



Neglected for almost a century: rediscovering and redescribing the enigmatic endemic species *Messor fodorii* Rösler, 1942 stat. nov. (Hymenoptera: Formicidae) from Chios Island (Greece)

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Abstract

The genus *Messor* Forel, 1890 currently comprises 171 valid species and subspecies, with highest diversity in the Mediterranean and Central Asia. Greece hosts at least 16 species, although the taxonomic status of some needs to be further investigated. Amongst these, six species are island endemics, either restricted to a single Aegean island or distributed across several islands in the archipelago. Despite recent studies on the harvester ants of Greece, the case of *Messor antennatus fodorii* Rösler, 1942, remained unresolved amongst Greek representatives. This enigmatic harvester ant was first collected almost a century ago, in 1935, from Chios Island, situated in the northeastern part of the Aegean Sea. The lack of both a type and additional material has led to its exclusion from checklists and identification keys, leaving its status as uncertain. From April 24th to May 5th 2025, we conducted field surveys in Chios, Oinousses and Psara islands to investigate the presence and taxonomic status of *M. antennatus fodorii*. Upon investigation, the harvester ant is raised to the species level *Messor fodorii* Rösler, 1942 stat. nov., designating a neotype, providing a re-description, a morphometric comparison of species in the *M. hellenius* complex, ecological notes and an updated identification key to Greek representatives of the *Messor hellenius* species complex.

Key words: ants, Aegean islands, identification key, *Messor*, taxonomy, redescription

Περίληψη

Το γένος *Messor* Forel, 1890 περιλαμβάνει 171 έγκυρα είδη και υποείδη, με τη μεγαλύτερη ποικιλότητα στη Μεσόγειο και την Κεντρική Ασία. Η Ελλάδα φιλοξενεί τουλάχιστον 16 είδη, αν και η ταξινομική κατάσταση ορισμένων ειδών πρέπει να διερευνηθεί περαιτέρω. Μεταξύ αυτών, έξι είδη είναι ενδημικά νησιών, είτε περιορίζονται σε ένα μόνο νησί του Αιγαίου είτε κατανέμονται σε διάφορα νησιά του αρχιπελάγους. Παρά τις πρόσφατες μελέτες για τα μυρμήγκια της Ελλάδας, η περίπτωση του *Messor antennatus fodorii* Rösler, 1942, παρέμεινε ανεπίλυτη μεταξύ των Ελλήνων εκπροσώπων. Αυτό το αιγιματικό μυρμήγκι συλλέχθηκε για πρώτη φορά πριν από σχεδόν έναν αιώνα, το 1935, από το νησί της Χίου, που βρίσκεται στο βορειοανατολικό τμήμα του Αιγαίου Πελάγους. Η έλλειψη δείγματος «τύπου» και πρόσθετου υλικού οδήγησε στον αποκλεισμό του από καταλόγους και κλειδες αναγνώρισης, αφήνοντας την κατάσταση του ως αβέβαιη. Από τις 24 Απριλίου έως τις 5 Μαΐου 2025, πραγματοποιήσαμε επιτόπιες έρευνες στα νησιά Χίος, Οινούσες και Ψαρά για να διερευνήσουμε την παρουσία και την ταξινομική κατάσταση του *M. antennatus fodorii*. Μετά από έρευνα, το μυρμήγκι αναβαθμίζεται στο επίπεδο του είδους *Messor fodorii* Rösler, 1942 stat. nov., ορίζοντας

ένα νεότυπο, παρέχοντας μια νέα περιγραφή, μια μορφολογική σύγκριση των ειδών του συμπλέγματος *M. hellenius*, οικολογικές σημειώσεις και μια ενημερωμένη κλείδα αναγνώρισης για τους ελληνικούς εκπροσώπους του συμπλέγματος ειδών *M. hellenius*.

Introduction

The genus *Messor* Forel, 1890 currently comprises 134 valid species and 37 subspecies (Bolton 2026), with a higher species diversity in the Mediterranean and Central Asia (Janicki *et al.* 2016; Guénard *et al.* 2017). Greece constitutes an important centre of diversity and rarity for Mediterranean ants (Kass *et al.* 2022), hosting more than 300 species (Borowiec & Salata 2012, 2013, 2022, 2025). More specifically, the genus *Messor* is represented by at least 16 species, although the status of some taxa needs to be further investigated through the use of molecular tools (Borowiec & Salata 2025). Amongst these, six species are island endemics restricted to singular or widespread in numerous Aegean islands i.e. *Messor concolor* Santschi, 1927 and *Messor creticus* Salata & Borowiec, 2019 from Crete, *Messor veneris* Salata, Georgiadis & Borowiec, 2023 from Cyclades, *Messor danaes* Salata, Georgiadis & Borowiec, 2023 from Cyclades and Dodecanese, as well as *Messor kardamenaes* Salata & Borowiec, 2023 and *Messor carpathous* Menozzi, 1936 from Dodecanese (Santschi 1927; Menozzi 1936; Salata & Borowiec 2019; Salata *et al.* 2023; Borowiec *et al.* 2024; Borowiec & Salata 2025; Demetriou *et al.* 2025). These species highlight the importance of the Aegean archipelago, as a ‘natural laboratory of evolution’ (Mylonas & Triantis 2009; Sfenthourakis & Triantis 2017).

Despite recent progress in documenting the myrmecofauna of Greek islands (e.g. Borowiec & Salata 2018; Salata *et al.* 2020; Borowiec *et al.* 2021, 2022, 2024; Scupola & Borowiec 2023; Demetriou *et al.* 2025), the elusive harvester ant *Messor antennatus fodorii* Rösler, 1942 constitutes an interesting case due to its uncertain taxonomic status, restricted distribution, and rarity. This enigmatic ant was first collected in 1935 from Chios Island (*locus typicus*: Agios Georgios), in the northeastern part of the Aegean Sea. It was then described by Rösler in 1942 and again in 1951 in two separate scientific publications (Rösler 1942, 1951) as a subspecies of *Messor antennatus* Emery, 1908, a species native to North Africa (Morocco and Algeria) (Emery 1908; Santschi 1929; Cagniant 1964; Cagniant & Espalader 1998). Nearly a century after its first and only collection, it has not been recorded from Chios nor any other Greek or Turkish locality (Kiran & Karaman 2012, 2020; Scupola & Borowiec 2023; Borowiec & Salata 2025). Subsequently, it was not included in the checklists of Chios published by Collingwood (1993) as well as Scupola & Borowiec (2023), while it was also left out of the revision of Greek *Messor* taxa published by Salata *et al.* (2019). Furthermore, the taxonomic status of *M. antennatus fodorii* is regarded as “unclear”, and thus, this taxon has not been included in the most recent identification keys (Salata *et al.* 2019; Borowiec & Salata 2025). Its ecology is unknown and the type specimens seem to have been lost (Salata *et al.* 2019). Although the holotype of the subspecies is said to have been deposited at the Natural History Museum Sibiu (NHMS) in Romania (AntWeb 2025), an investigation of ants deposited at the institution does not mention any specimens of *M. antennatus fodorii* (Markó & Csósz 2002). Upon subsequent communication with the Natural History Museum Sibiu (NHMS) and the Hungarian Natural History Museum (HNHM), curators confirmed the absence of any deposited specimens (Drs. Zoltan Vas and Sándor Csósz pers. comm.).

Herein, we report the finding of the taxon nearly a century after its original collection, during a survey carried out from April 24th to May 5th 2025 on the islands of Chios, Oinousses, and Psara to assess the presence and taxonomic status of the taxon. Based on the collected material, the harvester ant is raised to the species level *Messor fodorii* Rösler, 1942 **stat. nov.** Herein, we also designate a neotype, provide a re-description for the species, ecological notes, and perform morphological comparisons with other species of the *Messor hellenius* complex (i.e. *M. hellenius* and *M. ponticus*). An identification key to Greek representatives of the *Messor hellenius* complex is provided.

Materials and methods

Study area

With an area of approximately 842 km², Chios is the 5th largest Aegean Island, situated at its northeastern part

and separated from the coasts of Çesme peninsula (Türkiye) in the east by a narrow strait (approx. 5 km). Chios is bordered by the islands of Lesvos in its north, Ikaria in the south, Psara and Antipsara in its northwest and the small islands of Oinousses within the strait. According to the latest 30-year climatic data, the climate of Chios is temperate Mediterranean with a mean annual precipitation under 100 mm and mean minimum and maximum daily temperatures ranging from 10 to 24°C and from 13 to 28°C within the year, respectively (Meteoblue 2026). Most of its northern and central part is included within the NATURA 2000 network (GR413001, GR4130003), with hilly and mountainous habitats, including Mt Pelineo (1,297 m alt.) and Mt Epos (1,188 m alt.) formed by limestones. Its typical vegetation includes pine, oak and maple forests as well as plane trees covering areas with seasonal streams. The southern region (Mastichochochia—mastic villages) is more arid, devoid of mountains and only with small hills under 350 m alt., and overgrown with mastic trees, mastic cultivations, madrones, maquis and phrygana (Boratyński *et al.* 1987).

In between Chios and the Turkish coast (Çesme Peninsula) lie the islands of Oinousses, a cluster of one larger and eight smaller islands. Oinousses hold a population of approximately one thousand inhabitants with frequent movement between the largest island and the main island of Chios. The island is mostly covered in phrygana with some sparse maquis, while it is in its entirety within the NATURA 2000 network (GR4130001). Lastly, situated off the northwestern coast of Chios, the island of Psara covers an area of approx. 43 km² and is inhabited by around 400 people. The island is more isolated, lying 81 km off the main island of Chios. The island's landscape is hilly, covered in phrygana and sparse maquis, with the island's highest point being "Profitis Ilias" (512 m alt.). All islands have a rich cultural and naval history.

Study period and sampling method

We visited the island of Chios as well as the neighbouring islets of Oinousses and Psara between April 23rd and May 5th, 2025, in search of *M. antennatus fodorii*, sampling a total of 97 sites in various habitat types, including both natural and anthropogenic landscapes, at altitudes ranging from sea level to 960 m (Figure 1; Appendix I). The most common sampling approach was direct sampling (hand collection) and searching for ant mounds. All specimens were maintained primarily in pure EtOH, partially in 75° EtOH. Specimens were deposited at the Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland (DBET), the Museum of Natural History, University of Wrocław, Poland (MNHW), and the Museum of Zoology of the National and Kapodistrian University of Athens, Athens, Greece (ZMUA).

Data analysis

Statistical analyses were conducted using R and RStudio software (RStudio Team 2025). Principal component analysis (PCA) was performed on all 20 body measurements. The analysis was done using the *stats* (R Core Team 2025) and *factoextra* (Kassambara & Mundt 2020) packages. The Kruskal-Wallis test and Dunn's post hoc test (with Bonferroni correction, which reduces the risk of false detection of differences between groups) were performed for all measurements and morphometric indices using the *FSA* package (Ogle *et al.* 2026). The functions included in the *ggplot2* (Wickham 2016) and *dplyr* (Wickham 2023) packages were used to prepare all visualisations of statistical analyses.

Visualisation and specimen photography

Specimens were photographed using Nikon SMZ18 and Nikon SMZ 1500 stereomicroscopes, Nikon D5200 camera, and Helicon Focus software. Maps were created in QGIS, a free, open-source Geographic Information System Version 3.44.2 (<https://qgis.org/en/site/>).

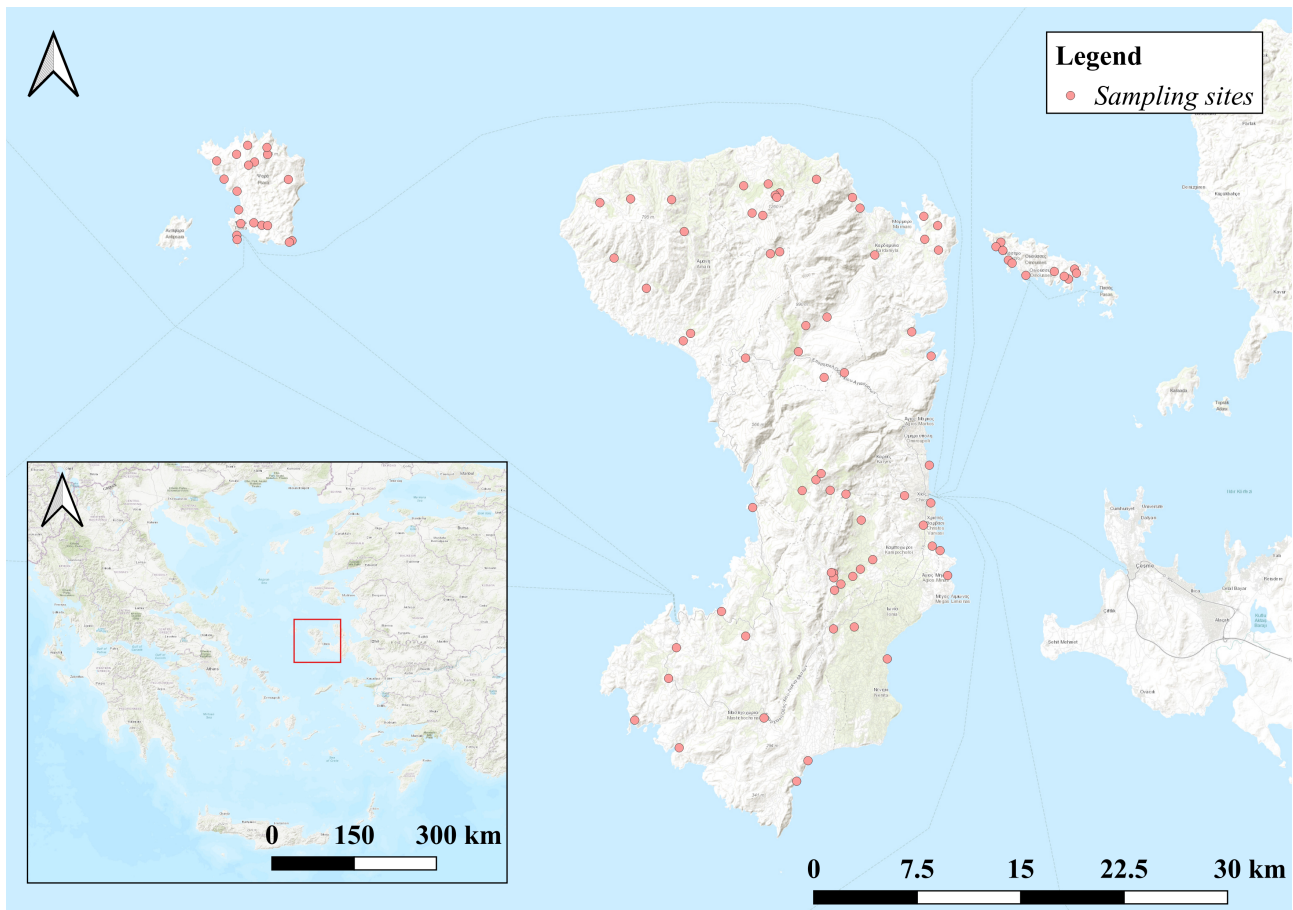


FIGURE 1. Sampled sites in Chios, Oinousses and Psara between April 23rd to May 5th 2025.

Measurements

[after Orou *et al.* (2023), modified]

CL Maximum median length of head capsule. The head must be carefully tilted so the maximum length is positioned in the measuring plane.

CW Maximum head width including compound eyes. The largest distance between profiles of the two compound eyes in full-face view.

POC Post ocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring position of

CL Caudal measuring point: median occipital margin; frontal measuring point: median head at the level of the posterior eye margin.

EL Eye length. Maximum diameter of the compound eye.

FR Minimum distance of the frontal carinae.

FL Maximum distance of frontal carinae.

AnScD Torular lamellae distance. Distance between distalmost edges of torular lamellae.

ML Diagonal length of the alitrunk in profile. Measured in lateral view from the anteriormost point of anterior pronotal slope to the caudalmost point of the lateral metapleural lobe.

MW Maximum width of pronotum.

NOL Petiole node length. Measured in lateral view, from the center of the petiolar spiracle to the posterior profile.

PEW Petiole width. The maximum width of petiole in dorsal view.

SL Scape length. The maximum straight-line scape length excluding the articular condyle.

HTL Hind tibia length. Measured from the distalmost point of the tibia to the proximal end where the tibia is narrowest in profile.

ScBw Maximum distance of the anterior corner at scape base from the anterior surface of the condylar neck.

ScBaC Maximum distance between the corners at scape base.

PrOC Malar distance. It is the shortest distance between the anteriormost margin of the compound eye and the closest margin of head capsule by the mandibular joint.

PEDW Pedicel width. Measured in frontal view; the maximum width of the pedicel taken perpendicularly to its longitudinal axis. The measurement was taken at the widest visible point of the pedicel.

PEDL Pedicel length. Measured in frontal view; the maximum visible length of the pedicel taken along its longitudinal axis.

AN03W Width of Antennal Segment III. Maximum width of antennal segment III (immediately following the pedicel) measured in frontal view. The width was taken at the broadest visible point perpendicular to the segment's long axis.

AN03L Length of Antennal Segment III. Maximum length of antennal segment III measured in frontal view.

CS = (HL + HW) / 2

All measurements are given in mm.

Pilosity

The nomenclature describing the pilosity inclination degree follows Wilson (1955). Appressed (0–5°) hairs run parallel or nearly parallel to the body surface. Decumbent hairs stand 5–20°, subdecumbent hair stands 20–60°, suberect 60–80°, and erect 80–90° from the surface (see Fig. 3 in Wilson 1955). The surface sculpturing glossary follows Harris (1979).

Museum and collection abbreviations

DBET Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland;

MNHW Museum of Natural History, University of Wrocław, Poland;

ZMUA Zoology Museum of the National and Kapodistrian University of Athens, Athens, Greece.

Results

Morphometric analyses

PCA analysis confirmed the hypotheses regarding the differentiation of *M. fodorii* from *M. hellenius* and *M. ponticus* by forming separate clusters based on basic body measurements (Table 1; Figure 2). The clusters of *M. hellenius* and *M. ponticus* clearly overlap. The first two components of this PCA analysis explain 92.7% of the variation between these species (Table 1; Figure 2).

The Kruskal-Wallis test showed that there are significant differences between groups for each body measurement and index, with only the FR/CS, EL/CS and PEDL/AN03L indices showing no significant differences between the three species. The Dunn's post hoc test showed significant differences in most measures and indices between *M. fodorii* and *M. hellenius* and between *M. fodorii* and *M. ponticus*. For the species *M. hellenius* and *M. ponticus*, a significant difference occurs only for POC/CL. The p-values for the Kruskal-Wallis test, for all measurements and indices, and Dunn's post hoc test, for all measurements and indices (for species pairs), are provided in Appendices II and III (significant differences are marked in bold).

Synopsis of members of the Messor structor group from the Eastern Mediterranean Region [after Steiner et al. (2018), Lapeva-Gjonova et al. (2025) and Lapeva-Gjonova and Borowiec (2026)]

Messor fodorii (Rösler, 1942) **stat. nov.***

Messor hellenius Agosti & Collingwood, 1987*

Messor ibericus Santschi, 1931*

Messor mcarthuri Steiner, Csősz, Markó, Gamisch, Rinnhofer, Folterbauer, Hammerle, Stauffer, Arthofer & Schlick-Steiner, 2018*

TABLE 1. Measurements and indices of 30 morphological characters for *Messor hellenius*, *M. fodorii* and *M. ponticus*, comprising the *M. hellenius* species complex (in mm).

Measurements and indices	<i>M. hellenius</i> (n = 18)	<i>M. fodorii</i> (n = 10)	<i>M. ponticus</i> (n = 10)
CL	2.32 ± 0.22 (1.96–2.62)	1.49 ± 0.27 (1.18–1.98)	2.43 ± 0.25 (1.94–2.84)
CW	2.54 ± 0.28 (2.08–2.98)	1.51 ± 0.32 (1.18–2.15)	2.69 ± 0.34 (2.07–3.26)
POC	0.91 ± 0.09 (0.79–1.05)	0.54 ± 0.11 (0.41–0.74)	1.01 ± 0.14 (0.78–1.25)
PrOC	0.94 ± 0.09 (0.79–1.05)	0.58 ± 0.13 (0.45–0.84)	0.96 ± 0.11 (0.78–1.18)
FR	0.64 ± 0.07 (0.53–0.74)	0.39 ± 0.07 (0.32–0.53)	0.67 ± 0.07 (0.51–0.77)
FL	0.65 ± 0.07 (0.53–0.74)	0.39 ± 0.07 (0.32–0.54)	0.67 ± 0.07 (0.51–0.77)
AnScD	0.76 ± 0.07 (0.65–0.85)	0.48 ± 0.09 (0.39–0.65)	0.79 ± 0.08 (0.62–0.89)
SL	1.73 ± 0.14 (1.54–1.93)	1.31 ± 0.19 (1.10–1.66)	1.77 ± 0.14 (1.52–1.97)
ScBaC	0.23 ± 0.03 (0.19–0.27)	0.16 ± 0.02 (0.13–0.20)	0.23 ± 0.03 (0.18–0.27)
ScBw	0.11 ± 0.02 (0.09–0.15)	0.07 ± 0.01 (0.06–0.10)	0.12 ± 0.02 (0.09–0.16)
ML	2.65 ± 0.27 (2.25–3.00)	1.91 ± 0.27 (1.61–2.36)	2.82 ± 0.28 (2.36–3.25)
NOL	0.56 ± 0.08 (0.47–0.71)	0.37 ± 0.06 (0.28–0.45)	0.59 ± 0.11 (0.42–0.76)
EL	0.41 ± 0.05 (0.33–0.49)	0.27 ± 0.04 (0.21–0.33)	0.43 ± 0.06 (0.34–0.52)
HTL	1.75 ± 0.14 (1.54–1.94)	1.28 ± 0.17 (1.08–1.53)	1.82 ± 0.16 (1.61–2.15)
PEW	0.43 ± 0.04 (0.37–0.49)	0.30 ± 0.04 (0.25–0.35)	0.48 ± 0.09 (0.38–0.68)
MW	1.39 ± 0.14 (1.17–1.58)	0.92 ± 0.13 (0.75–1.16)	1.43 ± 0.16 (1.16–1.70)
PEDW	0.10 ± 0.01 (0.09–0.12)	0.09 ± 0.01 (0.07–0.10)	0.11 ± 0.01 (0.09–0.12)
PEDL	0.26 ± 0.02 (0.23–0.29)	0.19 ± 0.01 (0.17–0.22)	0.28 ± 0.02 (0.24–0.32)
AN03W	0.10 ± 0.01 (0.09–0.12)	0.08 ± 0.01 (0.06–0.09)	0.11 ± 0.01 (0.10–0.12)
AN03L	0.21 ± 0.03 (0.17–0.25)	0.15 ± 0.02 (0.13–0.17)	0.22 ± 0.02 (0.19–0.24)
CS	2.43 ± 0.25 (2.02–2.80)	1.50 ± 0.29 (1.18–2.07)	2.56 ± 0.29 (2.01–3.05)
POC/CL	0.39 ± 0.02 (0.36–0.41)	0.36 ± 0.01 (0.33–0.38)	0.41 ± 0.02 (0.39–0.45)
FR/CS	0.27 ± 0.02 (0.23–0.28)	0.26 ± 0.01 (0.24–0.27)	0.26 ± 0.01 (0.25–0.28)
MW/CS	0.57 ± 0.01 (0.56–0.59)	0.62 ± 0.03 (0.56–0.66)	0.56 ± 0.02 (0.53–0.58)
PEW/CS	0.18 ± 0.01 (0.16–0.18)	0.20 ± 0.02 (0.17–0.23)	0.19 ± 0.02 (0.17–0.24)
ML/CS	1.09 ± 0.05 (0.96–1.15)	1.28 ± 0.07 (1.14–1.36)	1.11 ± 0.05 (1.04–1.18)
SL/CS	0.71 ± 0.02 (0.68–0.76)	0.88 ± 0.05 (0.80–0.94)	0.70 ± 0.04 (0.63–0.76)
EL/CS	0.17 ± 0.01 (0.15–0.18)	0.18 ± 0.02 (0.16–0.21)	0.17 ± 0.01 (0.15–0.19)
PEDL/PEDW	2.49 ± 0.27 (2.09–2.90)	2.21 ± 0.12 (2.00–2.43)	2.58 ± 0.20 (2.36–2.91)
PEDL/AN03L	1.24 ± 0.12 (1.08–1.45)	1.28 ± 0.08 (1.13–1.39)	1.29 ± 0.11 (1.13–1.45)

Messor muticus (Nylander, 1849)

Messor odrysarum Lapeva-Gjonova & Borowiec, 2026

Messor oertzeni Forel, 1910*

Messor ponticus Steiner, Csősz, Markó, Gamisch, Rinnhofer, Folterbauer, Hammerle, Stauffer, Arthofer & Schlick-Steiner, 2018*

Messor structor (Latreille, 1798)*

(* species present in Greece)

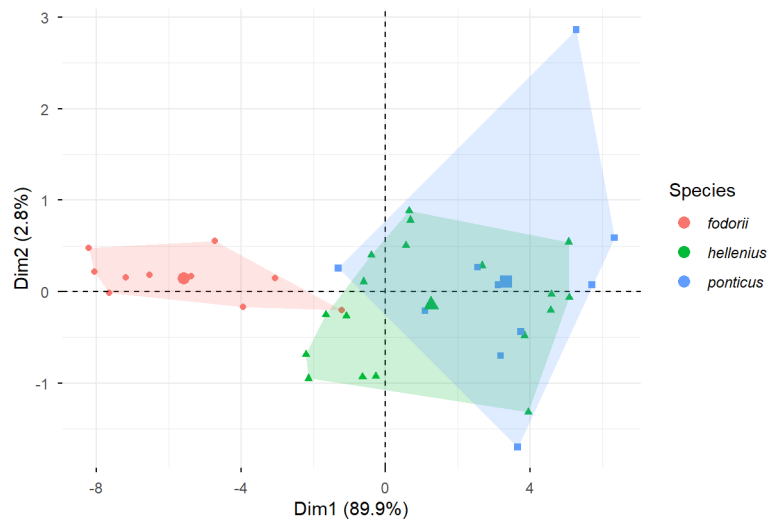


FIGURE 2. Principal Component Analysis (PCA) based on 20 morphometric characters measured for species of the *Messor hellenius* complex, *Messor fodorii* (red circles), *M. hellenius* (green triangles) and *M. ponticus* (blue squares). Each point represents an individual specimen, and the enlarged points are the barycentres for each species.

Update to the key to the Greek *Messor*

In the key to the Greek *Messor* proposed by Borowiec & Salata (2025), *M. fodorii* runs to couplet 15 and the key is modified as follow:

1. Smooth area with diffused costae to costulae present also between eyes and vertex. Ventral sides of head with numerous long J-shaped setae. In Greece form with mostly striate head *M. hellenius* Agosti & Collingwood, part
- Whole head between eyes and vertex with distinct costae. Ventral sides of head with predominately short C-shaped setae. 2.
2. Major workers smaller, CL: 1.49 ± 0.27 , SL: 1.31 ± 0.19 , ML: 1.91 ± 0.27 . Dorsal part of pronotum with up to 15 long and erect setae, central part of propodeal dorsum with weaker sculpture; the distal part of the first gastral tergite with sparse setae, the distance between setae is usually larger than their length *M. fodorii* Rösler, 1942
- Major workers larger, CL: 2.43 ± 0.25 , SL: 1.77 ± 0.14 , ML: 2.82 ± 0.28 . Dorsal part of pronotum with at least 20 long and erect setae, central part of propodeal dorsum usually with strong rugulae; the distal part of the first gastral tergite with dense setae, the distance between setae is shorter than their length (most often as long as half the length of setae). *M. ponticus* Steiner et al.

Species redescription

Messor fodorii Rösler, 1942 stat. nov.

Figures 3, 4

Messor antennatus var. *fodorii* Rösler, 1942: 55.

Messor antennatus var. *fodorii* Rösler, 1951: 92.

Material examined. Neotype (designated here): Collection MNHW | MNHW-GR03806 || GREECE, Aeg., Chios | Agios Georgios Sykousis | 370 m, 38.321 / 26.057 | 1 V 2025, S. Salata || *Messor* | *fodorii* | det. L. Borowiec || NEOTYPE (DBET). Topotypes: 15 workers (pin) and 23 (EtOH): the same data as the neotype (DBET, ZMUA). Other material: 5 workers (pin) 39 (EtOH): Collection MNHW | MNHW-GR03807 || GREECE, Aeg., Chios | Agia Markela Komis, 2 m | 38.1985 / 26.0376 | 5 V 2025, S. Salata || *Messor* | *fodorii* | det. L. Borowiec (DBET).

Comparative note. *Messor fodorii* belongs to the *Messor hellenius* complex within the *Messor structor* group. The complex consists of three species (*M. hellenius*, *M. fodorii*, and *M. ponticus*), and differs from the remaining members of the *structor* group in the lack of (or presence of reduced) sculpture on the posterior head. *Messor fodorii*

differs from both congeners in overall small body size in major workers (for this study only major workers with fully developed sculpture were measured) CL: 1.49 ± 0.27 (1.18–1.98) vs 2.32 ± 0.22 (1.96–2.62) in *hellenius* and 2.43 ± 0.25 (1.94–2.84) in *ponticus*, CW: 1.51 ± 0.32 (1.18–2.15) vs 2.54 ± 0.28 (2.08–2.98) in *hellenius* and 2.69 ± 0.34 (2.07–3.26) in *ponticus*, ML: 1.91 ± 0.27 (1.61–2.36) vs 2.65 ± 0.27 (2.25–3.00) in *hellenius* and 2.82 ± 0.28 (2.36–3.25) in *ponticus*, and SL/CS: 0.88 ± 0.05 (0.80–0.94) vs 0.71 ± 0.02 (0.68–0.76) in *hellenius* and 0.70 ± 0.04 (0.63–0.76) in *ponticus* (Table 1). Additionally, *M. fodorii* differs from *M. hellenius* in the presence of, sometimes weak, sculpture on the posterior frons and the lack of long J-shaped setae on the ventral side of the head. *Messor fodorii* is the most similar to *M. ponticus*, except for the distinct difference in body size; it also differs in the density of setae covering the gaster and propodeal dorsum. In all studied samples, majors of *M. fodorii* have up to 15 long and erect setae on the pronotal dorsum, while in *M. ponticus*, majors have at least 20 long and erect setae. The gaster setosity appears to show more pronounced differences in setosity. In *M. fodorii*, setae are distinctly sparse, especially on the distal part of the first gastral tergite, where the distance between setae is usually larger than their length. Whereas in *M. ponticus* the distance between setae is usually shorter than their length (most often it is equal to half the length of setae). See also taxonomic note below.

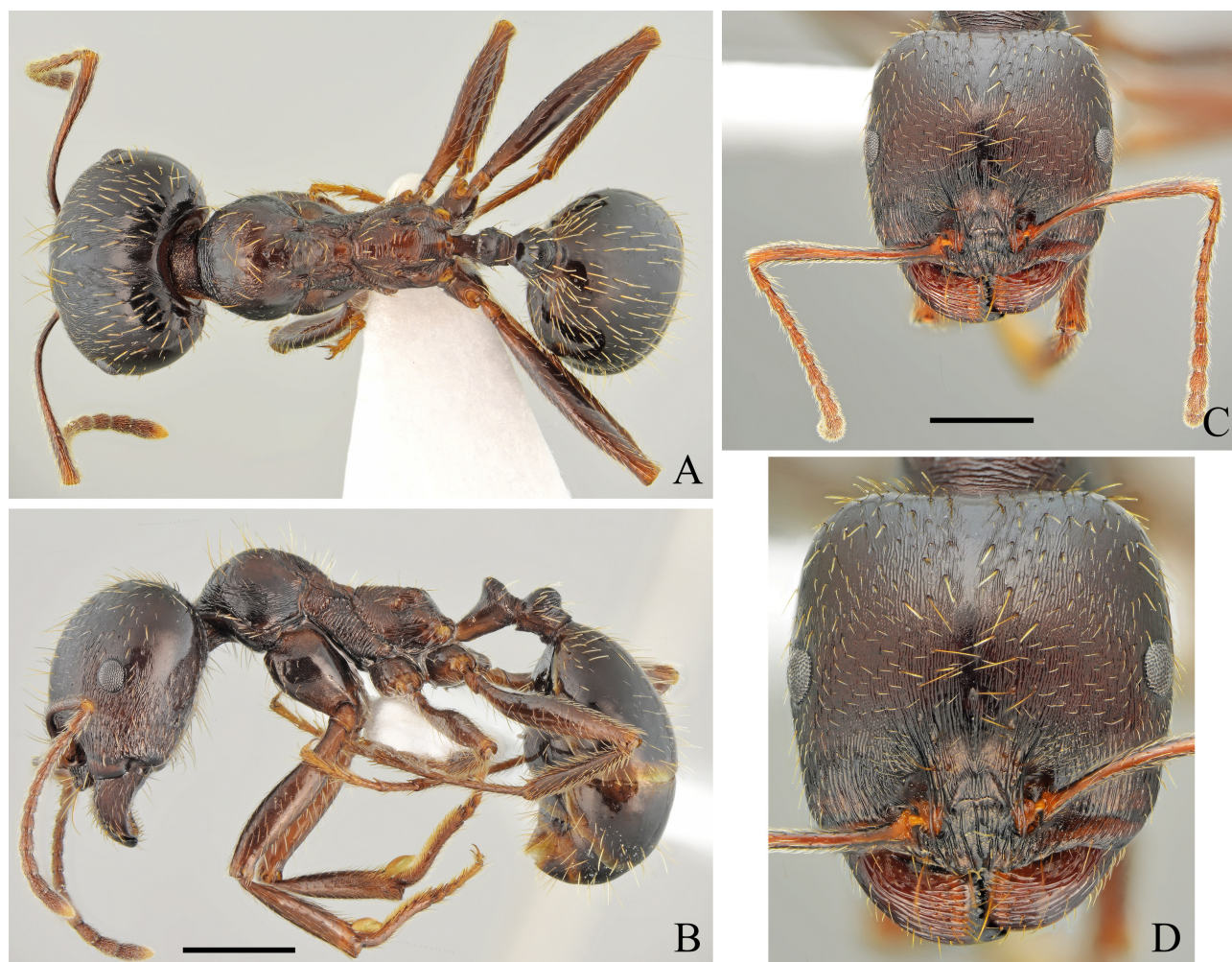


FIGURE 3. Habitus of *Messor fodorii* Rösler, 1942 stat. nov. major worker, dorsal (A) and lateral view (B). Head dorsal view (C, D).

Redescription. Major worker. Measurements: see Table 1. **Color.** Blackish brown with brighter patches on mesosomal dorsum; legs, mandibles and antenna brown to dark brown. Sometimes mesosoma and posterior part of head dorsum slightly brighter than the rest of the body. **Head.** Subrectangular, sides subparallel, posterior margin concave (Figure 3). Anterior clypeal margin indistinctly convex, finely crenulate, with shallow median emargination; with a row of up to 10 long marginal, yellowish setae, the longest as long as or longer than the length of clypeus. Clypeus without appressed pubescence, laterally with a group of a few long, erect setae; whole surface

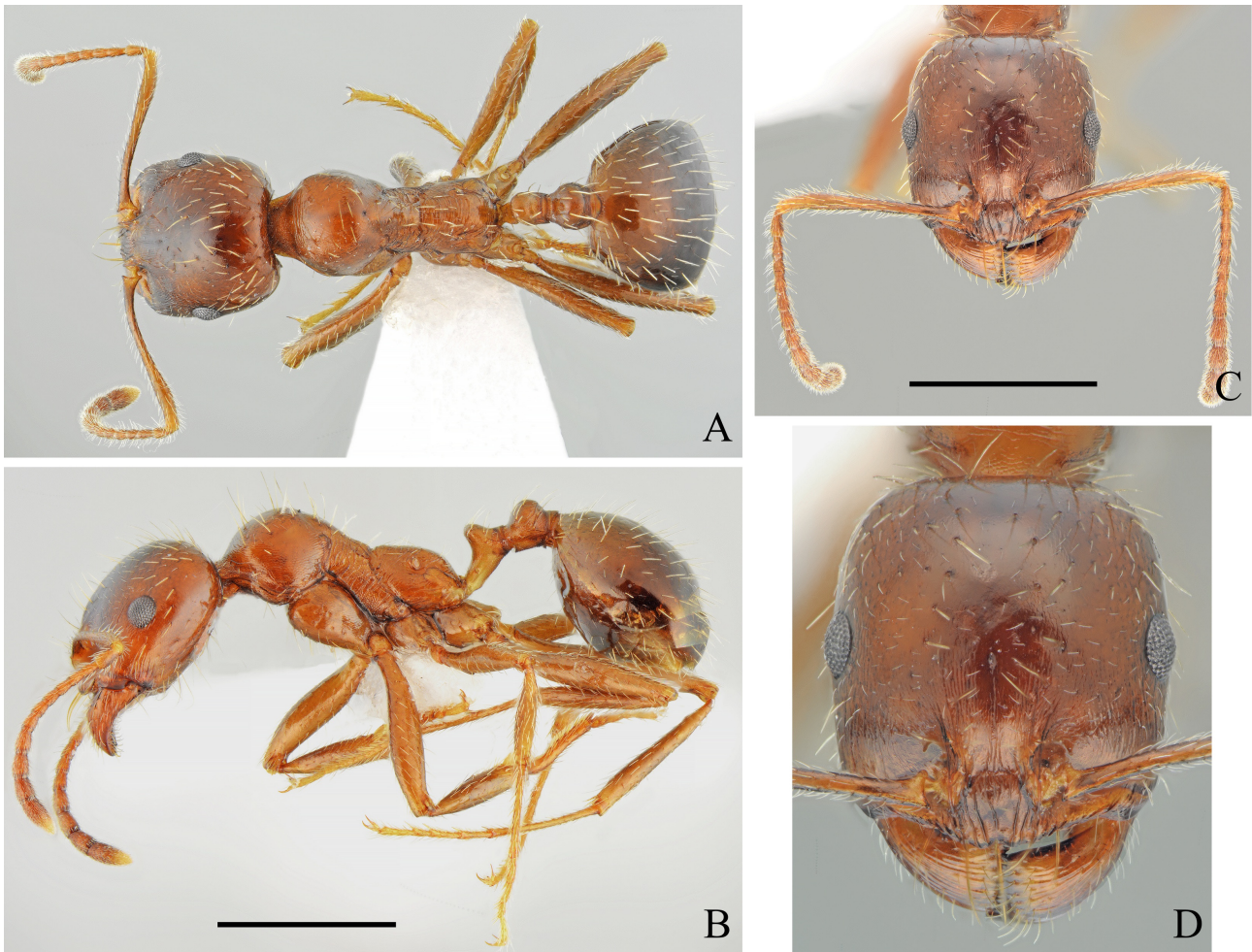


FIGURE 4. Habitus of *Messor fodorii* Rösler, 1942 stat. nov. minor worker, dorsal (A) and lateral view (B). Head dorsal view (C, D).

with dense and thick costae with imbricate interspaces, median keel absent (Figure 3). Eyes small and oval. Frontal triangle shallowly impressed, with several longitudinal costulae and diffusely microreticulate interspaces, shiny. Frontal carinae short, slightly extending beyond frontal lobes, running slightly posterolateral. Antennal fossa deep, never surrounded by semicircular costulae, but rather costulae run posteriad, surface with very fine microcostulae. Head with very fine and dense costulae with imbricate interspaces, only area posterolateral from eyes with distinctly reduced sculpture, imbricate. Overall head sculpture weakening posteriorly, and posterior part sometimes with costulae fading posteriad with predominant imbricate cover; head appears dull. Head covered with sparse, moderately long, decumbent to semierect setae. Frontal lobes with up to two long erect setae, and frons behind frontal carinae with few long erect setae. Ventral part of the head and inner margin of mandibles with numerous, long, erect setae, usually straight or occasionally C-shaped, psammophore (i.e. long J-shaped hairs on the ventral part of the head forming a distinct “beard-like” structure) absent. Antennal scape moderately elongate, in frontal view apically slightly curved; base of scape strongly extended, both outer and inner corners angulate. Funiculus distinctly longer than scape, pedicel elongated, approximately 2.5 x as long as wide at apex, not flattened dorsoventrally. Scape imbricate, shiny, covered with long and sparse, white, decumbent to subdecumbent setae. Mandibles rounded, with deep grooves, surface shiny with a few long and short yellow setae, cutting edge (masticatory margin) in large majors dentate or with serrulate edge. **Mesosoma.** Moderately long; promesonotum low and regularly convex in profile with pronotum not bulging above mesonotal plate, pronotal sides regularly rounded. Propodeum placed lower than promesonotum, flat anteriorly, sides posteriorly carinate, propodeal angle distinctly angulate never with subangulate denticles, posterior slope oblique. Promesonotum dorsally indistinctly and sparsely rugulose, interspaces smooth to imbricate; pronotum laterally costulate, costulae thin and dense with imbricate interspaces; lateral mesonotum

with thick and dense costae with imbricate interspaces; propodeum with sparser and thick costae with imbricate to smooth interspaces. Surface and setation of mesosoma moderately dense, pronotum with up to 15 long, yellow, erect setae, lateral sides of the pronotum without or anteriorly, with a few thin and short suberect setae, mesonotum with up to 35 long, erect setae, propodeal dorsum with up to 15, moderately long suberect setae, approximately 1/2 shorter than setae on promesonotum. **Waist and gaster.** Petiole moderately elongate, with moderately long pedicel and moderately high triangular node, thin. Whole surface of petiole with indistinct and sparse costulae with imbricate interspaces. Petiolar node subangulate in profile, top and lateral sides of node with up to 10 erect setae. Postpetiole subglobular, surface distinctly costulate with imbricate interspaces, surface with up to 20 long erect setae. Whole first gastral tergite smooth to very indistinctly imbricate, shiny; covered with extremely sparse and short appressed setae and moderately dense, long, semierect setae. **Legs.** Elongate, femora moderately swollen centrally, tibiae moderately widened apically, mid and hind tarsi longer than tibiae. Whole femora smooth, dorsally and laterally covered with sparse and long, decumbent and subdecumbent and ventrally semierect to erect setae. Tibiae covered with sparse and long decumbent to semierect setae.

Minor worker. Color. Predominates a pale form with the entire body brown to bright brown with darker patches on dorsal head and gaster. Some specimens with the same colouration as major workers. **Head.** Subrectangular, but more rounded in frontal view, approximately as long as wide, behind eyes more regularly rounded, occipital margin of the head straight. Sculpture of head weaker, whole surface imbricate with additional weak and indistinct costulae on anterior part of head. **Mesosoma.** As slender as in majors. Sculpture of mesosoma reduced, predominantly imbricate with some additional sparse costulae on mesonotum and propodeum. Propodeal angle well marked and not armed. Setation and surface of mesosoma as in majors but with lower number of setae (Figure 4). **Waist and gaster.** Waist imbricate and with lower number of erect setae. Gaster smooth and shiny. Remaining characters as in major workers.

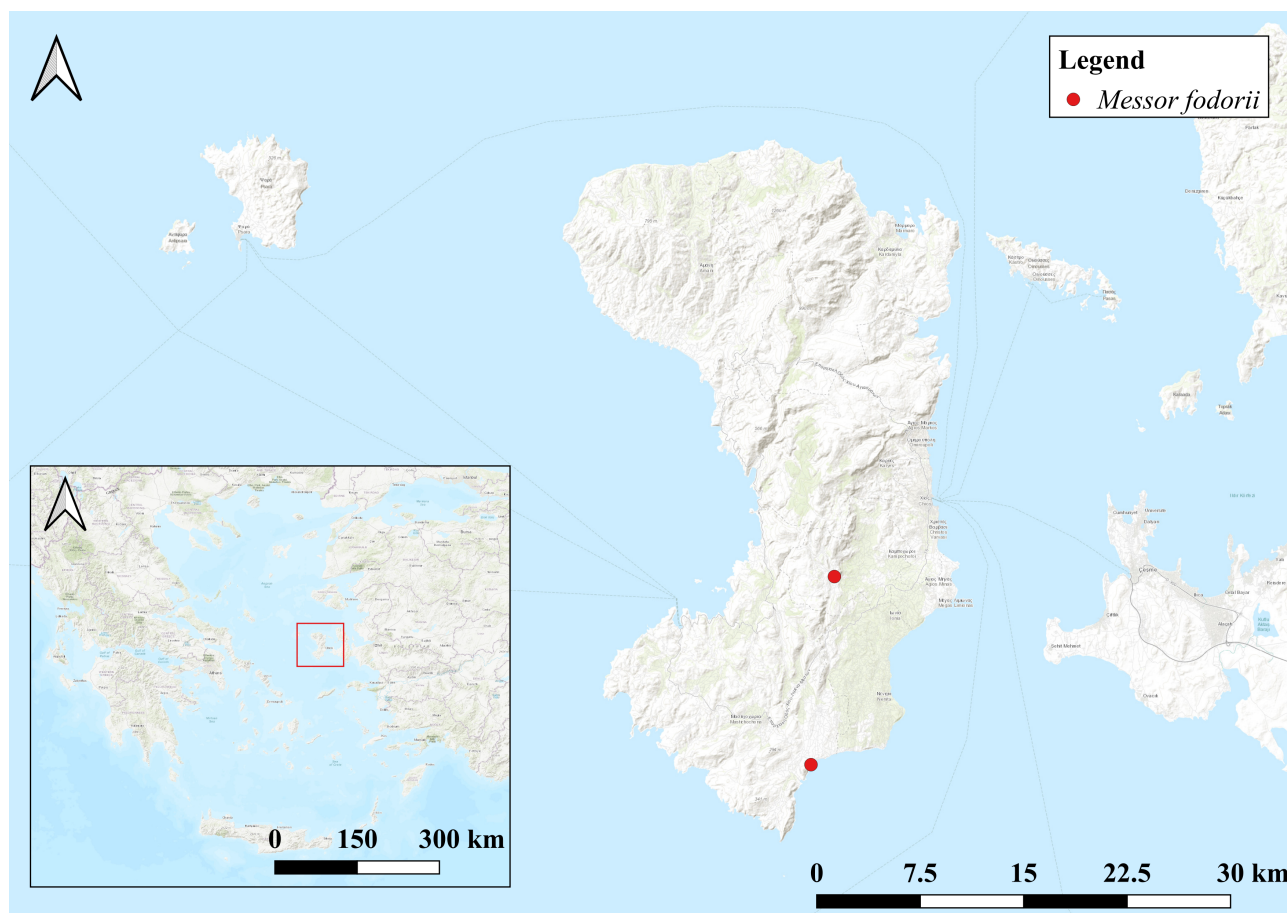


FIGURE 5. Distributional map of *Messor fodorii* in Chios (NE Aegean).

Biological notes. The species is thermophilous and granivorous. Out of all 97 sampled localities (Figure 1; Appendix I), *M. fodorii* was collected from only two sites on the island of Chios (Figure 5). Specimens were collected from two human-modified habitats, the *locus typicus*, i.e. the village of Agios Georgios (urban area) and a beach, both at low altitudes (370 and 2 meters) (Appendix I: localities CH34 and CH64, respectively). The only other *Messor* species in these localities was *M. wasmanni*. *Messor hellenius* was widespread on the island, while *M. ponticus* is only known from Thrace and Macedonia in Greece (Borowiec & Salata 2025). Foraging workers were observed nesting in pavement cracks and roadsides in urban areas, entering narrow circular holes which could not be excavated. As such, we could not locate any sexual forms. We did not observe the species nesting under stones or creating mounds typical of those of other *Messor* spp. Therefore, we hypothesize *Messor fodorii* may create deeper and narrower borrows, which are hard to locate and excavate, necessitating further research on its nesting habits and phenology of males and queens.

Discussion

In this article, we re-discover and re-describe *Messor fodorii* stat. nov. after nearly a century from its first and only collection. The taxonomic status of the species is investigated, raising the taxon to the species rank, designating a neotype, and comparing it with other species of the *Messor hellenius* complex (*M. hellenius*, *M. ponticus*). Additionally, as the species was previously known only from its *locus typicus* (Agios Georgios), we report the species one additional locality (Agia Markella) despite extensive fieldwork throughout the island, and lastly, provide ecological data.

Herein, we designate a neotype for *M. fodorii* due to its complex and uncertain taxonomic status. Despite exhaustive research, we could not locate type specimens of this taxon, and its description is insufficient and sometimes confusing. Thus, the name was overlooked by all taxonomic studies focusing on the Eastern-Mediterranean *Messor*. We concluded that establishing a neotype will clarify the taxonomic status and species-group affiliation of this species and further advance studies on this genus in this region. Based on the original description, Rösler (1942) described the species from a specimen intermediate between minor and major workers. The most ambiguous aspect of the description concerns the shape of the pedicel, which is characterized as “very thickened and large compared to the second” antennomere. This raises the question of which species served as the basis for comparison—a detail absent from the original description. One may therefore assume that the reference species had a distinctly flattened pedicel, as is the case in *M. structor*. However, when comparing the PEDL/PEDW indices for *M. fodorii*, it is clearly thicker than in the two remaining species (*M. hellenius* and *M. ponticus*) (see Table 1). We believe that establishing a neotype will help to resolve the taxonomic status concern of one of the most neglected ant species in this region.

Another concern that can be resolved by establishing a neotype is the relationship among the three taxa in the *hellenius* complex. As mentioned by Borowiec & Salata (2025), the infraspecific variation observed within populations of *M. ponticus* and *M. hellenius* is significant and considerably overlaps between these species. This was also evident in the PCA analysis (Figure 1), showing significant overlap between morphological characters except in one character being statistically significant (POC/CL). While *M. fodorii* is morphologically more similar to *M. ponticus*, its specimens with weaker sculpture can be confused with *M. hellenius*. Nevertheless, PCA analysis clearly clusters specimens of *M. fodorii* as a morphologically distinct taxonomic unit (Figure 1). While resolving this question is beyond the scope of this work, we assume that the relationship between these species can be determined only from molecular data. If all three species are in fact conspecific, *M. fodorii* holds priority over the remaining two species names.

Based on the available data, *M. fodorii* appears to be endemic to the island of Chios. No specimens were collected from Psara or Oinousses islands, although sampling on the latter island was restricted to a single day. Future studies could assess the potential presence of *M. fodorii* around the coasts of Çeşme peninsula (Türkiye), given the proximity of the Turkish mainland to the island. Similar cases notably include *Aphaenogaster aktaci* Kiran & Tezcan, 2008, known only from the Greek island of Lesbos and continental Türkiye (Salata *et al.* 2021), although the endemic status of the species is also highly plausible.

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APPENDIX I. Table of localities where specimens of *M. fodorii* were searched for from 24th April to the 5th May 2025, including data on habitats, assigned locality codes, island, elevation in meters and decimal latitude and longitude.

Date	Habitat	Locality code	Locality name	Island	Elevation (m)	Latitude	Longitude
24.04.2025	phrygana, chapel, spring	PS01	Agios Isidoros	Psara	115	38.58833	25.54689
24.04.2025	phrygana	PS02	Profitis Ilias	Psara	500	38.5925	25.58914
24.04.2025	phrygana	PS03	Karvouni, Agias Kiouras (Agias Matronis)	Psara	260	38.57631	25.60639
24.04.2025	seasonal creek, small lake	PS04	near Dodeka Apostoloi loc. 2	Psara	250	38.58764	25.57833
24.04.2025	monastery environs	PS05	Korakia, Moni Koimiseos Theotokou monastery	Psara	330	38.59706	25.58864
24.04.2025	phrygana, chapel	PS06	Panagia Vatousena	Psara	120	38.59842	25.57261
24.04.2025	phrygana, olive trees	PS07	near Dodeka Apostoloi loc. 1	Psara	200	38.58556	25.57333
24.04.2025	beach	PS08	Ftelio beach	Psara	5	38.5765	25.55306
24.04.2025	beach, dry riverbed	PS09	Archontiki beach	Psara	5	38.5687	25.5638
25.04.2025	phrygana	PS10	Kastri, Faros Kokkinopoulo	Psara	40	38.5366	25.6094
25.04.2025	phrygana, beach, dry stream	PS11	Fanari beach	Psara	20	38.53561	25.60719
25.04.2025	heterogeneous landscape (phrygana, reeds, dry stream, cultivated plants)	PS12	Limnos Psaron	Psara	15	38.54661	25.58439
25.04.2025	olive trees, maquis	PS13	Limnos Psaron loc. 2	Psara	30	38.54639	25.58911
25.04.2025	phrygana, <i>Juncus</i> , <i>Tamarix</i>	PS14	Achladokampos	Psara	10	38.54819	25.57769
25.04.2025	urban area and port	PS15	Psara town	Psara	10	38.54006	25.56364
25.04.2025	phrygana, pedestrian road	PS16	Mavri Rachi	Psara	15	38.53731	25.56389
25.04.2025	pond, dry riverbed and surrounding phrygana	PS17	Xirokampos, Zoodochos Pigi	Psara	60	38.5926	25.5634
25.04.2025	beach, phrygana	PS18	Lakka beach	Psara	10	38.5566	25.5652
25.04.2025	roadsides, phrygana	PS19	Vigla environs	Psara	45	38.5477	25.5669
26.04.2025	port, dirt road with <i>Tamarix</i> and flowering plants	CH01	Kastelo, Alieftiko Katafygio Ag. Paraskevis	Chios	1	38.3908	26.1383
26.04.2025	beach with reeds, <i>Tamarix</i> and flowering plants	CH02	Lekonio beach	Chios	1	38.3353	26.1472
26+28+ 30.04.2025	urban area and port	CH03	Chios town and port	Chios	5	38.3663	26.1395
26.04.2025	cultivated land, houses, <i>Quercus</i> trees	CH04	1.2 km E of Zyfias	Chios	65	38.3294	26.0913
26.04.2025	village entrance, roadsides, cultivated land	CH05	Agios Georgios Sykousis loc. 1	Chios	350	38.3206	26.0589
26.04.2025	urban area, roadsides inside village	CH06	Agios Georgios Sykousis loc. 2	Chios	360	38.3176	26.059

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APPENDIX I. (Continued)

Date	Habitat	Locality code	Locality name	Island	Elevation (m)	Latitude	Longitude
26.04.2025	lake with <i>Quercus</i> , <i>Pistacia lentiscus</i> var. <i>chia</i> , <i>Ceratonia siliqua</i> and olive trees	CH07	Agios Georgios artificial lake	Chios	110	38.3185	26.0748
27.04.2025	maquis, dry riverbed	CH08	Chavouna, Panagia Mariniotissa	Chios	280	38.5057	25.9035
27.04.2025	stream valley with <i>Platanus orientalis</i> , <i>Quercus</i> spp. and <i>Smyrnum</i>	CH09	800 m ESE of Trypes	Chios	230	38.5253	25.8767
27.04.2025	stream valley with <i>Platanus orientalis</i> , <i>Quercus</i> spp. and <i>Smyrnum</i>	CH10	Agio Galas, tou Vouda o Kremos	Chios	190	38.5612	25.8649
27.04.2025	stream valley with <i>Platanus orientalis</i> , <i>Quercus</i> spp. and <i>Smyrnum</i>	CH11	Kosmados	Chios	340	38.5637	25.8904
27.04.2025	pine forest, stream	CH12	1 km N Afrodisia	Chios	435	38.5632	25.9244
27.04.2025	pine forest, phrygana, wind turbines	CH13	500 m S Chalandra	Chios	500	38.5425	25.9349
27.04.2025	riverbed, large river with low flow	CH14	Chori	Chios	10	38.4716	25.9341
27.04.2025	maquis, beach	CH15	Akrotiri Pyrgos, Vigla Trachili	Chios	5	38.3633	25.9917
28.04.2025	recently burnt pine forest	CH16	1 km ESE Avgonyma	Chios	575	38.3743	26.0328
28.04.2025	sparse pine forest, dirt road, rocky substrate	CH17	2 km ENE Avgonyma, Seles	Chios	705	38.3813	26.0442
28.04.2025	pine forest, maquis	CH18	Agios Fanourios chapel	Chios	270	38.372	26.0691
28.04.2025	Maquis	CH19	900 m N Dafnonas	Chios	225	38.3551	26.0818
28.04.2025	plant nursery	CH20	Chios, plant nursery 1	Chios	25	38.371	26.1177
28.04.2025	pine forest with grasses and rocky substrate	CH21	Paralia Pantoukios	Chios	40	38.4617	26.1398
28.04.2025	urban area and port	CH22	Lagkada	Chios	0	38.4774	26.1237
29.04.2025	gorge with river	CH23	Mana Nerou gorge, Dipotamos river	Chios	50	38.5646	26.0745
29.04.2025	sparse maquis, rocky substrate	CH24	Pelinnaion Mt., Viki refuge loc. 1	Chios	640	38.5676	26.0141
29.04.2025	maquis, roadsides, small stream	CH25	Pelinnaion Mt., Viki refuge loc. 2	Chios	690	38.5661	26.0104
29.04.2025	pine forest	CH26	Pelinnaion Mt., 1 km SW Viki refuge	Chios	600	38.5734	26.0046
29.04.2025	gorge with deciduous trees	CH27	Kampia	Chios	330	38.5722	25.9842
29.04.2025	maquis with <i>Acer</i> trees	CH28	Pelinnaion Mt., Zoodochos Pigi chapel, near mountain top	Chios	960	38.553	26.0001
29.04.2025	pine and <i>Acer</i> forest	CH29	Pelinnaion Mt., Makria Skala	Chios	670	38.5545	25.9912

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APPENDIX I. (Continued)

Date	Habitat	Locality code	Locality name	Island	Elevation (m)	Latitude	Longitude
30.04.2025	plant nursery	CH30	Chios, plant nursery 2	Chios	5	38.3382	26.1407
01.05.2025	maquis and dirt road	CH31	500 m S of Zyfiias	Chios	90	38.3232	26.0811
01.05.2025	old olive orchard, pine forest, maquis	CH32	900 m SE of Agios Georgios Sykousis, Agios Kosmas	Chios	235	38.3135	26.0649
01.05.2025	sparse pine forest, maquis	CH33	Agios Georgios Sykousis, Isia	Chios	430	38.3095	26.0596
01.05.2025	urban habitat	CH34	Agios Georgios Sykousis, Agios Georgios church	Chios	370	38.321	26.057
01.05.2025	burnt and sparse pine forest, rocky substrate	CH35	2.5 km ESE Avgonyma, Seles	Chios	770	38.3854	26.0485
01.05.2025	archaeological site, monastery, stream	CH36	Nea Moni monastery	Chios	430	38.3745	26.056
02.05.2025	Maquis	CH37	750 m S Elata, Achlada	Chios	165	38.2796	25.9859
02.05.2025	port and beach	CH38	Agia Eirini beach	Chios	3	38.2957	25.9658
02.05.2025	roadsides, beach, phrygana	CH39	Mesta environs	Chios	75	38.2721	25.9284
02.05.2025	beach, meadow, maquis	CH40	Trachilia, Avlonia beach	Chios	2	38.2249	25.8938
02.05.2025	maquis	CH41	Olympoi environs	Chios	160	38.2521	25.9219
02.05.2025	archaeological site, olive grove, maquis	CH42	Sanctuary of Apollo Fanaios, Kato Fana beach	Chios	10	38.2069	25.9307
02.05.2025	urban area, parking lot	CH43	Pyrgi	Chios	100	38.2263	26.0011
02.05.2025	dry riverbed, agricultural area	CH44	Myrmigki	Chios	220	38.2856	26.076
02.05.2025	urban area	CH45	Katarraktis	Chios	1	38.2648	26.1034
03.05.2025	sparse maquis	CH46	Taxiarchis	Chios	95	38.5524	26.1337
03.05.2025	sparse maquis	CH47	Mpampakas, Stasima	Chios	145	38.5464	26.1452
03.05.2025	moist pine forest, dry riverbed	CH48	Megali Vigla, Agios Stamatios Chiopolitis	Chios	145	38.5464	26.1452
03.05.2025	old olive orchard, chapel, pine forest	CH49	Trygona, 750 m E Marmaro	Chios	7	38.5375	26.1345
03.05.2025	old olive orchard, chapel, pine forest	CH49	2.5 km ESE Marmaro, Agia Eirini chapel	Chios	100	38.5305	26.1459
03.05.2025	stream valley with <i>Platanus orientalis</i>	CH50	Nagos, Nagos spring	Chios	20	38.5577	26.0808
03.05.2025	heterogeneous landscape, cultivation, maquis, roadsides	CH51	Amades, Agios Nikolaos	Chios	320	38.5764	26.0446
03.05.2025	Acer forest	CH52	Pelinnaion Mt., Viki refuge loc. 3	Chios	720	38.5647	26.0117
03.05.2025	urban area	CH53	Kardamila	Chios	45	38.5273	26.093
04.05.2025	pine forest with a stream	CH54	near Fyta loc. 1	Chios	540	38.5281	26.0064
04.05.2025	pine forest with a stream	CH55	near Fyta loc. 2	Chios	666	38.5294	26.0141
04.05.2025	oak forest, olive orchard, <i>Pistacia lentiscus</i> var. <i>chia</i>	CH56	1.5 km SE Volissos	Chios	15	38.4764	25.9402

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APPENDIX I. (Continued)

Date	Habitat	Locality code	Locality name	Island	Elevation (m)	Latitude	Longitude
04.05.2025	pine forest clearing, phrygana	CH57	1 km ESE Katavasi, Arion dry stream	Chios	500	38.4604	25.9858
04.05.2025	riverbed (low flow), quarry, maquis	CH58	3.5 km SW Pityous, Mitsouras	Chios	475	38.4646	26.0296
04.05.2025	maquis, small artificial pond	CH59	2 km SW Pityous, Koilani	Chios	675	38.4815	26.0358
04.05.2025	urban area	CH60	Pityous	Chios	450	38.487	26.0534
04.05.2025	phrygana, rocky substrate	CH61	4.5 km S Pityous, Amygdalia	Chios	710	38.4478	26.051
04.05.2025	phrygana and chapel park	CH62	4 km SSE Pityous, Agios Georgios Florianos	Chios	515	38.4509	26.0678
05.05.2025	Beach	CH63	Emporeios, Mavra Volia	Chios	10	38.1851	26.0282
05.05.2025	Beach	CH64	Agia Markela Komis	Chios	2	38.1985	26.0376
05.05.2025	sandy beach, urban area	CH65	Karfas, Paralia Karfas	Chios	3	38.3191	26.1535
05.05.2025	garden and orchard	CH66	Chandri	Chios	20	38.3518	26.1333
05.05.2025	roadside, phrygana	CH67	near Tholopotami	Chios	260	38.284325	26.058741
30.04.2025	pine forest	OIN101	Aspalathrokampos	Oinousses	50	38.5182	26.2588
30.04.2025	meadow with <i>Juncus</i>	OIN102	Aspalathrokampos beach environs	Oinousses	5	38.5155	26.2604
30.04.2025	Maquis	OIN103	Marmara	Oinousses	10	38.5117	26.2538
30.04.2025	phrygana, roadside	OIN104	Fourkero	Oinousses	10	38.5135	26.2502
30.04.2025	dry stream with pine trees	OIN105	Vrisidia	Oinousses	30	38.5166	26.242
30.04.2025	urban area, port	OIN106	Oinousses town, port	Oinousses	5	38.5141	26.2184
30.04.2025	monastery, small pine forest, phrygana	OIN107	Monastery of the annunciation of Theotokos	Oinousses	75	38.5356	26.1976
30.04.2025	Phrygana	OIN108	“Pagkaki” near monastery	Oinousses	20	38.5327	26.1936
30.04.2025	phrygana (hillside), beach	OIN109	Hatzali beach	Oinousses	1	38.5303	26.1993
30.04.2025	maquis (<i>Pistacia lentiscus</i> var. <i>chia</i> , <i>Pinus</i>)	OIN110	Kastro, Kampos Fokias	Oinousses	5	38.524	26.2039
30.04.2025	maquis (<i>Pistacia lentiscus</i> var. <i>chia</i> , <i>Pinus</i>)	OIN111	Kastro, near Taxiarches chapel	Oinousses	30	38.522	26.207

APPENDIX II. P-value of Kruskal-Wallis test for all measurements and indices. Significant differences are highlighted in bold.

Measurements and indices	p-value	Measurements and indices	p-value
CL	p<0.001	PEDW	p<0.001
CW	p<0.001	PEDL	p<0.001
POC	p<0.001	AN03W	p<0.001
PrOC	p<0.001	AN03L	p<0.001
FR	p<0.001	CS	p<0.001
AnScD	p<0.001	POC/CL	p<0.001
SL	p<0.001	FR/CS	0.3258
ScBaC	p<0.001	MW/CS	p<0.001
ScBw	p<0.001	PEW/CS	p<0.01
ML	p<0.001	ML/CS	p<0.001
NOL	p<0.001	SL/CS	p<0.001
EL	p<0.001	EL/CS	0.2033
HTL	p<0.001	PEDL/PEDW	p<0.001
PEW	p<0.001	PEDL/AN03L	0.6178
MW	p<0.001		

APPENDIX III. P-value of Dunn's test for all measurements and indices for species pairs examined. Significant differences are highlighted in bold.

Measurements and indices	Comparison pair		
	<i>fodorii-hellenius</i>	<i>fodorii-ponticus</i>	<i>hellenius-ponticus</i>
CL	p<0.01	p<0.001	0.44514
CW	p<0.001	p<0.001	0.53720
POC	p<0.01	p<0.001	0.13164
PrOC	p<0.001	p<0.001	1.0
FR	p<0.001	p<0.001	0.54522
AnScD	p<0.01	p<0.001	0.31393
SL	p<0.001	p<0.001	1.0
ScBaC	p<0.001	p<0.001	1.0
ScBw	p<0.01	p<0.001	0.63659
ML	p<0.01	p<0.001	0.50184
NOL	p<0.01	p<0.001	0.74816
EL	p<0.001	p<0.001	0.85015
HTL	p<0.001	p<0.001	0.70826
PEW	p<0.01	p<0.001	0.27183
MW	p<0.001	p<0.001	0.84761
PEDW	p<0.01	p<0.001	0.58949
PEDL	p<0.001	p<0.001	0.17443
AN03W	p<0.001	p<0.001	1.0
AN03L	p<0.001	p<0.001	0.45638
CS	p<0.01	p<0.001	0.47161
POC/CL	0.05669	p<0.001	p<0.05
FR/CS	0.75246	1.0	0.57255
MW/CS	p<0.05	p<0.001	0.09653
PEW/CS	p<0.001	0.05876	0.83370
ML/CS	p<0.001	p<0.001	1.0
SL/CS	p<0.01	p<0.001	0.26257
EL/CS	0.56847	0.24518	1.0
PEDL/PEDW	p<0.05	p<0.001	0.49012
PEDL/AN03L	1.0	1.0	1.0