also highly structured with a high intraspecific divergence (p. dist. = 3.3%).

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Lech Borowiec thanks Jolanta Świętojańska (University of Wrocław) for her assistance during field trips. We wish to thank Cecília Corbella for her help in the laboratory and all the colleagues and amateurs who helped us collecting the specimens sequenced in this study: Andrea Montechiarini, Antonio Alicata, Carlo Legittimo, Celal Karaman, David Drinic, Elia Nalini, Elisabetta Sbrega, Emiliano Mori, Enrico Schifani, Fede García, Gerard Talavera, Giorgia Mocilnik, György Makranczy, Joan Carles Hinojosa, Kadri Kiran, Leonardo Dapporto, Leonardo Platania, Luca Berton, Matteo D'Ambrosio, Mattia Francesco D'amato, Nicolò Crosato, Nikola Balevic, Paola Ferruzzi, Roberto Piras, Roberto Viviano, Sämi Schär, Stefano Menchetti, Tomislav Kragujević. Support for this research was provided by 'la Caixa' Foundation (ID 100010434) to Mattia Menchetti (grant LCF/BQ/DR20/11790020), by grant BG-RRP-2.004-0008 SUMMIT-3.3 to Albena Lapeva-Gjonova, and by grant PID2022-139689NB-I00 (MICIU/AEI/10.13039/501100011033 and ERDF, EU) and 2021-SGR-00420 (Departament de Recerca i Universitats, Generalitat de Catalunya) to Roger Vila.

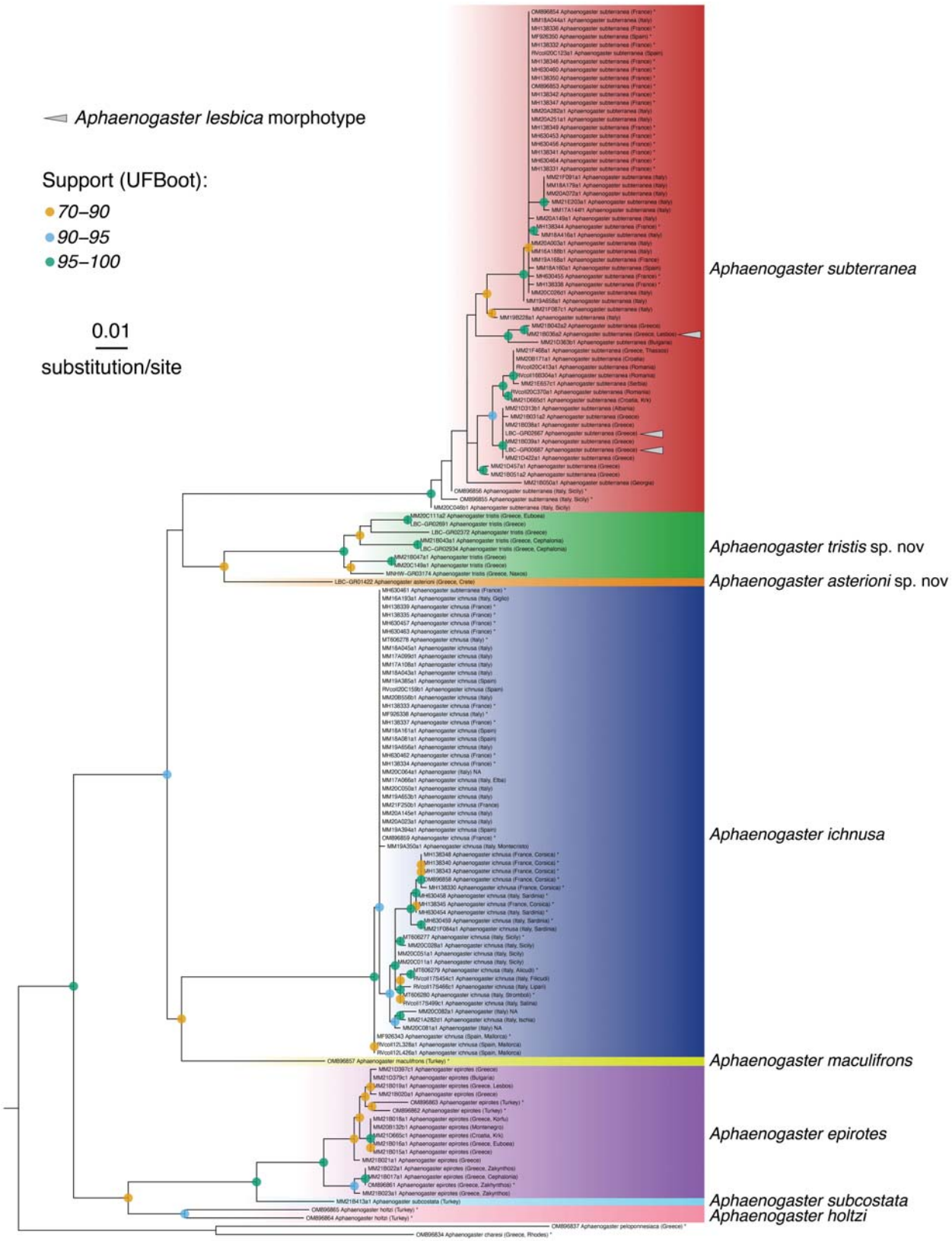

Figure 50. Maximum likelihood tree based on mitochondrial COI sequences, produced with IQ-tree. Bootstrap values above 70 are indicated by colours on the nodes and the voucher or GenBank accession numbers, species names, and countries and islands are shown in the tip labels. Grey arrows indicate the *A. lesbica* morphotype.

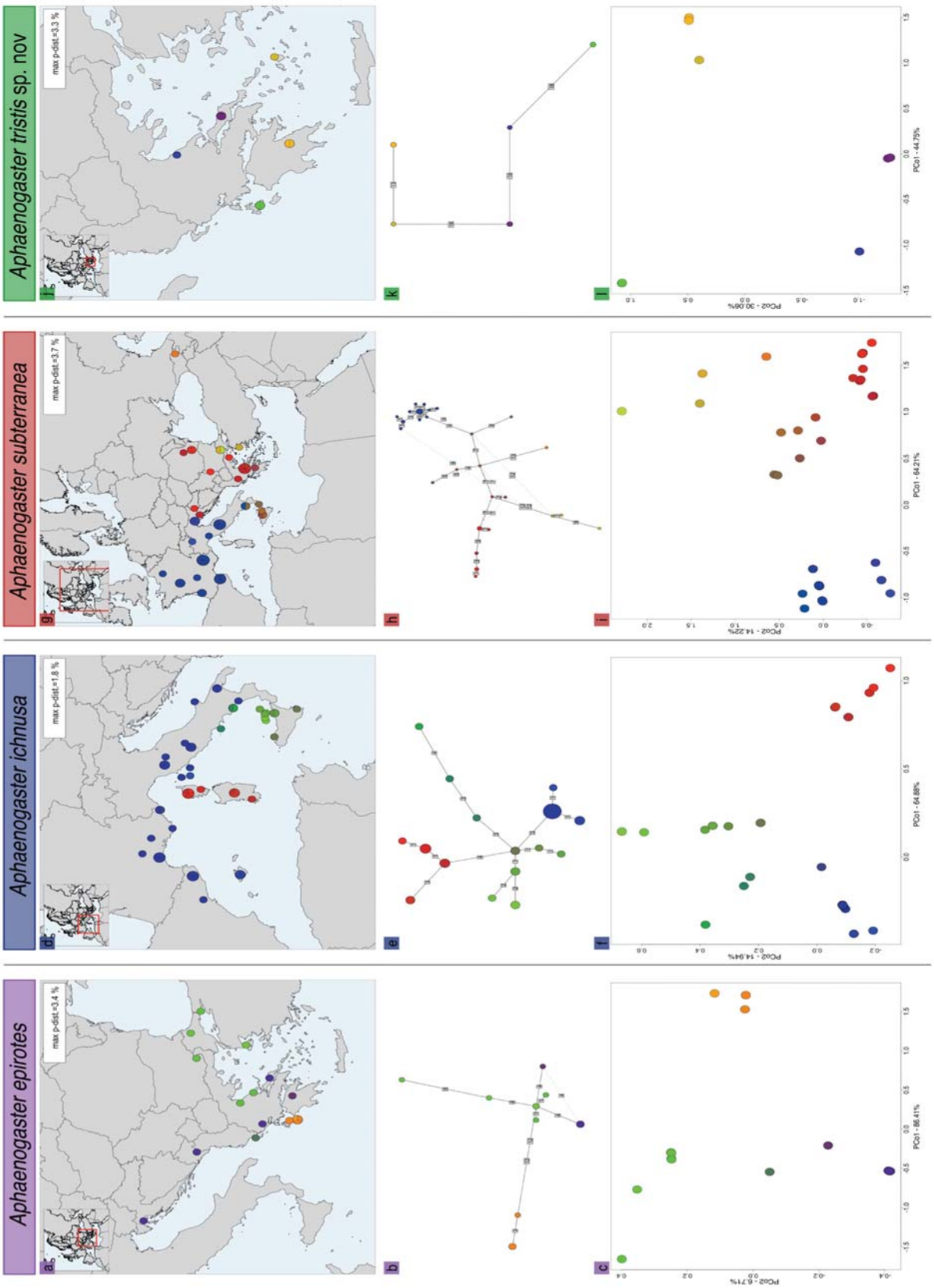

Figure 51. Spatial genetic structure of *A. epirotes* (a), *A. ichnusa* (d), *A. subterranea* (g) and *A. tristis* sp. nov. (j) and their respective haplotype networks (b,e,h,k) based on COI sequences. Colours match the bidimensional colour space of the PCoA projection (c,f,i,l). Insets show the max intraspecific p-dist.

This work represents a combination of results achieved by DZ during his work on a master thesis submitted to the University of Wroclaw broadened with an extensive experience, knowledge and additional data provided by the remaining authors.

References

Alicata, A. and E. Schifani. 2019. Three endemic *Aphaenogaster* from the Siculo-Maltese archipelago and the Italian Peninsula: part of a hitherto unrecognized species group from the Maghreb? (Hymenoptera: Formicidae: Myrmicinae). Acta Entomologica Musei Nationalis Pragae, 59: 1–16. 10.2478/aemnp-2019-0001.

Boer, P. 2013. Revision of the European ants of the *Aphaenogaster testaceopilosa*-group (Hymenoptera: Formicidae). Tijdschrift voor Entomologi, 156: 57–93.

Bolton, B. 1982. Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). Bulletin of the British Museum (Natural History), Entomology series, 45: 307–370.

Bolton, B. 1995. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Massachusetts, USA, 504 pp.

Bolton, B. 2023. An online catalog of the ants of the world. Available from https://antcat.org. (accessed 12 December 2023).

Borowiec, L. and S. Salata. 2018. Notes on ants (Hymenoptera: Formicidae) of Samos Island, Greece. Annals of the Upper Silesian Museum in Bytom, Entomology, 27: 1–13. 10.5281/zenodo.1481802.

Bračko, G., Kiran, K., Karaman, C., Salata, S. and L. Borowiec. 2016. Survey of the ants (Hymenoptera: Formicidae) of the Greek Thrace. Biodiversity Data Journal, 4: 1–44. https://doi.org/10.3897/BDJ.4.e7945.

Bračko, G., Lapeva-Gjonova, A., Salata, S., Borowiec, L. and S. Polak. 2019. *Aphaenogaster illyrica*, a new species from the mountains of the Balkan Peninsula (Hymenoptera, Formicidae). ZooKeys, 862: 89–107. https://doi.org/10.3897/zookeys.862.32946.

Branstetter, M.G., Longino, J.T., Reyes-López, J.L., Brady, S.G. and T.R. Schultz. 2022. Out of the temperate zone: A phylogenomic test of the biogeographical conservatism hypothesis in a contrarian clade of ants. Journal of Biogeography, 49: 1640–1653. https://doi.org/10.1111/jbi.14462.

Csősz, S. and B.L. Fisher. 2016. Toward Objective, Morphology-Based Taxonomy: A Case Study on the Malagasy *Nesomyrmex sikorai* Species Group (Hymenoptera: Formicidae). PLoS ONE, 11(4): e0152454. https://doi.org/10.1371/journal.pone.0152454.

Dapporto, L., Menchetti, M., Vodă, R., Corbella, C., Cuvelier, S., Djemadi, I., Gascoigne-Pees, M., Hinojosa, J. C., Lam, N. T., Serracanta, M., Talavera, G., Dincă, V. and R. Vila. 2022. The atlas of mitochondrial genetic diversity for Western Palaearctic butterflies. Global Ecology and Biogeography, 31: 2184–2190. https://doi.org/10.1111/geb.13579.

deWaard, J.R., Ivanova, N.V., Hajibabaei, M. and P.D.N. Hebert. 2008. Assembling DNA barcodes. Analytical protocols. *In*: Martin CC, Martin CC (Eds) Environmental Genomics. Methods in Molecular Biology, vol 410. Humana Press, Totowa & New Jersey: 275–294. https://doi.org/10.1007/978-1-59745-548-0_15.

Emery, C. 1895. Sopra alcune formiche della fauna mediterranea. Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna (5)5: 59–75 [pagination of separate: 291–307].

Emery, C. 1898. Beiträge zur Kenntniss der palaearktischen Ameisen. Öfversigt af Finska Vetenskaps-Societetens Förhandlingar, 20: 124–151.

Emery, C. 1908. Beiträge zur Monographie der Formiciden des paläarktischen Faunengebietes. (Hym.) (Fortsetzung.) III. Die mit *Aphaenogaster* verwandte Gattungengruppe. Deutsche Entomologische Zeitschrift, 1908: 305–338.

Emery, C. 1915. Definizione del genere *Aphaenogaster* e partizione di esso in sottogeneri. *Parapheidole* e *Novomessor* nn. gg. Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna, Classe di Scienze Fisiche (n.s.), 19: 67–75.

Folmer, O., Black, M., Hoeh, W., Lutz, R. and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3: 294–299. https://pubmed.ncbi.nlm.nih. gov/7881515.

Galkowski, C., Aubert, C. and R. Blatrix. 2019. *Aphaenogaster ichnusa* Santschi, 1925, bona species, and redescription of *Aphaenogaster subterranea* (Latreille, 1798) (Hymenoptera, Formicidae). Sociobiology, 66(3): 420–425. https://doi.org/10.13102/sociobiology.v66i3.3660.

Gómez, K., Martinez, D. and X. Espadaler. 2018. Phylogeny of the ant genus *Aphaenogaster* (Hymenoptera: Formicidae) in the Iberian Peninsula, with the description of a new species. Sociobiology, 65(2): 215–224. https://doi.org 10.13102/sociobiology.v65i2.2099.

Harris, R.A. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology, State of California Department of Food and Agriculture, 28: 1–31.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. and L.S. Jermiin. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods, 14: 587–589. https://doi.org/10.1038/nmeth.4285.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. and A. Drummond. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics, 28(12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199.

Kiran, K., Aktaç, N. and S. Tezcan. 2008. Three new species of ants (genus *Aphaenogaster*, Hymenoptera: Formicidae) from Türkiye. Biológia (Bratislava), 63(5): 689–695. https://doi.org/10.2478/s11756-008-0123-y.

Kiran, K., and C. Karaman. 2020. Additions to the Ant Fauna of Turkey (Hymenoptera, Formicidae). Zoosystema, 42(18): 285–329. https://doi.org/10.5252/zoosystema2020 v42a18.

Kiran, K., and C. Karaman. 2021. Ant fauna (Hymenoptera: Formicidae) of Central Anatolian Region of Türkiye. Turkish Journal of Zoology, 45: 161–196. doi:10.3906/zoo-2008-6.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D.,

Woodhams, M.D., von Haeseler, A. and R. Lanfear. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution, 37: 1530–1534. https://doi.org/10.1093/molbev/msaa015.

Moradloo, S., Fard, R. N., Rad, S. P. and B. Taylor. 2015. Records of ants (Hymenoptera: Formicidae) from Northern Iran. Zoology in the Middle East, 61: 168–173. http://dx.doi.org/10.1080/09397140.2015.1020611.

Salata, S. and L. Borowiec. 2018. Redescription of *Aphaenogaster muschtaidica* Emery, 1908 with a key to *gibbosa* species group. Asian Myrmecology, 10: e010002. 10.20362/am.010002.

Salata, S., Karaman, C., Kiran, K. and L. Borowiec. 2021. Review of the *Aphaenogaster splendida* species-group (Hymenoptera: Formicidae). Annales Zoologici (Warsaw), 71: 297–343. 10.3161/00034541ANZ2021.71.2.008.

Santschi, F. 1925. Fourmis d'Espagne et autres espèces paléarctiques (Hymenopt.). EOS. Revista Española de Entomología, 1: 339–360.

Schifani, E., Costa, S., Mei, M. and A. Alicata. 2021. A new species for the Italian fauna: *Aphaenogaster strioloides*, not *A. crocea*, inhabits Pantelleria Island (Hymenoptera: Formicidae). Fragmenta Entomologica, 53(1): 21–24. 10.13133/2284-4880/482.

Schifani, E., Alicata, A., Menchetti, M., Borowiec, L., Fisher, B. L., Karaman, C., Kiran, K., Oueslati, W., Salata, S. and R. Blatrix. 2022. Revisiting the morphological species groups of West-Palearctic *Aphaenogaster* ants (Hymenoptera: Formicidae) under a phylogenetic perspective: toward an evolutionary classification. Arthropod Systematics and Phylogeny, 80: 627–648. 10.3897/asp.80.e84428.

Schifani, E., Alicata, A., Borowiec, L., García, F., Gentile, V., Gómez, K., Nalini, E., Rigato, F., Schär, S., Scupola, A., Vila, R. and M. Menchetti. 2023. Unrecognized for centuries: distribution and sexual caste descriptions of the West European *Aphaenogaster* species of the *subterranea* group (Hymenoptera, Formicidae). ZooKeys, 1153: 141–156. [online early] 10.3897/zookeys.1153.98297.

Schär, S., Menchetti, M., Schifani, E., Hinojosa, J.C., Platania, L., Dapporto, L. and R. Vila. 2020. Integrative biodiversity inventory of ants from a Sicilian archipelago reveals high diversity on young volcanic islands (Hymenoptera: Formicidae). Organisms Diversity & Evolution, 20(3): 405–416. https://doi.org/10.1007/s13127-020-00442-3.

Schulz, A. 1994. *Aphaenogaster graeca* nova species (Hym: Formicidae) aus dem Olymp-Gebirge (Griechenland) und eine Gliederung der Gattung *Aphaenogaster*. Beiträge zur Entomologie, 44: 417–429. https://doi.org/10.21248/contrib.entomol.44.2.417-429.

Wilson, E. O. 1955. A monographic revision of the ant genus *Lasius*. Bulletin of the Museum of Comparative Zoology, 113: 1–201.

Viehmeyer, H. 1922. Neue Ameisen. Archiv für Naturgeschichte, (A)88(7): 203–220.

Vonshak, M. and A. Ionescu-Hirsch. 2010 (2009). A checklist of the ants of Israel (Hymenoptera: Formicidae). Israel Journal of Entomology, 39: 33–55.

Table 1. GenBank accession numbers of newly generated COI sequences of species belonging to the *Aphaenogaster subterranea* species group.

Voucher	Accession number	Species	Legit	Country	LocLatitude	LocLongitude
LBC-GR01422	PP476387	*asterioni*	Salata, Sebastian	Greece	35.3336	24.6848
LBC-GR02372	PP476391	*tristis*	Borowiec, Lech	Greece	39.80844	22.68604
LBC-GR02691	PP476390	*tristis*	Borowiec, Lech	Greece	38.63619	23.81488
LBC-GR02934	PP476389	*tristis*	Borowiec, Lech	Greece	38.1571	20.62602
MM20C111a2	PP476432	*tristis*	Borowiec, Lech	Greece	38.63619	23.81488
MM20C149a1	PP476433	*tristis*	Borowiec, Lech	Greece	37.25344	22.59165
MM21B047a1	PP476450	*tristis*	Borowiec, Lech	Greece	37.22055	22.59165
MNHWGR03174	PP476388	*tristis*	Salata, Sebastian	Greece	37.14237	25.53209
MM20B132b1	PP476423	*epirotes*	Balevic, Nikola	Montenegro	42.45132	19.27469
MM21B015a1	PP476435	*epirotes*	Borowiec, Lech	Greece	39.34366	20.76352
MM21B016a1	PP476436	*epirotes*	Borowiec, Lech	Greece	38.6366	23.79593
MM21B017a1	PP476437	*epirotes*	Borowiec, Lech	Greece	38.12872	20.79576
MM21B018a1	PP476438	*epirotes*	Borowiec, Lech	Greece	39.74749	19.86375
MM21B019a1	PP476439	*epirotes*	Borowiec, Lech	Greece	39.32012	26.24461
MM21B020a1	PP476440	*epirotes*	Borowiec, Lech	Greece	39.48621	22.95425
MM21B021a1	PP476441	*epirotes*	Borowiec, Lech	Greece	37.79238	22.41455
MM21B022a1	PP476442	*epirotes*	Borowiec, Lech	Greece	37.72325	20.96123
MM21B023a1	PP476443	*epirotes*	Borowiec, Lech	Greece	37.78617	20.73706
MM21D379c1	PP476456	*epirotes*	Lapeva-Gjonova, Albena	Bulgaria	41.6297	25.8961
MM21D397c1	PP476457	*epirotes*	Lapeva-Gjonova, Albena	Greece	40.1542	22.3687
MM21D665c1	PP476460	*epirotes*	Salata, Sebastian	Croatia	45.15039	14.52427
MM16A193a1	PP476395	*ichnusa*	Mori, Emiliano	Italy	42.33586	10.91628
MM17A066a1	PP476396	*ichnusa*	Platania, Leonardo	Italy	42.75523	10.17051
MM17A099d1	PP476397	*ichnusa*	Menchetti, Mattia	Italy	40.6696	17.21613
MM17A108a1	PP476398	*ichnusa*	Menchetti, Mattia	Italy	40.88582	16.69287
MM18A043a1	PP476400	*ichnusa*	Menchetti, Mattia	Italy	43.86041	11.23954
MM18A045a1	PP476402	*ichnusa*	Mori, Emiliano	Italy	43.08852	10.98478
MM18A081a1	PP476403	*ichnusa*	Menchetti, Mattia	Spain	41.62077	2.014744
MM18A161a1	PP476405	*ichnusa*	Menchetti, Mattia; Sbrega, Elisabetta	Spain	41.98786	2.825964
MM19A350a1	PP476409	*ichnusa*	Platania, Leonardo	Italy	42.33353	10.29959
MM19A385a1	PP476410	*ichnusa*	Menchetti, Mattia	Spain	41.72705	2.278615
MM19A394a1	PP476411	*ichnusa*	Menchetti, Mattia	Spain	41.72668	2.276936
MM19A653b1	PP476412	*ichnusa*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	42.30114	12.16667
MM19A656a1	PP476413	*ichnusa*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	42.55203	12.71365
MM20A023a1	PP476417	*ichnusa*	Menchetti, Mattia	Italy	43.51312	11.80468
MM20A145e1	PP476419	*ichnusa*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	42.54898	12.8594
MM20B556b1	PP476425	*ichnusa*	D'Ambrosio, Matteo	Italy	41.93264	16.04951
MM20C011a1	PP476426	*ichnusa*	Schifani, Enrico	Italy	36.97935	15.07832
MM20C028a1	PP476428	*ichnusa*	Bertoni, Luca	Italy	38.02581	14.77567
MM20C050a1	PP476430	*ichnusa*	Nalini, Elia	Italy	43.85376	7.932088
MM20C051a1	PP476431	*ichnusa*	Viviano, Roberto	Italy	38.16928	13.12617
MM20C064a1	PP476481	*ichnusa*	Borowiec, Lech	Italy	39.79967	15.9101
MM20C081a1	PP476480	*ichnusa*	Borowiec, Lech	Italy	40.08709	15.39717
MM20C082a1	PP476479	*ichnusa*	Borowiec, Lech	Italy	40.08709	15.39717
MM21A282d1	PP476434	*ichnusa*	Ferruzzi, Paola; Menchetti, Stefano	Italy	40.75842	13.87101
MM21F084a1	PP476464	*ichnusa*	Piras, Roberto	Italy	39.82933	8.737026
MM21F250b1	PP476467	*ichnusa*	García, Fede	France	44.12408	5.26447
RVcoll12L328a1	PP476469	*ichnusa*	Talavera, Gerard	Spain	39.725	3.208
RVcoll12L426a1	PP476470	*ichnusa*	Talavera, Gerard	Spain	39.643	2.469
RVcoll17S454c1	PP476472	*ichnusa*	Vila, Roger	Italy	38.571	14.562

Table 1. Continued.

Voucher	Accession number	Species	Legit	Country	LocLatitude	LocLongitude
RVcoll17S466c1	PP476473	*ichnusa*	Hinojosa, Joan Carles; Schär, Sämi; Vila, Roger	Italy	38.5053	14.9301
RVcoll17S499c1	PP476474	*ichnusa*	Menchetti, Mattia; Schär, Sämi	Italy	38.5624	14.8444
RVcoll20C159b1	PP476475	*ichnusa*	Menchetti, Mattia; Vila, Roger; Hinojosa, Joan Carles	Spain	41.2578	0.742599
MM21B413a1	PP476453	*subcostata*	Kiran, Kadri; Karaman, Celal	Türkiye	36.7512	30.42076
LBC-GR00687	PP476392	*subterranea*	Borowiec, Lech	Greece	40.35945	22.25878
LBC-GR02667	PP476393	*subterranea*	Borowiec, Lech	Greece	38.56562	23.93159
MM16A188b1	PP476394	*subterranea*	Mori, Emiliano	Italy	43.94071	12.77235
MM17A144f1	PP476399	*subterranea*	Mocilnik, Giorgia	Italy	45.67054	13.80044
MM18A044a1	PP476401	*subterranea*	Menchetti, Mattia	Italy	43.85802	11.2392
MM18A160a1	PP476404	*subterranea*	Menchetti, Mattia; Sbrega, Elisabetta	Spain	41.98713	2.827922
MM18A179a1	PP476406	*subterranea*	Legittimo, Carlo	Italy	45.64363	13.81473
MM18A416a1	PP476407	*subterranea*	D'Amato, Mattia Francesco	Italy	40.6988	14.73752
MM19A168a1	PP476408	*subterranea*	Suchan, Tomasz	France	43.4261	2.617569
MM19A658a1	PP476414	*subterranea*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	42.4249	12.15536
MM19B228a1	PP476415	*subterranea*	Ritrovato, Roberto	Italy	38.85834	16.60056
MM20A003a1	PP476416	*subterranea*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	41.93135	12.49988
MM20A072a1	PP476418	*subterranea*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	43.43176	12.10014
MM20A149a1	PP476420	*subterranea*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	42.53929	12.72292
MM20A251a1	PP476421	*subterranea*	Menchetti, Mattia; Dapporto, Leonardo	Italy	42.21712	14.06076
MM20A282a1	PP476422	*subterranea*	Menchetti, Mattia; Sbrega, Elisabetta	Italy	44.18545	10.38004
MM20B171a1	PP476424	*subterranea*	Kragujevi, Tomislav	Croatia	45.71239	15.81252
MM20C026d1	PP476427	*subterranea*	Schifani, Enrico	Italy	44.768878	10.314738
MM20C046b1	PP476429	*subterranea*	Viviano, Roberto	Italy	37.87472	14.01778
MM21B031a2	PP476444	*subterranea*	Borowiec, Lech	Greece	39.1464	21.26745
MM21B036a2	PP476445	*subterranea*	Borowiec, Lech	Greece	39.32734	26.21009
MM21B038a1	PP476446	*subterranea*	Borowiec, Lech	Greece	40.00868	22.59654
MM21B039a1	PP476447	*subterranea*	Borowiec, Lech	Greece	39.99133	22.44169
MM21B042a2	PP476448	*subterranea*	Borowiec, Lech	Greece	41.06043	25.92451
MM21B043a1	PP476449	*subterranea*	Borowiec, Lech	Greece	38.15258	20.63944
MM21B050a1	PP476451	*subterranea*	Salata, Sebastian	Georgia	41.91278	45.4637
MM21B051a2	PP476452	*subterranea*	Borowiec, Lech	Greece	38.03864	22.25566
MM21D313b1	PP476454	*subterranea*	Lapeva-Gjonova, Albena	Albania	40.23843	20.64326
MM21D363b1	PP476455	*subterranea*	Lapeva-Gjonova, Albena	Bulgaria	42.0133	26.65374
MM21D422a1	PP476458	*subterranea*	Borowiec, Lech	Greece	38.58249	21.97418
MM21D457a1	PP476459	*subterranea*	Borowiec, Lech	Greece	38.17058	21.96326
MM21D665d1	PP476461	*subterranea*	Salata, Sebastian	Croatia	45.15039	14.52427
MM21E203a1	PP476462	*subterranea*	Montechiarini, Andrea	Italy	46.11373	9.261755
MM21E657c1	PP476463	*subterranea*	Drinic, David	Serbia	43.2575	22.54339
MM21F087c1	PP476465	*subterranea*	Alicata, Antonio	Italy	38.21282	15.88123
MM21F091a1	PP476466	*subterranea*	Crosato, Nicolò	Italy	45.99207	12.2915
MM21F468a1	PP476468	*subterranea*	Borowiec, Lech	Greece	40.7579	24.69427
RVcoll16B304a1	PP476471	*subterranea*	Makranczy, Gyorgy	Romania	45.0969	28.3858
RVcoll20C123a1	PP476478	*subterranea*	Menchetti, Mattia; Vila, Roger; Hinojosa, Joan Carles	Spain	41.668115	1.615106
RVcoll20C370a1	PP476476	*subterranea*	Vila, Roger; Hinojosa, Joan Carles; Talavera, Gerard	Romania	45.77011	26.99483
RVcoll20C413a1	PP476477	*subterranea*	Vila, Roger; Hinojosa, Joan Carles; Talavera, Gerard	Romania	44.43802	26.06454

Table 2. Distribution data of the investigated non-type material of species belonging to the *Aphaenogaster subterranea* species group.

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
asterioni	near Sfinari	Greece	35.41332	23.57353	120 m	GBC
asterioni	Zimbragou	Greece	35.44366	23.762845	234 m	BFUS
epirotes	Dajti	Albania	41.36192	19.91073	1054 m	BFUS
epirotes	Muzina 2	Albania	39.94019	20.22367	564 m	BFUS
epirotes	East Rhodopes. Gaberovo	Bulgaria	41.6297	25.8961	NA	MMC
epirotes	Eastern Rhodopes. Bryagovets	Bulgaria	41.6505	25.8181	336 m	BFUS
epirotes	Eastern Rhodopes. Chernichino	Bulgaria	41.5888	25.848	640 m	BFUS
epirotes	Eastern Rhodopes. Gaberovo	Bulgaria	41.6297	25.894	535 m	BFUS
epirotes	Eastern Rhodopes. Ivanovo	Bulgaria	41.8661	25.883	137 m	BFUS
epirotes	Eastern Rhodopes. Madzharovo	Bulgaria	41.6533	25.8872	297 m	BFUS
epirotes	Eastern Rhodopes. Odrintsi	Bulgaria	41.4502	26.138	217 m	BFUS
epirotes	Eastern Rhodopes. Oreshino	Bulgaria	41.46722	26.090833	276 m	BFUS
epirotes	Eastern Rhodopes. Siniger	Bulgaria	41.3865	25.7626	575 m	BFUS
epirotes	Eastern Rhodopes. Strazhets	Bulgaria	41.3788	25.8505	456 m	BFUS
epirotes	Eastern Rhodopes. Susam	Bulgaria	41.97103	25.3347	313 m	BFUS
epirotes	Eastern Rhodopes. Svirachi	Bulgaria	41.4766	26.1088	294 m	BFUS
epirotes	Maleshevska Mt. Mikrevo	Bulgaria	41.61305	23.1883	235 m	BFUS
epirotes	Sakar. Matochina	Bulgaria	41.8519	26.546	168 m	BFUS
epirotes	Strandzha Mt. Kosti	Bulgaria	42.0938	27.7886	280 m	BFUS
epirotes	Strandzha Mt. Malko Tarnovo. Propada	Bulgaria	41.9817	27.49222	385 m	BFUS
epirotes	Struma valley. General Todorov	Bulgaria	41.4659	23.2564	98 m	BFUS
epirotes	Struma valley. Kamenitsa	Bulgaria	41.65	23.167	240 m	BFUS
epirotes	Struma valley. Kresna gorge	Bulgaria	41.7952	23.1574	260 m	BFUS
epirotes	Struma valley. Yavorov station	Bulgaria	41.7533	23.1516	190 m	BFUS
epirotes	Malinska	Croatia	45.15038	14.5242	NA	MMC
epirotes	1 km S of Loucha	Greece	37.78414	20.72732	495 m	MNHW
epirotes	1 km SW of Ano Kerasia	Greece	39.48063	22.94874	580 m	MNHW
epirotes	1.2 km NE of Anafonitria	Greece	37.85489	20.64124	475 m	MNHW
epirotes	1.2 km SE of Loucha	Greece	37.78617	20.73706	445 m	MNHW
epirotes	1.2 km SW of Ano Vasilikos loc. 2	Greece	37.72325	20.96123	75 m	MNHW
epirotes	1.2 km SW of Ano Vasilikos loc. 2. Zakynthos	Greece	37.72325	20.96123	75 m	MMC
epirotes	1.4 km E of Ano Volimes	Greece	37.87594	20.68525	430 m	MNHW
epirotes	1.5 km N of Exo Chora	Greece	37.81446	20.68826	460 m	MNHW
epirotes	1.7 km NW of Pastra	Greece	38.1084	20.74085	335 m	MNHW
epirotes	1.9 km W of Maries	Greece	37.818	20.65556	290 m	MNHW
epirotes	2 km W Iti	Greece	38.73333	22.38333	836 m	MNHW
epirotes	2.5 km N of Kanalia	Greece	39.5226	22.88144	520 m	MNHW
epirotes	2.5 km NE of Maries	Greece	37.8299	20.70151	475 m	MNHW
epirotes	2.6 km SW of Glifada	Greece	38.6366	23.79593	650 m	MNHW
epirotes	3.4 km NE of Skalochori	Greece	39.27923	26.10926	292 m	MNHW
epirotes	500 m SW Therapeio centre	Greece	41.57517	26.18551	78 m	MNHW
epirotes	580 m SW of Lithakia	Greece	37.71491	20.8242	225 m	MNHW
epirotes	6 km NNW of Melia	Greece	41.00519	26.08169	310 m	MNHW
epirotes	600 m W of Panagia	Greece	40.73359	24.71967	335 m	MNHW
epirotes	670 m NE of Keri	Greece	37.66532	20.8214	185 m	MNHW
epirotes	880 m S of Orthonies	Greece	37.84462	20.69843	390 m	MNHW
epirotes	Ag. Spyridon beach n. Acharavi	Greece	39.7918	19.8181	13 m	MNHW
epirotes	Agrafa. Neochori	Greece	39.27323	21.73299	981 m	MNHW
epirotes	Ano Kerasia	Greece	39.48621	22.95425	660 m	MNHW
epirotes	Ano Meria	Greece	40.46641	25.67348	109 m	MNHW
epirotes	Argennos	Greece	39.35494	26.2661	548 m	MNHW
epirotes	Assos	Greece	39.34366	20.76352	440 m	MNHW
epirotes	Assos. Preveza. Epirus	Greece	39.34366	20.76352	440 m	MMC
epirotes	Gyftika Helicopter Airport loc. 2	Greece	37.1538	24.48086	171 m	MNHW

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
epirotes	Holomontas. Stagira	Greece	40.52896	23.74872	539 m	MNHW
epirotes	Ipsilometopo	Greece	39.32012	26.24461	485 m	MNHW
epirotes	Kalamata. suburban area	Greece	37.02334	22.13753	4 m	MNHW
epirotes	Kalivia-Kastro rd. loc. 2	Greece	40.6586	24.60666	135 m	MNHW
epirotes	Kardaras	Greece	37.6285	22.03	982 m	MNHW
epirotes	Kastro. Apostolus Waterfall	Greece	40.69069	24.66275	383 m	MNHW
epirotes	Kato Olimbos Mts. 6.1 km S of Kalipefki	Greece	39.91322	22.4641	855 m	MNHW
epirotes	Ligona Valley	Greece	39.32734	26.21009	229 m	MNHW
epirotes	Livia Mts. loc. 1	Greece	37.83018	20.71619	600 m	MNHW
epirotes	Meteora. ad St Nicolaos Anapausas	Greece	39.72275	21.62498	335 m	MNHW
epirotes	Mt. Olympus. Krevatia	Greece	40.15425	22.36873	975 m	BFUS
epirotes	Mt. Olympus. Litohoro vic.	Greece	40.09677	22.49301	470 m	MNHW
epirotes	Mt. Pandokrator	Greece	39.7438	19.8714	785 m	NHMC
epirotes	n. Karia loc. 1	Greece	37.63885	22.55093	697 m	MNHW
epirotes	n. Skotini	Greece	37.79238	22.41455	910 m	MNHW
epirotes	near Agia Triada	Greece	40.16738	22.39801	378 m	MNHW
epirotes	Nymfes	Greece	39.75478	19.79535	162 m	MNHW
epirotes	Old Perithia	Greece	39.76159	19.87412	467 m	MNHW
epirotes	Olympus Mt. Krevatia	Greece	40.1542	22.3687	NA	MMC
epirotes	Paleopoli	Greece	40.50436	25.52957	14 m	MNHW
epirotes	Panagia Kakaviotissa	Greece	39.87239	25.10797	161 m	MNHW
epirotes	Pandokrator. Korfu	Greece	39.74749	19.86375	736 m	MMC
epirotes	Parnon Mts. ad Charadros	Greece	37.33509	22.67388	654 m	MNHW
epirotes	Parnon Mts. 1.4 km NE of Sitena	Greece	37.30126	22.65989	749 m	MNHW
epirotes	Parnon Mts. rd to Sitena	Greece	37.27447	22.65289	772 m	MNHW
epirotes	Platamonas Castle hill	Greece	40.0073	22.59696	60 m	MNHW
epirotes	Poros-Skala rd.	Greece	38.12813	20.79509	13 m	MNHW
epirotes	rd. Sykaminia-Vigla	Greece	39.35468	26.30483	395 m	MNHW
epirotes	road Skala-Poros	Greece	38.12872	20.79576	5 m	MNHW
epirotes	road Skala-Poros. Cephalonia	Greece	38.1287	20.7958	5 m	MMC
epirotes	Saint Athanasius	Greece	36.69865	24.35182	49 m	MNHW
epirotes	Skala vic. loc. 3	Greece	38.08505	20.7926	50 m	MNHW
epirotes	Sotiras	Greece	40.71634	24.56997	242 m	MNHW
epirotes	Strinilas	Greece	39.73963	19.84265	632 m	MNHW
epirotes	Taygetos Mts. 0.6 km W of Artemisia	Greece	37.09877	22.22287	660 m	MNHW
epirotes	W of Kampi	Greece	37.78161	20.68078	165 m	MNHW
epirotes	Waterfalls of Milos	Greece	36.69332	24.37778	183 m	MNHW
epirotes	Podgorica (Gorica park)	Montenegro	42.45131	19.27469	NA	MMC
epirotes	10 km N Mugla	Türkiye	NA	NA	NA	MHNG
epirotes	Col de Boruera	Türkiye	NA	NA	NA	MHNG
epirotes	Marmaris	Türkiye	NA	NA	NA	MHNG
holtzi	Üzümbağı, İspir-Erzurum	Türkiye	40.7231	41.3261	1438 m	MNHW
holtzi	cca. 12 km E Karakurt	Türkiye	NA	NA	NA	MNHW
holtzi	Tunceli-Ovacik	Türkiye	NA	NA	1100 m	MHNG
ichnusa	2 km SW of Corte	France	42.289	9.132	480 m	MNHW
ichnusa	Draguignan	France	43.52304	6.45533	175 m	MNHW
ichnusa	Mont Ventoux	France	44.1241	5.26447	NA	MMC
ichnusa	Bosco delle Pianelle, Martina Franca, Taranto	Italy	40.6696	17.216128	NA	MMC
ichnusa	Cavagrande del Cassibile	Italy	36.9793	15.078315	NA	MMC
ichnusa	Cipressa	Italy	43.8538	7.93209	NA	MMC
ichnusa	Filicudi	Italy	38.5709	14.562	NA	MMC
ichnusa	Foresta di Mercadante, Cassano delle Murge, Bari	Italy	40.8858	16.6929	NA	MMC
ichnusa	Galati Mamertino	Italy	38.02580	14.7757	NA	MMC

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
ichnusa	Lipari	Italy	38.50529	14.93009	511 m	MMC
ichnusa	Monte Arci. Oristano	Italy	39.82933	8.73702	NA	MMC
ichnusa	Monte Bulgheria n. Poderia	Italy	40.08709	15.39717	380 m	MNHW
ichnusa	Monte Genuardo	Italy	37.6955	13.1532	NA	MMC
ichnusa	Monte Morello. Sesto Fiorentino. Florence	Italy	43.86040	11.239535	NA	MMC
ichnusa	Monte Pecoraro	Italy	38.16928	13.1262		MMC
ichnusa	Monte Petroso	Italy	38.01984	12.842762	270 m	MNHW
ichnusa	Montecristo	Italy	42.3335	10.29959	NA	MMC
ichnusa	Morro Reatino. Rieti	Italy	42.54899	12.859404	NA	MMC
ichnusa	n. Buonvicino	Italy	39.68705	15.90079	462 m	MNHW
ichnusa	n. San Sosti loc. 1	Italy	39.66698	16.00754	429 m	MNHW
ichnusa	Orsomarso	Italy	39.79967	15.9101	184 m	MNHW
ichnusa	Orsomarso vic. Fiume Argentino Valley	Italy	39.79454	15.92558	158 m	MNHW
ichnusa	Orsomarso. Cosenza	Italy	39.79967	15.9101	184 m	MMC
ichnusa	Parco Della Colombaia. Forio. Ischia	Italy	40.75842	13.871005	NA	MMC
ichnusa	Peschici-Vieste litoranea. Peschici	Italy	41.93264	16.049512	NA	MMC
ichnusa	Poggio Terneti. Isola del Giglio	Italy	42.33586	10.91627	NA	MMC
ichnusa	Ponte Buriano. Arezzo	Italy	43.5131	11.80467	NA	MMC
ichnusa	Prata. Grosseto	Italy	43.08851	10.984779	NA	MMC
ichnusa	Punta del Lago. Viterbo	Italy	42.30114	12.1667	NA	MMC
ichnusa	Salina	Italy	38.5624	14.8444	788 m	MMC
ichnusa	Vallebuia. Elba Island	Italy	42.7552	10.17051	NA	MMC
ichnusa	between rd. 35 to Tossa de Mar	Spain	41.733	2.883	123 m	MNHW
ichnusa	Bunyola vic. W slope of Namarich	Spain	39.7	2.71666	390 m	MNHW
ichnusa	Cabaces. Tarragona	Spain	41.2578	0.7426	NA	MMC
ichnusa	Castell de Santueri n. Felanitx	Spain	39.41666	3.16666	310 m	MNHW
ichnusa	Ermita San Salvador n. Felanitx	Spain	39.45	3.16666	310 m	MNHW
ichnusa	Figaró-Montmany. Barcelona	Spain	41.72705	2.27861	NA	MMC
ichnusa	Girona	Spain	41.98786	2.825964	NA	MMC
ichnusa	Malgrat de Mar	Spain	41.63333	2.71666	50 m	MNHW
ichnusa	Mallorca. Puig Galatzó	Spain	39.643	2.46899	439 m	MMC
ichnusa	Mallorca. Santa Margalida	Spain	39.725	3.208	36 m	MMC
ichnusa	Montseny	Spain	41.75	2.04	590 m	MNHW
ichnusa	Montseny. Piscines del Montseny	Spain	41.7611	2.3879	400 m	MNHW
ichnusa	Parc Natural de Sant Llorenç del Munt i l'Obac. Barcelona	Spain	41.6207	2.01474	NA	MMC
maculifrons	Akşehir-Eskiler Vill.	Türkiye	38.15431	31.52139	1770 m	MNHW
maculifrons	ancient Termessos	Türkiye	36.96666	30.45	1018 m	MNHW
subcostata	1.3 km S of Kastania	Greece	37.74216	26.69263	350 m	MNHW
subcostata	Nera	Greece	36.913	26.94	15 m	MNHW
subcostata	Pandroso	Greece	37.73165	26.82803	670 m	MNHW
subcostata	Vigla	Greece	37.7	26.63333	15 m	MNHW
subcostata	5km N Alanya. Umliegendes Berglan	Türkiye	NA	NA	500 m	MHNG
subcostata	Antalya- Merkez-Hisarçandır Vill.	Türkiye	36.7512	30.42076	837 m	MMC
subterranea	Repisht 3	Albania	42.247	19.5812	852 m	MNHW
subterranea	Shalës	Albania	40.2384	20.6433	873 m	MNHW
subterranea	Aëtos (Aytos)	Bulgaria	NA	NA	NA	MHNG
subterranea	Batovo	Bulgaria	43.40508	27.95052	60 m	BFUS
subterranea	Belasitsa Mt. Kamena	Bulgaria	41.36463	23.07567	449 m	BFUS
subterranea	Black Sea coast - Chernomorec	Bulgaria	42.41666	27.6	100 m	MNHW
subterranea	Brodilovo vill. Papiya loc.	Bulgaria	42.1133	27.8361	258 w	MNHW
subterranea	Domlyan vill. 2	Bulgaria	42.5408	24.9407	369 m	MNHW
subterranea	East Rhodopes. Belopoltsi	Bulgaria	41.5141	25.8072	577 m	BFUS
subterranea	Eastern Rhodopes. Dolno lukovo	Bulgaria	41.36381	26.06563	120 m	BFUS

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
subterranea	Eastern Rhodopes. Huhla	Bulgaria	41.57233	26.07183	134 m	BFUS
subterranea	Eastern Rhodopes. Ivaylovgrad. Armira	Bulgaria	41.51056	26.08056	270 m	BFUS
subterranea	Eastern Rhodopes. Madzharovo	Bulgaria	41.6533	25.8872	297 m	BFUS
subterranea	Eastern Rhodopes. Malka chinka	Bulgaria	41.4	25.5222	384 m	BFUS
subterranea	Eastern Rhodopes. Meden buk	Bulgaria	41.38038	26.02505	134 m	BFUS
subterranea	Eastern Rhodopes. Mezek	Bulgaria	41.73528	26.08194	226 m	BFUS
subterranea	Eastern Rhodopes. Odrintsi	Bulgaria	41.4502	26.138	217 m	BFUS
subterranea	Eastern Rhodopes. Oreshino	Bulgaria	41.46722	26.09083	276 m	BFUS
subterranea	Eastern Rhodopes. Plevun	Bulgaria	41.4589	26.0146	415 m	BFUS
subterranea	Eastern Rhodopes. Senoklas	Bulgaria	41.6066	25.9394	285 m	BFUS
subterranea	Gaberovo vill.	Bulgaria	41.6297	25.894	535 m	MNHW
subterranea	Goleshovo vill.	Bulgaria	41.4213	23.625	1094 m	MNHW
subterranea	Gorna Breznitsa vill.	Bulgaria	41.7507	23.1093	482 m	MNHW
subterranea	Kamena vill.	Bulgaria	41.3591	23.0734	479 m	MNHW
subterranea	Karlukovo	Bulgaria	43.1573	24.0858	300 m	BFUS
subterranea	Kiten	Bulgaria	42.2383	27.7725	18 m	BFUS
subterranea	Kosti vill. St. Ilia loc.	Bulgaria	42.0589	27.7633	38 m	MNHW
subterranea	Kozhuh. Rupite	Bulgaria	41.45997	23.25311	185 m	BFUS
subterranea	Lakovo	Bulgaria	42.0598	26.7322	186 m	BFUS
subterranea	Madzharovo	Bulgaria	41.6206	25.8856	280 m	MNHW
subterranea	Malko Gradishte vill.	Bulgaria	41.59	25.5029	554 m	MNHW
subterranea	Malko Tarnovo	Bulgaria	41.9794	27.5138	348 m	MNHW
subterranea	Malko Tarnovo. Propada loc.	Bulgaria	41.9817	27.4922	385 m	MNHW
subterranea	Mladezhko vill. along the river	Bulgaria	42.1517	27.3619	222 m	MNHW
subterranea	Pirin Mt. Bukovo	Bulgaria	41.696	23.705	598 m	BFUS
subterranea	Pirin Mt. Vlahi	Bulgaria	41.7417	23.2319	543 m	BFUS
subterranea	Piyavets vill.	Bulgaria	41.4878	25.4615	578 m	MNHW
subterranea	Pryaporets vill.	Bulgaria	42.4508	25.5219	356 m	MNHW
subterranea	Sakar. Studena	Bulgaria	41.904	26.407	276 m	BFUS
subterranea	Senovo	Bulgaria	43.6538	26.3466	164 m	BFUS
subterranea	Shumnatitsa vill.	Bulgaria	41.2862	25.3731	411 m	MNHW
subterranea	Sinemorets vill. Butamyata loc.	Bulgaria	42.0528	27.9869	17 m	MNHW
subterranea	South Pirin. Kalimantsi	Bulgaria	41.46373	23.48675	312 m	BFUS
subterranea	Strandzha Mt. Kosti	Bulgaria	42.09389	27.78694	280 m	BFUS
subterranea	Strandzha Mt. Kalovo	Bulgaria	42.1387	27.5357	324 m	BFUS
subterranea	Strandzha Mt. Mladezhko	Bulgaria	42.1517	27.3619	222 m	BFUS
subterranea	Strandzha Mt. Sinemorets. Veleka mouth	Bulgaria	42.0608	27.9653	5 m	BFUS
subterranea	Strandzha Mt. Slivarovo	Bulgaria	41.96056	27.6597	224 m	BFUS
subterranea	Strandzha. Fazanovo	Bulgaria	42.1647	27.7342	60 m	BFUS
subterranea	Strandzha. Propada	Bulgaria	41.98167	27.49222	377 m	BFUS
subterranea	Strandzha. Sinemorets	Bulgaria	42.06083	27.9653	5 m	BFUS
subterranea	Strandzha. Sinemorets. Butamyata	Bulgaria	42.05278	27.98694	17 m	BFUS
subterranea	Valcha plyana	Bulgaria	42.0133	26.6537	307 m	BFUS
subterranea	Varna. Botanical garden	Bulgaria	43.2358	28.0021	41 m	BFUS
subterranea	Vrachanski karst. Darvodeltsi river	Bulgaria	43.1783	23.5775	534 m	BFUS
subterranea	Vratsa. Voyvodin dol	Bulgaria	43.18667	23.53139	600 m	BFUS
subterranea	Vratsata loc.	Bulgaria	43.1909	23.5303	432 m	MNHW
subterranea	Yavornitsa vill.	Bulgaria	41.3578	23.0504	600 m	MNHW
subterranea	Zemen. Shegava	Bulgaria	42.39306	22.71028	523 m	BFUS
subterranea	4 km NW of Grabarje	Croatia	45.245	18.00333	160 m	GBC
subterranea	Horvati. Zagreb. forest nearby	Croatia	45.71238	15.812519	NA	MMC
subterranea	Malinska	Croatia	45.15039	14.5242	NA	MMC
subterranea	Mt. Senjsko bilo. 7 km NW of Krasno	Croatia	NA	NA	1100 m	MNHW
subterranea	near Kloštar, Limski kanal	Croatia	45.14167	13.70667	120 m	GBC
subterranea	17 km W of Brive-la-Gaillarde	France	45.101	1.3	170 m	MNHW

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
subterranea	2 km S of Brive-la-Gaillarde	France	45.129	1.491	140 m	MNHW
subterranea	Draguignan	France	43.54637	6.48804	400 m	MNHW
subterranea	Ferrals-les-Montagnes	France	43.42610	2.617569	NA	MMC
subterranea	Saint-Aubin-de-Médoc	France	44.925	-0.729	40 m	MNHW
subterranea	Okatse canyon	Georgia	42.4484	42.54885	475 m	MNHW
subterranea	Telavi forest	Georgia	41.91278	45.46377	823 m	MNHW
subterranea	Telavi walls	Georgia	41.92171	45.47211	713 m	MNHW
subterranea	Telavi. Kakheti	Georgia	41.91278	45.4637	823 m	MMC
subterranea	1 km N of Palaghia	Greece	40.9194	25.86687	329 m	MNHW
subterranea	1.2 km NW of A. Kotsanopoulo	Greece	39.23467	20.70309	170 m	MNHW
subterranea	1.3 km NE of Athamania	Greece	39.37919	21.23158	850 m	MNHW
subterranea	1.3 km SW of Kato Drosini	Greece	41.21515	25.59189	255 m	MNHW
subterranea	1.4 km N of Agia Triada	Greece	38.57225	23.93041	890 m	MNHW
subterranea	1.4 km W of Neo Pagontas	Greece	38.6755	23.53914	260 m	MNHW
subterranea	1.5 km SW of Koutourla	Greece	38.62838	23.92772	695 m	MNHW
subterranea	1.6 km N Xirolivado	Greece	38.98628	21.21172	300 m	MNHW
subterranea	1.6 km NW of Dadia	Greece	41.13659	26.20799	39 m	MNHW
subterranea	1.6 km NW of Kato Seta	Greece	38.55105	23.92852	765 m	MNHW
subterranea	1.8 km S of Thassos	Greece	40.7579	24.69427	100 m	MNHW
subterranea	1.9 km NE of Kanali	Greece	39.06969	20.71734	115 m	MNHW
subterranea	12 km S of Livadero	Greece	41.2351	24.1936	500 m	NHMC
subterranea	2 km NW of Kottani	Greece	41.32143	25.07343	312 m	MNHW
subterranea	2 km S of Skoulikaria	Greece	39.158	21.27393	890 m	MNHW
subterranea	2.2 km SE of Stropones	Greece	38.5997	23.9001	735 m	MNHW
subterranea	2.3 km S of Sikies	Greece	39.27264	20.6813	215 m	MNHW
subterranea	2.4 km SE of Pachtouri	Greece	39.45672	21.27687	655 m	MNHW
subterranea	2.5 km SE of Pentalofos	Greece	41.63021	26.20642	205 m	MNHW
subterranea	2.5 km SW of Thermes	Greece	41.34488	24.96146	658 m	MNHW
subterranea	2.7 km NW of Lefkimi	Greece	41.03864	26.16716	218 m	MNHW
subterranea	2.7 km SE of Stropones	Greece	38.59851	23.9085	855 m	MNHW
subterranea	2.8 km W of Dadia	Greece	41.1241	26.19078	141 m	MNHW
subterranea	3 km N of Kanalia	Greece	39.52494	22.8887	555 m	MNHW
subterranea	3 km NE of Steni	Greece	38.59785	23.86556	955 m	MNHW
subterranea	3 km NW of Petrota	Greece	41.71235	26.11475	194 m	MNHW
subterranea	3 km S of Thassos	Greece	40.74456	24.6975	272 m	MNHW
subterranea	3 km W of Timfristos	Greece	38.91666	21.91666	908 m	MNHW
subterranea	3.7 km SW of Metochi	Greece	38.60402	23.91683	830 m	MNHW
subterranea	4.4 km NW of Lefkimi	Greece	41.05035	26.15935	278 m	MNHW
subterranea	5 km SW of Pentalofos	Greece	41.63514	26.12102	411 m	MNHW
subterranea	5.5 km SW of Pentalofos	Greece	41.63331	26.11415	435 m	MNHW
subterranea	500 m SW Therapeio centre	Greece	41.57517	26.18551	78 m	MNHW
subterranea	570 m NW of Drosia	Greece	38.61705	23.59089	140 m	MNHW
subterranea	6 km NNW of Melia	Greece	41.00519	26.08169	310 m	MNHW
subterranea	6.6 km NE of Leptokarya	Greece	41.10698	25.96444	932 m	MNHW
subterranea	600 m W of Panagia	Greece	40.73359	24.71967	335 m	MNHW
subterranea	650 m NE of Seta	Greece	38.53777	23.92516	725 m	MNHW
subterranea	7 km W of Dadia	Greece	41.12062	26.14339	295 m	MNHW
subterranea	700 m E of Kanali	Greece	39.0638	20.70621	50 m	MNHW
subterranea	700 m N of Agia Triada	Greece	38.56562	23.93159	810 m	MNHW
subterranea	Acheron Gorge	Greece	39.28772	20.68153	190 m	MNHW
subterranea	ad Potamia	Greece	40.71867	24.71943	212 m	MNHW
subterranea	ad. Reresi	Greece	38.50798	21.99851	198 m	MNHW
subterranea	Ag. Ilias	Greece	39.79367	19.87508	191 m	MNHW
subterranea	Agia Triada	Greece	38.5594	23.93304	875 m	MNHW
subterranea	Agrafa. 1.4 km N of Oxia	Greece	39.37049	21.59365	1073 m	MNHW

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
subterranea	Agrafa. 700 m SW of Anthiro	Greece	39.19559	21.74626	827 m	MNHW
subterranea	Agrafa. 970 m N of Elatos	Greece	39.24775	21.68767	970 m	MNHW
subterranea	Agrafa. ad Longa	Greece	39.2537	21.71575	833 m	MNHW
subterranea	Agrafa. Filakti	Greece	39.3037	21.67199	1125 m	MNHW
subterranea	Agrafa. Koutsodimos	Greece	39.32301	21.6985	859 m	MNHW
subterranea	Agrafa. Vragiana	Greece	39.21302	21.63568	1101 m	MNHW
subterranea	Ainos Mts. loc. 3. Cephalonia	Greece	38.15258	20.63944	1330 m	MMC
subterranea	Aliki	Greece	40.60335	24.74164	18 m	MNHW
subterranea	Ano Kerasia	Greece	39.48621	22.95425	660 m	MNHW
subterranea	Aroania Mts. n. Agridi	Greece	38.03864	22.25566	1000 m	MNHW
subterranea	Chorepiskopi-Valanio rd. loc. 3	Greece	39.73027	19.75743	150 m	MNHW
subterranea	Chrisopigi	Greece	39.11252	21.20878	580 m	MNHW
subterranea	Dadia	Greece	41.12367	26.21939	134 m	MNHW
subterranea	Dadia forest. Tres Vryses	Greece	41.11395	26.02515	648 m	MNHW
subterranea	E of Kechrokampos	Greece	41.154	24.704	450 m	MNHW
subterranea	E of Nymfes	Greece	39.75047	19.8057	179 m	MNHW
subterranea	Elatou-Ano Chora rd. loc. 1	Greece	38.58664	21.95837	1290 m	MNHW
subterranea	Enos Mts. loc. 2	Greece	38.15273	20.6393	1336 m	MNHW
subterranea	Erimanthos Mts. 1.25 km m NW of Neochori	Greece	38.05346	21.97405	913 m	MNHW
subterranea	Erimanthos Mts. 870 m NW of Neochori	Greece	38.05432	21.98038	908 m	MNHW
subterranea	Erimanthos Mts. ad. Flampoura	Greece	38.04458	21.99947	644 m	MNHW
subterranea	Fiona gorge loc. 2	Greece	40.4759	25.64054	243 m	MNHW
subterranea	Gria Vathra ad Therma	Greece	40.48716	25.6113	198 m	MNHW
subterranea	Holomontas. 3.9 km SE of Varvara	Greece	40.54601	23.69197	730 m	MNHW
subterranea	Holomontas. 4.5 km SE of Varvara	Greece	40.54458	23.70115	719 m	MNHW
subterranea	Holomontas. ad Polygyros	Greece	40.38264	23.46007	704 m	MNHW
subterranea	Holomontas. n. Arnea	Greece	40.46666	23.55	790 m	MNHW
subterranea	Holomontas. n. Taxiarhis	Greece	40.4	23.51666	594 m	MNHW
subterranea	Holomontas. Pente Vryses rest area	Greece	40.57649	23.71999	453 m	MNHW
subterranea	Holomontas. Stagira	Greece	40.52896	23.74872	539 m	MNHW
subterranea	Holomontas. Stagira-Neochori rd.	Greece	40.51666	23.7	512 m	MNHW
subterranea	Holomontas. Taxiarhis-Paleokastro rd.	Greece	40.41666	23.5	896 m	MNHW
subterranea	Holomontas. Vrastama-Taxiarhis rd.	Greece	40.38333	23.51666	626 m	MNHW
subterranea	Kardaras-Vitina rd. loc. 1	Greece	37.62478	22.27755	1163 m	MNHW
subterranea	Kassandra. Kassandrino-Polihrono rd.	Greece	40.000	23.43333	100 m	MNHW
subterranea	Kassandra. Loutra	Greece	39.91666	23.58333	22 m	MNHW
subterranea	Kassandra. Siviri-Elani rd.	Greece	40.03333	23.35	41 m	MNHW
subterranea	Kastro. Apostolus Waterfall	Greece	40.69069	24.66275	383 m	MNHW
subterranea	Kato Olimbos Mts. 1 km SE of Ano Skotina	Greece	39.98556	22.53947	770 m	MNHW
subterranea	Kato Olimbos Mts. 1.1 km W of Ano Skotina	Greece	39.99097	22.5198	940 m	MNHW
subterranea	Kato Olimbos Mts. 6.2 km S of Sikaminea	Greece	39.90736	22.37109	760 m	MNHW
subterranea	Kato Olympus Mts. Pandeleimonas-Ano Skotina rd.	Greece	39.9851	22.54676	738 m	MNHW
subterranea	Kato Olympus Mts. road to Pandeleimonas	Greece	39.9888	22.59519	279 m	MNHW
subterranea	Kato Olympus. north of the road	Greece	39.97531	22.43501	995 m	MNHW
subterranea	Klimatia	Greece	39.74123	19.78953	311 m	MNHW
subterranea	Komnina-Livera	Greece	41.1595	24.6961	450 m	NHMC
subterranea	Ligona Valley	Greece	39.32734	26.21009	229 m	MNHW
subterranea	Menoikio Mt. Mikropoli;	Greece	41.18266	23.79965	745 m	BFUS
subterranea	Meteora. ad St Nicolaos Anapausas	Greece	39.72275	21.62498	335 m	MNHW

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
subterranea	Metsovo	Greece	39.7694	21.1904	977 m	MNHW
subterranea	Moni Agiou Panteleimonos	Greece	40.70643	24.59932	742 m	MNHW
subterranea	Mt Ditiko Mainalo. 1.4 km S of Limbovisi	Greece	37.57132	22.18845	1131 m	MNHW
subterranea	Mt Ditiko Mainalo. 1.6 km NW of Chrisivitsi	Greece	37.55723	22.19665	1125 m	MNHW
subterranea	Mt Ditiko Mainalo. ad Limbovisi	Greece	37.58202	22.19006	1186 m	MNHW
subterranea	Mt Fonias. ad Kantaratika	Greece	40.46092	25.64199	892 m	MNHW
subterranea	Mt. Falakro	Greece	41.2939	24.0948	1300 m	NHMC
subterranea	Mt. Kapsalo NW of Lefkimi	Greece	41.09038	26.13448	572 m	MNHW
subterranea	Mt. Olympus. 1.6 km SW of Litohoro	Greece	40.08929	22.48804	575 m	MNHW
subterranea	Mt. Olympus. 3.9 km E of Karya	Greece	39.99133	22.44169	790 m	MNHW
subterranea	Mt. Olympus. 4.6 km E of Karya	Greece	39.99709	22.44375	830 m	MNHW
subterranea	Mt. Olympus. 5.3 km E of Olimpiada	Greece	40.00989	22.31096	800 m	MNHW
subterranea	Mt. Olympus. 6.2 km NE of Karya	Greece	40.00703	22.46108	935 m	MNHW
subterranea	Mt. Olympus. Ag. Joannis n. Litohoro	Greece	40.08377	22.48775	580 m	MNHW
subterranea	Mt. Olympus. Litohoro vic.	Greece	40.09677	22.49301	470 m	MNHW
subterranea	Mt. Olympus. Old Ag. Moni Dionizou vic.	Greece	40.09207	22.42658	870 m	MNHW
subterranea	Mt. Olympus. Prionia loc. 1	Greece	40.08523	22.40733	1065 m	MNHW
subterranea	Mt. Olympus. Prionia-Mt. Olympus trail loc. 1	Greece	40.08122	22.400123	1200 m	MNHW
subterranea	Mt. Ossa ski center	Greece	39.80844	22.68604	1520 m	MNHW
subterranea	Mt. Ossa. 1.3 km SE of Karitsa	Greece	39.88331	22.77258	360 m	MNHW
subterranea	Mt. Ossa. 1.9 km NW of Karitsa	Greece	39.84991	22.74069	435 m	MNHW
subterranea	Mt. Ossa. 2.4 km SE of Karitsa	Greece	39.82632	22.77557	425 m	MNHW
subterranea	Mt. Ossa. 600 m SE of Karitsa	Greece	39.84009	22.76983	300 m	MNHW
subterranea	Mt. Ossa. Karitsa-Spilia rd. km 2.7	Greece	39.84991	22.74069	510 m	MNHW
subterranea	Mt. Ossa. Karitsa-Spilia rd. km 3.5	Greece	39.84663	22.7216	680 m	MNHW
subterranea	Mt. Ossa. Kokkino Nero	Greece	39.83389	22.79379	3 m	MNHW
subterranea	Mt. Pandokrator	Greece	39.74749	19.86375	736 m	MNHW
subterranea	Mt. Pandokrator loc. 2	Greece	39.73221	19.84825	748 m	MNHW
subterranea	N of Avandas loc. 1	Greece	40.94276	25.91075	97 m	MNHW
subterranea	N of Avandas loc. 2	Greece	40.94644	25.90533	101 m	MNHW
subterranea	N of Avandas loc. 3	Greece	40.97921	25.91529	151 m	MNHW
subterranea	n. Analipsi	Greece	39.47045	20.76412	780 m	MNHW
subterranea	n. Avra	Greece	40.92227	25.67666	247 m	MNHW
subterranea	n. Evrostina	Greece	38.07386	22.39388	662 m	MNHW
subterranea	n. Giannioti loc. 1	Greece	39.1464	21.26745	950 m	MNHW
subterranea	n. Giannioti loc. 2	Greece	39.14579	21.2725	945 m	MNHW
subterranea	n. K. Kotsanopoulo	Greece	39.19554	20.72153	95 m	MNHW
subterranea	n. Kanali	Greece	39.05458	20.70207	15 m	MNHW
subterranea	n. Leptokarya	Greece	41.06553	25.90852	753 m	MNHW
subterranea	n. Lippa	Greece	39.46813	20.75004	783 m	MNHW
subterranea	n. Vlahokerasea	Greece	37.37659	22.39035	887 m	MNHW
subterranea	n. Vourgareli	Greece	39.37527	21.19403	795 m	MNHW
subterranea	near Agia Triada	Greece	40.16738	22.39801	378 m	MNHW
subterranea	near old monastery of Agios Dionysios	Greece	40.09394	22.42635	863 m	MNHW
subterranea	Nestos river n. Komnina	Greece	41.169	24.6966	100 m	NHMC
subterranea	Nymfes	Greece	39.75478	19.79535	162 m	MNHW
subterranea	Nymfes waterfall	Greece	39.75076	19.80541	158 m	MNHW
subterranea	Olympus Mts. Monastery St. Dionysios	Greece	40.09633	22.420415	1001 m	BFUS
subterranea	Olympus Mts. Fotina-Petra rd. loc. 1	Greece	40.21229	22.31785	249 m	MNHW
subterranea	Olympus Mts. Fotina-Petra rd. loc. 2	Greece	40.20049	22.3167	386 m	MNHW
subterranea	Olympus Mts. Leptokaria-Karia rd.	Greece	40.0373	22.52403	227 m	MNHW
subterranea	Olympus Mts. Litochoro-Ag. Ioannis rd.	Greece	40.08993	22.48833	575 m	MNHW
subterranea	Olympus Mts. Litochoro-Faragi Enipeas	Greece	40.10449	22.49286	322 m	MNHW

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
subterranea	Olympus Mts. Litochoro-Olympus rd.	Greece	40.10747	22.45951	1055 m	MNHW
subterranea	Olympus Mts. Petra vic.	Greece	40.17741	22.32991	584 m	MNHW
subterranea	Olympus Mts. Prionia	Greece	40.0859	22.406982	1059 m	BFUS
subterranea	Ossa Mts. Ag. Dimitrios Mon. n. Stomio	Greece	39.85903	22.74025	162 m	MNHW
subterranea	Ossa Mts. Omoli-Stomio rd. loc. 2	Greece	39.8708	22.69751	84 m	MNHW
subterranea	Ossa Mts. Stomio-Karitsa rd.	Greece	39.85775	22.74714	137 m	MNHW
subterranea	Panagia	Greece	40.72903	24.72557	298 m	MNHW
subterranea	Panahaiko Mts. Rakita	Greece	38.1531	21.94737	1165 m	MNHW
subterranea	Panahaiko Mts. rd. Kounina-Rakita loc. 4	Greece	38.17058	21.96326	1056 m	MNHW
subterranea	Panahaiko Mts. rd. Kounina-Rakita loc. 6	Greece	38.16134	21.94786	1123 m	MNHW
subterranea	Parnon Mts. 600 m N of Nea Hora	Greece	37.37269	22.54888	638 m	MNHW
subterranea	Parnon Mts. ad Kastri	Greece	37.35639	22.52906	983 m	MNHW
subterranea	Parnon Mts. Nea Hora	Greece	37.3687	22.545	725 m	MNHW
subterranea	Parnon Mts. Kastanitsa	Greece	37.25847	22.64858	868 m	MNHW
subterranea	Partheno Dasos	Greece	41.5056	24.4288	995 m	NHMC
subterranea	Pieria Mts. 1.8 km E Rizomata	Greece	40.35607	22.23148	668 m	MNHW
subterranea	Pieria Mts. 2.3 km N Elatochori	Greece	40.33972	22.25685	748 m	MNHW
subterranea	Pieria Mts. 4.5 km N Elatochori	Greece	40.35945	22.25878	762 m	MNHW
subterranea	Pieria Mts. Aliakomonas Lake n. Sfikia	Greece	40.41376	22.19501	88 m	MNHW
subterranea	Pieria Mts. Fotina	Greece	40.22121	22.30627	398 m	MNHW
subterranea	Pieria Mts. Fotina-Skotina rd.	Greece	40.22074	22.29231	567 m	MNHW
subterranea	Pieria Mts. Ritini-Elatochori rd.	Greece	40.3026	22.26633	748 m	MNHW
subterranea	Pieria Mts. Skotina	Greece	40.20001	22.23222	649 m	MNHW
subterranea	Platamonas Castle	Greece	40.0057	22.59873	106 m	MNHW
subterranea	Platamonas Castle hill	Greece	40.00868	22.59654	12 m	MNHW
subterranea	Prasinada n. monastery	Greece	41.3694	24.5489	700 m	NHMC
subterranea	Psila Alonia	Greece	38.96255	21.19527	62 m	MNHW
subterranea	rd. Alexandroupolis-Kirki loc. 1	Greece	40.90222	25.83497	118 m	MNHW
subterranea	rd. Alexandroupolis-Kirki loc. 2	Greece	40.91697	25.81271	221 m	MNHW
subterranea	rd. Essymi-Leptokarya loc. 1	Greece	41.06043	25.92451	687 m	MNHW
subterranea	rd. Essymi-Leptokarya loc. 2	Greece	41.06121	25.9122	752 m	MNHW
subterranea	rd. Leptokarya-Mega Derio loc. 1	Greece	41.1186	25.94328	859 m	MNHW
subterranea	rd. Leptokarya-Mega Derio loc. 2	Greece	41.15638	25.92475	819 m	MNHW
subterranea	rd. Leptokarya-Mega Derio loc. 4	Greece	41.16249	25.95632	715 m	MNHW
subterranea	riveredge below old monastery of Agios Dionysios	Greece	40.09347	22.43066	800 m	MNHW
subterranea	road to Marble Beach loc. 2	Greece	40.73993	24.74711	262 m	MNHW
subterranea	road to P. Poroi loc. 4	Greece	39.96824	22.59625	370 m	MNHW
subterranea	SE of Thermes	Greece	41.35084	24.99243	439 m	MNHW
subterranea	Sithona. Parthenonas	Greece	40.1195	23.81297	305 m	MNHW
subterranea	Steni Dirfyos	Greece	38.58703	23.84533	480 m	MNHW
subterranea	Taygetos Mts. 0.6 km W of Artemisia	Greece	37.09877	22.22287	660 m	MNHW
subterranea	Taygetos Mts. 1.3 km S of Artemisia	Greece	37.08738	22.23378	870 m	MNHW
subterranea	Taygetos Mts. 1.5 km SW of Anavryti	Greece	37.0191	22.36003	990 m	MNHW
subterranea	Taygetos Mts. Nedoussa	Greece	37.14408	22.23208	690 m	MNHW
subterranea	Taygetos Mts. Piges	Greece	37.0968	22.24031	650 m	MNHW
subterranea	Taygetos Mts. rd. Kalamati-Sparta loc. 2	Greece	37.06412	22.26539	1290 m	MNHW
subterranea	Tetrazi Mts. 1km SE of Dassochori	Greece	37.33491	21.98344	670 m	MNHW
subterranea	Tetrazi Mts. Isaris	Greece	37.36644	22.01516	790 m	MNHW
subterranea	Valanio	Greece	39.73443	19.76401	150 m	MNHW
subterranea	Vlahokerasea-Kollines rd. loc. 1	Greece	37.36013	22.38003	1033 m	MNHW
subterranea	Vlahokerasea-Kollines rd. loc. 2	Greece	37.35144	22.38858	1064 m	MNHW
subterranea	W of Elatou	Greece	38.58249	21.97418	1077 m	MNHW
subterranea	Alpe di Corfino. Corfino. Lucca	Italy	44.18545	10.38003	NA	MMC

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
subterranea	Aspromonte. T. Vasi. Cosoleto. Reggio Calabria	Italy	38.21282	15.8812	NA	MMC
subterranea	Bagnaia. Viterbo	Italy	42.4249	12.1553	NA	MMC
subterranea	Catanzaro	Italy	38.85833	16.60056	NA	MMC
subterranea	Croce. Cava de' Tirreni. Salerno	Italy	40.6988	14.7375	NA	MMC
subterranea	Gradara. Pesaro Urbino	Italy	43.9407	12.77234	NA	MMC
subterranea	Gravedona	Italy	46.15	9.3	320 m	MNHW
subterranea	Lettomanoppello. Pescara	Italy	42.2171	14.06076	NA	MMC
subterranea	Marmore. Terni	Italy	42.53929	12.72292	NA	MMC
subterranea	Monte Morello. Sesto Fiorentino. Florence	Italy	43.85802	11.2392	NA	MMC
subterranea	Musso	Italy	46.11373	9.26175	NA	MMC
subterranea	n. Buonvicino	Italy	39.68705	15.90079	462 m	MNHW
subterranea	n. Fagnano loc. 1	Italy	39.53769	16.0489	753 m	MNHW
subterranea	n. Fagnano loc. 4	Italy	39.53761	16.03249	846 m	MNHW
subterranea	n. Grisolia loc. 3	Italy	39.71131	15.89413	585 m	MNHW
subterranea	n. San Sosti loc. 1	Italy	39.66698	16.00754	429 m	MNHW
subterranea	n. San Sosti loc. 2	Italy	39.67062	15.99461	520 m	MNHW
subterranea	n. Verbicaro loc. 4	Italy	39.73791	15.94564	368 m	MNHW
subterranea	Pontescodogna	Italy	44.73825	10.192025	117 m	MNHW
subterranea	Portella Arena	Italy	37.87472	14.017778	NA	MMC
subterranea	Prato. Città di Castello. Perugia	Italy	43.4318	12.10014	NA	MMC
subterranea	Trieste	Italy	45.67054	13.800438	NA	MMC
subterranea	Villa Ada. Rome	Italy	41.93135	12.499876	NA	MMC
subterranea	Vittorio Veneto TV	Italy	45.99207	12.291498	NA	MMC
subterranea	1 km S of Pikal, Cijevna River Valley	Montenegro	42.39583	19.38033	100 m	GBC
subterranea	2.5 km NE of Raborci	North Macedonia	41.40667	22.62667	320 m	GBC
subterranea	2 km SW of Crničani	North Macedonia	41.225	22.635	160 m	GBC
subterranea	Avra	Romania	45.77011	26.99483	NA	MMC
subterranea	Bucharest	Romania	44.43801	26.0645	NA	MMC
subterranea	Hamcearca. Creasta Cardonului	Romania	45.09689	28.3858	175 m	MMC
subterranea	Temska	Serbia	43.2575	22.54339		MMC
subterranea	Ivanovci	Slovenia	46.74	16.235	280 m	GBC
subterranea	Križišče (Stena), Dragonja	Slovenia	45.45167	13.66167	20 m	GBC
subterranea	Matavun (near parking)	Slovenia	45.66417	13.988	420 m	GBC
subterranea	Girona	Spain	41.98713	2.827922	NA	MMC
subterranea	rd. Angles-Osor	Spain	41.95	2.61666	203 m	MNHW
subterranea	Volca Santa Margarida n. Olot	Spain	42.13333	2.53333	700 m	MNHW
subterranea	8 km W Borçka	Türkiye	NA	NA	350 m	MHNG
subterranea	5 km E Hopa	Türkiye	NA	NA	100 m	MHNG
subterranea	Eregli-Balikoy	Türkiye	NA	NA	NA	MHNG
subterranea	Forêt de Belgrad (Belgrad Forest)	Türkiye	NA	NA	NA	MHNG
subterranea	Hopa-Kemalpasa	Türkiye	NA	NA	30 m	MHNG
subterranea	Keshiron	Türkiye	NA	NA	NA	MHNG
subterranea	Pirnalli. massif du Karkal Dağı (Kaçkar Dağı)	Türkiye	NA	NA	1600 m	MHNG
subterranea	Strandzha. Avcılar Köyü	Türkiye	41.896	27.866	182 m	BFUS
subterranea	SW Artvin	Türkiye	NA	NA	1900 m	MHNG
tristis	2.1 km S of Glifada	Greece	38.63619	23.81488	910 m	MNHW
tristis	3.7 km SW of Metochi	Greece	38.60402	23.91683	830 m	MNHW
tristis	3.8 km W of Tzanata	Greece	38.1355	20.70529	759 m	MNHW
tristis	3.96 km W of Penteli	Greece	36.9414	22.36268	1250 m	MNHW
tristis	Agios Andreas	Greece	38.15943	20.59734	501 m	MNHW

Table 2. Continued

Species	Locality name	Country	LocLatitude	LocLongitude	Elevation	LocatedAt
tristis	Agrafa. Elatos	Greece	39.24037	21.68717	1195 m	MNHW
tristis	Ainos Mts	Greece	38.14007	20.6606	1595 m	MNHW
tristis	Ainos Mts. loc. 3	Greece	38.15258	20.63944	1330 m	MNHW
tristis	Ainos Mts. loc. 4	Greece	38.1571	20.62602	1135 m	MNHW
tristis	E of Nymfes	Greece	39.75047	19.8057	179 m	MNHW
tristis	Enos Mts. loc. 2	Greece	38.15273	20.6393	1336 m	MNHW
tristis	Kardaras	Greece	37.6285	22.3	982 m	MNHW
tristis	Kardaras-Vitina rd. loc. 2	Greece	37.62753	22.26641	1287 m	MNHW
tristis	Katochori vic.	Greece	39.39402	22.99603	500 m	MNHW
tristis	Koranida	Greece	37.1424	25.5319	462 m	MNHW
tristis	Lakonia. 3.2 km NE Vamvakou	Greece	37.25343	22.59165	1370 m	MMC
tristis	Mt Ditiko Mainalo. 1.6 km NW of Chrisivitsi	Greece	37.55723	22.19665	1125 m	MNHW
tristis	Mt Mainalo. above Ski Centre loc. 2	Greece	37.65948	22.25973	1626 m	MNHW
tristis	Mt. Olympus. 6.2 km NE of Karya	Greece	40.00703	22.46108	935 m	MNHW
tristis	Mt. Ossa ski center	Greece	39.80844	22.68604	1520 m	MNHW
tristis	Mt. Ossa. Karitsa-Spilia rd. km 6	Greece	39.83615	22.69249	990 m	MNHW
tristis	Oros Taygetos. 20 km SW of Sparti	Greece	36.966	22.36	1950 m	MNHW
tristis	Parnon Mts. Mt Megali Tourla. Kefaloneri	Greece	37.29333	22.59179	1129 m	MNHW
tristis	Taygetos Mts. 2.5 km E of Saidona	Greece	36.88917	22.31053	1125 m	MNHW

Table 3. Comparative measurements and indices of species belonging to the *Aphaenogaster subterranea* species group.

	WORKER							
	A. asterioni n=10	*A. epirotes* n=10	*A. holtzi* n=9	*A. ichnusa* n=8	*A. maculifrons* n=10	*A. subterranea* n=58	*A. subcostata* n=7	*A. tristis* n=46
CL	1.00 ± 0.06	1.26 ± 0.09	1.15 ± 0.05	1.02 ± 0.06	1.08 ± 0.06	1.01 ± 0.09	1.28 ± 0.06	1.04 ± 0.07
	(0.84–1.08)	(1.08–1.36)	(1.09–1.27)	(0.94–1.11)	(1–1.19)	(0.82–1.16)	(1.19–1.37)	(0.89–1.18)
CW	0.89 ± 0.07	1.13 ± 0.1	1 ± 0.05	0.9 ± 0.07	0.96 ± 0.05	0.89 ± 0.1	1.15 ± 0.07	0.92 ± 0.09
	(0.71–0.96)	(0.94–1.25)	(0.94–1.12)	(0.81–1.01)	(0.87–1.07)	(0.65–1.08)	(1.05–1.25)	(0.74–1.06)
FRS	0.27 ± 0.02	0.36 ± 0.03	0.29 ± 0.02	0.26 ± 0.02	0.27 ± 0.01	0.25 ± 0.02	0.38 ± 0.02	0.26 ± 0.02
	(0.22–0.29)	(0.29–0.39)	(0.27–0.34)	(0.23–0.28)	(0.25–0.3)	(0.19–0.3)	(0.35–0.40)	(0.22–0.3)
EL	0.17 ± 0.01	0.23 ± 0.02	0.19 ± 0.01	0.18 ± 0.02	0.19 ± 0.01	0.19 ± 0.02	0.24 ± 0.01	0.18 ± 0.02
	(0.14–0.18)	(0.20–0.24)	(0.18–0.21)	(0.15–0.2)	(0.18–0.21)	(0.15–0.22)	(0.22–0.26)	(0.14–0.21)
MD	0.27 ± 0.02	0.31 ± 0.03	0.31 ± 0.01	0.27 ± 0.02	0.28 ± 0.01	0.26 ± 0.02	0.34 ± 0.02	0.27 ± 0.02
	(0.22–0.29)	(0.25–0.34)	(0.29–0.33)	(0.25–0.3)	(0.26–0.31)	(0.19–0.3)	(0.32–0.37)	(0.22–0.3)
SL	0.92 ± 0.04	1.09 ± 0.07	1.11 ± 0.06	0.97 ± 0.05	1.01 ± 0.04	0.97 ± 0.07	1.13 ± 0.05	1.01 ± 0.06
	(0.81–0.97)	(0.95–1.16)	(1.03–1.22)	(0.92–1.05)	(0.96–1.09)	(0.79–1.1)	(1.06–1.21)	(0.86–1.1)
ML	1.29 ± 0.08	1.65 ± 0.12	1.49 ± 0.08	1.31 ± 0.07	1.39 ± 0.07	1.32 ± 0.11	1.7 ± 0.09	1.35 ± 0.09
	(1.09–1.38)	(1.40–1.80)	(1.40–1.66)	(1.21–1.43)	(1.29–1.53)	(1.07–1.54)	(1.57–1.83)	(1.15–1.54)
SPST	0.17 ± 0.02	0.24 ± 0.03	0.22 ± 0.03	0.15 ± 0.02	0.18 ± 0.01	0.18 ± 0.03	0.28 ± 0.04	0.19 ± 0.03
	(0.12–0.2)	(0.17–0.27)	(0.18–0.29)	(0.13–0.17)	(0.16–0.2)	(0.11–0.23)	(0.22–0.34)	(0.14–0.26)
MPST	0.29 ± 0.02	0.35 ± 0.03	0.32 ± 0.02	0.28 ± 0.02	0.31 ± 0.02	0.29 ± 0.02	0.37 ± 0.02	0.3 ± 0.02
	(0.24–0.31)	(0.28–0.4)	(0.3–0.36)	(0.25–0.31)	(0.28–0.33)	(0.24–0.34)	(0.34–0.39)	(0.25–0.35)
PEH	0.27 ± 0.02	0.33 ± 0.02	0.33 ± 0.02	0.27 ± 0.01	0.3 ± 0.02	0.27 ± 0.02	0.35 ± 0.02	0.28 ± 0.02
	(0.22–0.29)	(0.29–0.36)	(0.31–0.37)	(0.26–0.29)	(0.27–0.32)	(0.22–0.32)	(0.32–0.37)	(0.25–0.31)
PEL	0.31 ± 0.02	0.38 ± 0.05	0.34 ± 0.02	0.3 ± 0.03	0.33 ± 0.02	0.32 ± 0.03	0.38 ± 0.02	0.31 ± 0.02
	(0.26–0.34)	(0.26–0.41)	(0.32–0.37)	(0.26–0.34)	(0.3–0.37)	(0.25–0.38)	(0.35–0.42)	(0.26–0.36)
PPH	0.27 ± 0.02	0.36 ± 0.03	0.31 ± 0.01	0.26 ± 0.01	0.29 ± 0.02	0.27 ± 0.03	0.38 ± 0.02	0.27 ± 0.02
	(0.22–0.3)	(0.33–0.4)	(0.29–0.35)	(0.24–0.28)	(0.26–0.32)	(0.21–0.32)	(0.34–0.41)	(0.22–0.31)
PPL	0.26 ± 0.02	0.35 ± 0.03	0.29 ± 0.02	0.25 ± 0.01	0.27 ± 0.01	0.26 ± 0.02	0.36 ± 0.02	0.27 ± 0.02
	(0.22–0.28)	(0.3–0.38)	(0.27–0.33)	(0.24–0.27)	(0.25–0.3)	(0.21–0.31)	(0.33–0.39)	(0.19–0.3)
HTL	0.76 ± 0.04	0.96 ± 0.06	0.92 ± 0.05	0.8 ± 0.04	0.83 ± 0.04	0.82 ± 0.07	0.98 ± 0.05	0.82 ± 0.05
	(0.66–0.81)	(0.81–1.03)	(0.83–1.03)	(0.74–0.85)	(0.78–0.91)	(0.66–0.93)	(0.92–1.06)	(0.7–0.92)
MW	0.59 ± 0.04	0.76 ± 0.06	0.64 ± 0.04	0.59 ± 0.04	0.61 ± 0.03	0.58 ± 0.05	0.76 ± 0.04	0.6 ± 0.04
	(0.49–0.64)	(0.63–0.83)	(0.59–0.73)	(0.54–0.65)	(0.56–0.67)	(0.45–0.69)	(0.71–0.84)	(0.5–0.68)
PEW	0.21 ± 0.01	0.26 ± 0.02	0.24 ± 0.01	0.21 ± 0.01	0.23 ± 0.01	0.21 ± 0.02	0.27 ± 0.02	0.2 ± 0.02
	(0.18–0.22)	(0.22–0.29)	(0.22–0.27)	(0.19–0.23)	(0.21–0.25)	(0.16–0.24)	(0.24–0.29)	(0.15–0.24)
PPW	0.27 ± 0.02	0.39 ± 0.03	0.31 ± 0.02	0.25 ± 0.02	0.28 ± 0.01	0.26 ± 0.02	0.39 ± 0.03	0.26 ± 0.02
	(0.22–0.29)	(0.33–0.44)	(0.29–0.35)	(0.22–0.27)	(0.26–0.31)	(0.21–0.3)	(0.35–0.43)	(0.2–0.3)
CS	0.95 ± 0.06	1.19 ± 0.09	1.08 ± 0.05	0.96 ± 0.06	1.02 ± 0.05	0.95 ± 0.09	1.21 ± 0.06	0.98 ± 0.07
	(0.78–1.02)	(1.01–1.31)	(1.02–1.2)	(0.88–1.06)	(0.94–1.13)	(0.74–1.12)	(1.12–1.31)	(0.82–1.12)
CS/SL	1.02 ± 0.03	1.09 ± 0.02	0.97 ± 0.02	0.99 ± 0.02	1.01 ± 0.02	0.98 ± 0.03	1.07 ± 0.02	0.97 ± 0.03
	(0.96–1.06)	(1.05–1.13)	(0.93–1)	(0.95–1.01)	(0.97–1.04)	(0.93–1.07)	(1.05–1.11)	(0.9–1.03)
CS/ML	0.73 ± 0.01	0.72 ± 0.01	0.72 ± 0.01	0.73 ± 0.01	0.73 ± 0.01	0.72 ± 0.01	0.71 ± 0.01	0.73 ± 0.02
	(0.71–0.74)	(0.71–0.74)	(0.71–0.73)	(0.71–0.74)	(0.72–0.76)	(0.69–0.74)	(0.71–0.72)	(0.68–0.75)
CS/SPST	5.61 ± 0.42	5.11 ± 0.34	5.04 ± 0.52	6.39 ± 0.43	5.76 ± 0.25	5.41 ± 0.45	4.42 ± 0.38	5.21 ± 0.49
	(5.03–6.46)	(4.73–5.94)	(4.12–5.83)	(5.69–7.08)	(5.39–6.16)	(4.66–6.68)	(3.85–5.09)	(4.29–6.57)
CS/EL	5.56 ± 0.16	5.25 ± 0.15	5.56 ± 0.17	5.51 ± 0.22	5.3 ± 0.11	4.96 ± 0.21	5.08 ± 0.09	5.44 ± 0.24
	(5.31–5.82)	(5.02–5.44)	(5.3–5.83)	(5.25–5.83)	(5.07–5.47)	(4.4–5.39)	(4.94–5.24)	5.03–5.94)