NeoBiota 88: 17–73 (2023)
doi: 10.3897/neobiota.88.106750
https://neobiota.pensoft.net

REVIEW ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Running rampant: the alien ants (Hymenoptera, Formicidae) of Cyprus

Jakovos Demetriou[1,2,3], Christos Georgiadis[4,5], Angeliki F. Martinou[2,3,6], Helen E. Roy[7], James K. Wetterer[8], Lech Borowiec[9], Evan P. Economo[10], Kostas A. Triantis[1], Sebastian Salata[9]

1 *Department of Ecology and Systematics, Faculty of Biology, National and Kapodistrian University of Athens, 15784 Athens, Greece* **2** *Joint Services Health Unit Cyprus, BFC RAF Akrotiri BFPO 57, Akrotiri, Cyprus* **3** *Enalia Physis Environmental Research Centre, Acropoleos 2, Aglantzia 2101, Nicosia, Cyprus* **4** *Museum of Zoology, National and Kapodistrian University of Athens, 15784 Athens, Greece* **5** *Section of Zoology and Marine Biology, Department of Biology, National and Kapodistrian University of Athens, 15784 Athens, Greece* **6** *Climate and Atmosphere Research Centre/ Care-C, The Cyprus Institute, Athalassa Campus, 20 Konstantinou Kavafi Street, 2121 Aglantzia, Nicosia, Cyprus* **7** *UK Centre for Ecology & Hydrology, Benson Lane, Crowmarsh Gifford, Oxfordshire, UK* **8** *Department of Biology, Harriet L. Wilkes Honors College, Florida Atlantic University, Jupiter, FL 33458, USA* **9** *University of Wrocław, Department of Biodiversity and Evolutionary Taxonomy, Myrmecological Laboratory, Przybyszewskiego 65, 51-148 Wrocław, Poland* **10** *Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Onnason, Okinawa, 904-0495, Japan*

Corresponding author: Jakovos Demetriou (jakovosdemetriou@gmail.com)

Academic editor: Wolfgang Rabitsch | Received 22 May 2023 | Accepted 19 September 2023 | Published 12 October 2023

Citation: Demetriou J, Georgiadis C, Martinou AF, Roy HE, Wetterer JK, Borowiec L, Economo EP, Triantis KA, Salata S (2023) Running rampant: the alien ants (Hymenoptera, Formicidae) of Cyprus. NeoBiota 88: 17–73. https://doi.org/10.3897/neobiota.88.106750

Abstract

Biological invasions are considered a major driver of biodiversity loss, particularly on islands. Invasive alien ants can often have severe consequences on native biodiversity. Here, we review published and new information on alien ant species found on the Mediterranean island of Cyprus, a biodiversity hotspot. Our checklist of alien ants of Cyprus includes a total of 17 species, of which nine are reported from Cyprus for the first time (*): *Camponotus* cf. *vitiosus* Smith, *Cardiocondyla mauritanica* Forel, 1890, *Cardiocondyla obscurior* Wheeler, W.M., 1929*, *Hypoponera punctatissima* (Roger, 1859)*, *Monomorium bicolor* Emery, 1877, *Nylanderia jaegerskioeldi* (Mayr, 1904), *Paratrechina longicornis* (Latreille, 1802), *Pheidole fadli* Sharaf, 2007*, *Pheidole indica* Mayr, 1879, *Solenopsis* sp. (thief ant)*, *Tetramorium bicarinatum* (Nylander, 1846)*, *Tetramorium caldarium* (Roger, 1857)*, *Tetramorium immigrans* Santschi, 1927*, *Tetramorium lanuginosum*

Mayr, 1870*, *Trichomyrmex destructor* (Jerdon, 1851), *Trichomyrmex mayri* (Forel, 1902)*, and *Wasmannia auropunctata* (Roger, 1863). We did not include three previously reported alien species for which we could not find supporting specimens [*Monomorium pharaonis* (Linnaeus, 1758), *Nylanderia vividula* (Nylander, 1846), *Solenopsis geminata* (Fabricius, 1804)], one based on a previous misidentification [*Cardiocondyla nuda* (Mayr, 1866)], and two species now considered native to Cyprus [*Hypoponera eduardi* (Forel, 1894), *Monomorium subopacum* (F. Smith, 1858)]. Literature records, specimens from field surveys and museum collections, the geographic origin of species, occupied habitats in Cyprus, and notes on invasiveness (spread and impact) are presented for each species. An identification key to distinguish alien from native ant species in Cyprus is provided, including widespread alien ants not yet known from Cyprus in order to support early detection, monitoring, and management efforts.

Keywords
biological invasions, checklist, first records, identification key, invasive alien species, social insects, tramp species

Introduction

Biological invasions are considered a major driver of global biodiversity loss, with profound impacts on the extinction risk and evolutionary histories of island species (Mooney and Cleland 2001; Reaser et al. 2007; Butchart et al. 2010; Russell et al. 2017; Leclerc et al. 2018; IPBES 2019). Of 520 ant species found transported outside their native range globally, almost half of them have managed to establish viable, self-sustaining populations in their invaded range, although only relatively few have been assessed as harmful (Wong et al. 2023). A recent study assessing socio-economic and environmental impacts of alien ants, documented 31 species as highly invasive (Gruber et al. 2022). Alien ants have been found to have adverse environmental impacts on native flora and fauna, largely through competition and predation, and in some cases lead to the extinction of native species. Additionally, alien ants have serious socio-economic impacts as household pests, and threaten human and animal health as both vectors of pathogens and through their venomous stings which may cause allergic reactions (Angulo et al. 2022; Gruber et al. 2022).

The Mediterranean Basin is a global biodiversity hotspot with a plethora of endemic species in need of conservation (Myers et al. 2000). Situated at the crossroad between three continents, Cyprus constitutes the 3rd largest Mediterranean island covering an area of 9,251 km^2. The island is a centre of endemism for Mediterranean plants hosting 146 endemic species and subspecies (8.85% endemism rate) (Hand et al. 2011, 2019; Cheikh Albassatneh et al. 2021) and is also considered a centre of endemism for mammals (Hadjisterkotis and Masala 1995) as well as European and Middle Eastern birds (Bibby et al. 1992). Regarding its insect biota, recent comprehensive studies on the wild bees of Cyprus indicate the presence of 21 endemic species of Anthophila (5.7% endemism rate) (Varnava et al. 2020). Data on other hymenopteran taxa remain unpublished or largely unknown.

The myrmecofauna of Cyprus is considered relatively understudied, with published reports of 65 native and nine alien species (Janicki et al. 2016; Guénard et al.

2017); constituting fewer species than the neighbouring island of Crete, an island of similar area, where 93 native and 10 alien species have been collected (Salata et al. 2020; Lapeva-Gjonova et al. in prep). Nonetheless, a number of endemic species and subspecies have been described from Cyprus, including *Cataglyphis aphrodite* Salata, Demetriou, Georgiadis & Borowiec, 2023, *Cataglyphis chionistrae* Salata, Demetriou, Georgiadis & Borowiec, 2023 (Salata et al. 2023a), *Crematogaster cypria* Santschi, 1930 (Salata and Borowiec 2015b), *Lasius cyperus* Seifert, 2020 (Seifert 2020), and *Oxyopomyrmex pygmalioni* Salata & Borowiec, 2015 (Salata and Borowiec 2015a), as well as subspecies such as *Crematogaster inermis aphrodite* Santschi, 1937, *Solenopsis fugax cypridis* Santschi, 1934 and *Temnothorax bulgaricus cypridis* (Santschi, 1930) (Santschi 1930, 1934, 1937). In addition, several more endemic taxa are currently being described (Salata, Demetriou, Georgiadis and Borowiec, unpubl. data).

The first checklist of the alien ants of Cyprus (Salata et al. 2019) and a recent review on the island's alien insect-fauna (Demetriou et al. 2023a) both included nine species of ants, though these checklists differed in four species. Here, we review published and new information on alien ants found on the Mediterranean island of Cyprus. We perform a focused study on the alien ant fauna of Cyprus, both to provide a more comprehensive list, and reconcile existing incongruences in the literature regarding ant species presence on the island. Considering the adverse environmental and socio-economic impacts of alien ants, an updated, annotated checklist is provided alongside an identification key to distinguish alien from native ant species of Cyprus. The presence of alien ants in the NATURA 2000 network and their land-cover usage are analysed and discussed.

Materials and methods

Data collection and specimen identification

A literature review was carried out to collate all available records of alien ants reported from Cyprus including species catalogued in the Global Ant Biodiversity Informatics (GABI) database (Janicki et al. 2016; Guénard et al. 2017) and scientific literature (Emery 1909, 1910; Georghiou 1977; Georgiadis et al. 2017; Salata et al. 2019; Demetriou et al. 2022, 2023a). In addition, specimens collected in the field by the authors on the island during 2012, 2021 and 2022, deposited in the collections of L. Borowiec and S. Salata (Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland – DBET), Ch. Georgiadis (Museum of Zoology of the University of Athens, Greece – ZMUA), J. Wetterer (Smithsonian National Museum of Natural History, Washington, USA) and J. Demetriou (pers. collection) as well as material in the Museum of Natural History of the University of Wroclaw, Poland (MNHW) and Natural History Museum of Crete (NHMC) were examined (Suppl. material 1).

The identification of the ants was performed by comparing the specimens with type material deposited in museum collections such as that of MNHW alongside regional

works on European ants and recent published revisions for genera and species complexes/groups (Agosti and Collingwood 1987; Seifert 2003, 2018, 2020; Czechowski et al. 2012; Seifert et al. 2017; Wagner et al. 2017).

Establishment status

The establishment status of alien ants was catalogued as Established i.e. "non-native species records with established populations in the wild" or Indoors introduced i.e. "non-native species records without established populations in the wild (e.g. in buildings, greenhouses, airports, quarantine surveys)" noting that within GABI the equivalent categories are given as exotic (= established) and indoors introduced (Janicki et al. 2016; Guénard et al. 2017). Lastly, the establishment status of data-deficient species is given as "Unknown".

The native origin of species was decided based on GABI accessed through the antmaps.org website (Janicki et al. 2016; Guénard et al. 2017) and available scientific literature on the native range of species. Each species was assigned to one or more biogeographic realms sensu Holt et al. (2013). Criteria in Essl et al. (2018) were also applied to determine whether some species could be regarded as alien or native.

Identification key

A dichotomous identification key to distinguish alien from native ant species inhabiting Cyprus was constructed using available scientific literature and specimens (Seifert 2003; Sharaf et al. 2016; Salata et al. 2020; Gotzek and Martinez 2021; Borowiec and Salata 2022). Additionally, several alien and invasive alien species included in the 100 of the world's worst invasive alien species (*Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta* and *Wasmannia auropunctata*) (GISD 2023), alien invasive species of Union Concern (*Solenopsis geminata*, *S. invicta*, *S. richteri* and *W. auropunctata*) (EU 2022/1203), species listed in a horizon scanning exercise (Peyton et al. 2019) (*L. humile* and *W. auropunctata*), alien ant species inhabiting the Eastern Mediterranean (Janicki et al. 2016; Guénard et al. 2017) as well as international and regional lists of widespread alien ants (Vonshak and Ionescu-Hirsch 2009; Wetterer 2009a, 2014a, b; Pospischil 2011; Borowiec 2014; Schifani 2019; Kiran and Karaman 2020; Salata et al. 2020; Pawluk et al. 2022a, b; Demetriou et al. 2023a) were added to the identification key to facilitate early detection, monitoring and management efforts across Cyprus.

Spread and invaded habitats

The distribution of alien ant species within Cyprus was mapped. A total of 281 georeferenced observations (Suppl. material 1) were pooled in QGIS Version 3.18.2 free and open source Geographic Information System (https://qgis.org/en/site/) and were assigned to their respective land cover and presence within the NATURA2000 network.

Boundaries and habitat types were based on the European layers of Corine Land Cover (CLC) project version CLC2018 and NATURA2000 sites, downloaded from Copernicus Land Monitoring Service and the European Environmental Agency, respectively. The occurrence of species within the boundaries of the protected RAMSAR site of Akrotiri (https://rsis.ramsar.org/RISapp/files/1375/pictures/GB1375map.pdf) (RAMSAR site code: 1375), was also documented. In addition to these distribution maps, information on occupied habitats are given, providing additional information alongside the broad CLC types. Therefore, with reference to the Copernicus Land Monitoring Service, records of ants within the following land-cover types were mapped: artificial surfaces, agricultural areas, forest and semi-natural areas, wetlands and water bodies as well as their respective sub-categories (https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html). The area of occupancy (AOO) and extent of occurrence (EOO) of species were calculated through GeoCAT in a 2 × 2 km^2 grid, following guidelines of the International Union for the Conservation of Nature (IUCN) for the assessment of extinction risk of taxa (IUCN 2001; Bachman et al. 2011).

Specimen photography

Photographs of specimens, unless stated otherwise, were taken by Prof. L. Borowiec using Nikon SMZ18 and Nikon SMZ 1500 stereomicroscopes, Nikon D5200 camera and Helicon Focus software. Locality data for each photographed specimen are provided in the figure titles.

Results

The updated checklist of alien ants of Cyprus currently comprises of 17 species (Table 1). Six species previously included on checklists were removed. In particular, records of *Cardiocondyla nuda* (Mayr, 1866), *Monomorium pharaonis* (Linnaeus, 1758), *Nylanderia vividula* (Nylander, 1846) and *Solenopsis geminata* (Fabricius, 1804) are considered as dubious, while *Hypoponera eduardi* (Forel, 1894) and *Monomorium subopacum* (Smith, F., 1858) are currently considered as native to the island. Furthermore, eleven species are added, including the recently detected invasive alien *Wasmannia auropunctata* (Roger, 1863) (Demetriou et al. 2022), *Camponotus* cf. *vitiosus* (Salata et al. 2023b) and newly presented records of *Pheidole fadli* Sharaf, 2007, *C. obscurior* Wheeler, W.M., 1929, *Tetramorium bicarinatum* (Nylander, 1846), *T. caldarium* (Roger, 1857), *T. immigrans* Santschi, 1927, *T. lanuginosum* Mayr, 1870, *Solenopsis* sp_CYP139, *T. mayri* (Forel, 1902), and *H. punctatissima* (Roger, 1859) (Tables 1, 2).

The five species with the highest AOO in decreasing order are *M. bicolor*, *P. indica*, *N. jaegerskioeldi*, *P. longicornis* and *W. auropunctata*, while regarding their EOO this order is: *T. bicarinatum*, *M. bicolor*, *P. indica*, *P. longicornis* and *N. jaegerskioeldi*, in decreasing order (Table 2). The majority of alien species have been collected in the island's lowlands, below the altitude of 500 m. Nevertheless, *M. bicolor* and *T. mayri*

Table 1. List of alien ants of Cyprus and accompanying notes including previous lists, (1) Salata et al. (2019), (2) Demetriou et al. (2023a), and updates from (3) Present study.

Subfamily	Tribe	Species	1	2	3	Notes
Formicinae	Camponotini	*Camponotus* cf. *vitiosus*			X	
	Lasiini	*Nylanderia jaegerskioeldi*	X	X	X	
		Paratrechina longicornis	X	X	X	
Myrmicinae	Attini	*Pheidole fadli*			X	New addition – new record
		Pheidole indica	X	X	X	
		Wasmannia auropunctata			X	
	Crematogastrini	*Cardiocondyla mauritanica*	X	X	X	
		Cardiocondyla nuda		X		Removed as dubious
		Cardiocondyla obscurior			X	New addition – new record
		Tetramorium bicarinatum			X	New addition – new record
		Tetramorium caldarium			X	New addition – new record
		Tetramorium immigrans			X	New addition – new record
		Tetramorium lanuginosum			X	New addition – new record
	Solenopsidini	*Monomorium bicolor*	X	X	X	
		Monomorium pharaonis	X	X		Removed as dubious
		Monomorium subopacum	X			Removed as native
		Solenopsis geminata	X	X		Removed as dubious
		Solenopsis sp_CYP139			X	New addition – new record
		Trichomyrmex destructor		X	X	
		Trichomyrmex mayri			X	New addition – new record
Ponerinae	Ponerini	*Hypoponera eduardi*	X			Removed as native
		Hypoponera punctatissima			X	New addition – new record
Total alien species			**9**	**9**	**17**	

have reached altitudes of 550 and 600 metres, respectively, and *C.* cf. *vitiosus* has been collected in the Cedar Valley protected area (CY2000006) at an altitude of approx. 1200 m. A total of seven alien species were collected from 20 protected areas within the NATURA 2000 and RAMSAR network. *Monomorium bicolor* was found in 15 protected sites, followed by *P. longicornis* and *T. mayri* each in three. The Akamas Peninsula (sites CY4000010 and CY4000023) was the protected area with the highest number of alien ants (hosting four alien species), followed by the Akrotiri Peninsula RAMSAR site with three alien species. The sites Koili – Mavrokolympos (CY4000008), Faros Kato Paphou (CY4000013), Alykes Larnakas (CY6000002) and Periochi Kosiis – Pallourokampou (CY6000009) each hosted two alien species, with the remaining protected areas having only one alien species (Suppl. material 2). Only three alien species have been reported from Cyprus during the 20th century. The remaining 14 species were recorded within the last decade (2012–2022).

According to the CLC analysis, 90% of georeferenced records of alien ants have been collected from anthropogenic habitats (Fig. 1). These include artificial surfaces (61%) and agricultural areas (29%), with further information provided in Suppl. material 1. Only 9% of records were associated with semi-natural and natural areas, with two records (1%) corresponding to inland water bodies, specifically ants collected close to water reservoirs.

Table 2. Spatiotemporal characteristics of alien ants species in Cyprus, including their area of occupancy (AOO) and extent of occurrence (EOO) in a 2 × 2 km² grid, altitudinal range in metres (rounded off to the nearest 50s), number and code(s) of occupied protected areas as well as the year of first official published record and associated reference.

No.	Taxonomy	Spread (km²)		Altitude range (m)	Protected areas		First official published record	
	Species	AOO	EOO		No.	Code(s)	Detection year	Reference
1	*Camponotus* cf. *vitiosus*	N/A	N/A	1200	2	CY2000006 CY2000016	2012	Salata et al. 2023b
2	*Nylanderia jaegerskioeldi*	80	4,728	0–400	5	CY4000008 CY4000010 CY4000023 CY6000009 RAMSAR1375	1910	Emery (1910)
3	*Paratrechina longicornis*	72	4,915	0–150	3	CY4000010 CY4000023 CY6000002	2012	Salata et al. (2019)
4	*Pheidole fadli*	N/A	N/A	100	0	N/A	2022	present study
5	*Pheidole indica*	100	4,963	0–400	2	CY4000008 CY4000013	2012	Salata et al. (2019)
6	*Wasmannia auropunctata*	60	410	0–300	0	N/A	2022	Demetriou et al. (2022)
7	*Cardiocondyla mauritanica*	36	4,043	0–150	0	N/A	1909	Emery (1909)
8	*Cardiocondyla obscurior*	16	65	0–50	0	N/A	2012	present study
9	*Tetramorium bicarinatum*	12	9.878	0–100	0	N/A	2022	present study
10	*Tetramorium caldarium*	N/A	N/A	100	0	N/A	2022	present study
11	*Tetramorium immigrans*	8	N/A	0–100	0	N/A	2022	present study
12	*Tetramorium lanuginosum*	28	247	0–100	2	CY4000010 CY4000023	2013	present study
13	*Monomorium bicolor*	264	6,318	0–600	15	CY3000007 CY3000008 CY4000003 CY4000005 CY4000007 CY4000010 CY4000013 CY4000019 CY4000020 CY4000021 CY4000023 CY4000025 CY6000002 CY6000009 RAMSAR1375	2012	Salata and Borowiec (2015b)
14	*Solenopsis* sp_CYP139	16	1,185	0–100	0	N/A	2022	present study
15	*Trichomyrmex destructor*	16	159	0–100	0	N/A	1925	Georghiou (1977)
16	*Trichomyrmex mayri*	32	4,074	0–550	3	CY2000004 CY2000013 RAMSAR1375	2022	present study
17	*Hypoponera punctatissima*	N/A	N/A	100	0	N/A	2022	present study

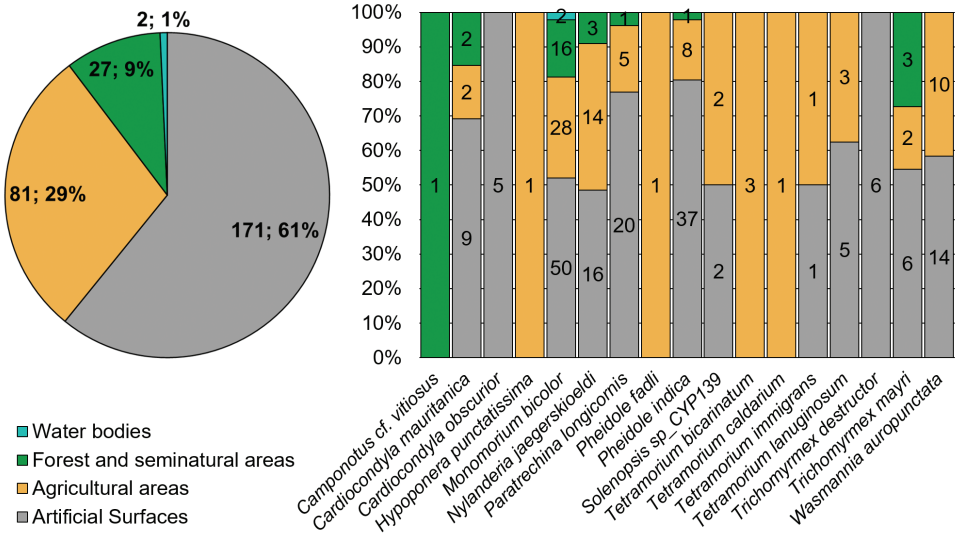

Figure 1. Number of georeferenced records of alien ants and respective percentage within broad Corine Land Cover (CLC) types in Cyprus (**A**). Percentage and number of georeferenced records for each species of alien ant collected in Cyprus per broad CLC type (**B**).

Commented checklist

Alien ants of Cyprus

Formicinae
Formicini

Camponotus* cf. *vitiosus
Fig. 2

Literature records. (Salata et al. 2023b).

Material examined. Suppl. material 1.

Origin. Sino-Japanese biogeographic realm.

Habitat details. Collected once from Cedar valley (Paphos), in high altitude (1196 m) in natural pine and cedar forest (Salata et al. 2023b).

Degree of establishment. Unknown.

Notes. A species resembling *C. vitiosus* was first recorded for the Mediterranean Basin from Israel, as *Camponotus* (*Myrmamblys*) sp. near *vitiosus* Smith, F., 1874 (Ionescu-Hirsch 2009). Specimens were intercepted at the Ashdod Port "in bamboo from China" (Ionescu-Hirsch 2009), while no additional records of the species have been provided since. A worker and a queen of the species were collected from the Cedar valley in 2012, situated within the Troodos mountain range, and the overlapping protected NATURA 2000 sites CY2000006 and CY2000016. Follow-up field surveys in 2022 provided no further material. In its native range (China, Japan and Korea),

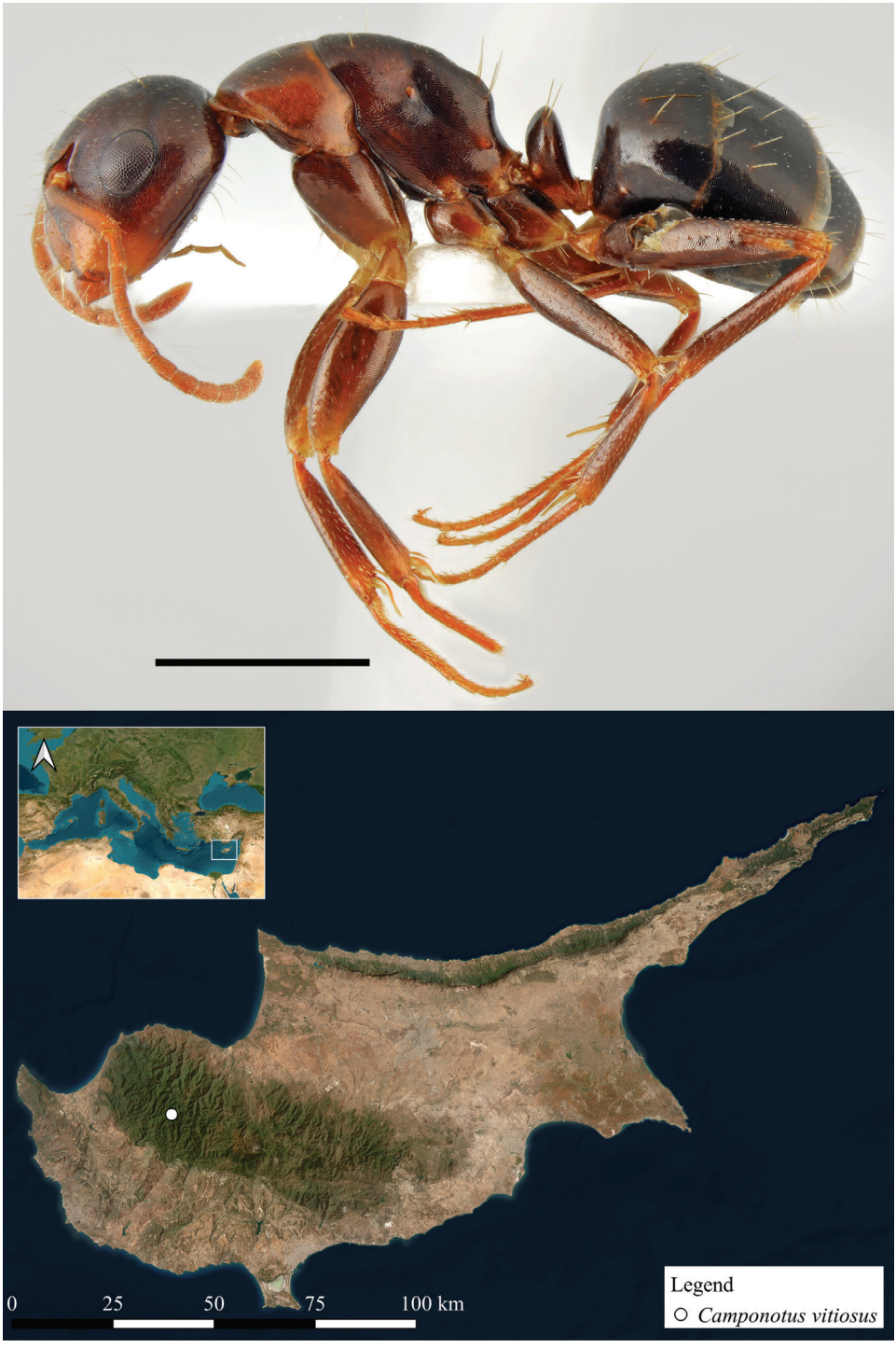

Figure 2. Habitus of minor worker of *Camponotus* cf. *vitiosus* (from Paphos, Cedar Valley) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

C. vitiosus has been collected both from urban and natural habitats in the lowlands and high mountains (Guénard and Dunn 2012; Kim and Lyu 2012; Park et al. 2014). The exact identity of this morphospecies will be further investigated with the help of molecular tools and sampling to retrieve any additional material.

Lasiini

***Nylanderia jaegerskioeldi* (Mayr, 1904)**
Fig. 3

Literature records. Emery (1910); Georgiadis et al. (2017); Salata et al. (2019).

Material examined. Suppl. material 1.

Origin. Africa and Arabian Peninsula (Afrotropical and Saharo-Arabian biogeographic realms).

Habitat details. Common synanthropic species collected from urban habitats, plant nurseries, and households as well as from semi-natural and natural habitats such as a beach, stream valley, canyon, pastureland, and a river bank.

Degree of establishment. Established.

Notes. In Sicily aggressive behaviour towards *Pheidole pallidula* (Nylander, 1849) has been observed, although typically across the Mediterranean *N. jaegerskioeldi* is mostly collected from anthropogenic habitats (Obregón Romero and Reyes López 2012; Schifani and Alicata 2018; Reyes-López and Taheri 2018). In Cyprus, the species has been found indoors as a household pest, as well as in five natural protected areas including the Akrotiri marsh RAMSAR site. More research on its impacts on native ant communities is required.

***Paratrechina longicornis* (Latreille, 1802)**
Fig. 4

Literature records. Salata et al. (2019).

Material examined. Suppl. material 1.

Origin. Indian subcontinent (Tseng et al. 2022) (Indomalayan biogeographic realm).

Habitat details. Common species in urban areas (garden, parks, parking lots, roadsides) and disturbed semi-natural habitats (beach, dirt road, field, waterfront).

Degree of establishment. Established.

Notes. This synanthropic species is widespread across Cyprus and has been collected from a variety of habitats. In Greece, *P. longicornis* can be found in the Dodecanese, inhabiting disturbed habitats in the lowlands and invading households (Borowiec and Salata 2022). Nevertheless, the species has been found to co-occur with native species, showing no signs of aggression (Salata et al. 2019). In Cyprus, the species can be found in urban and semi-natural habitats with evident human intervention and no adverse impact on native ant species has been observed. Nevertheless, detailed studies on the

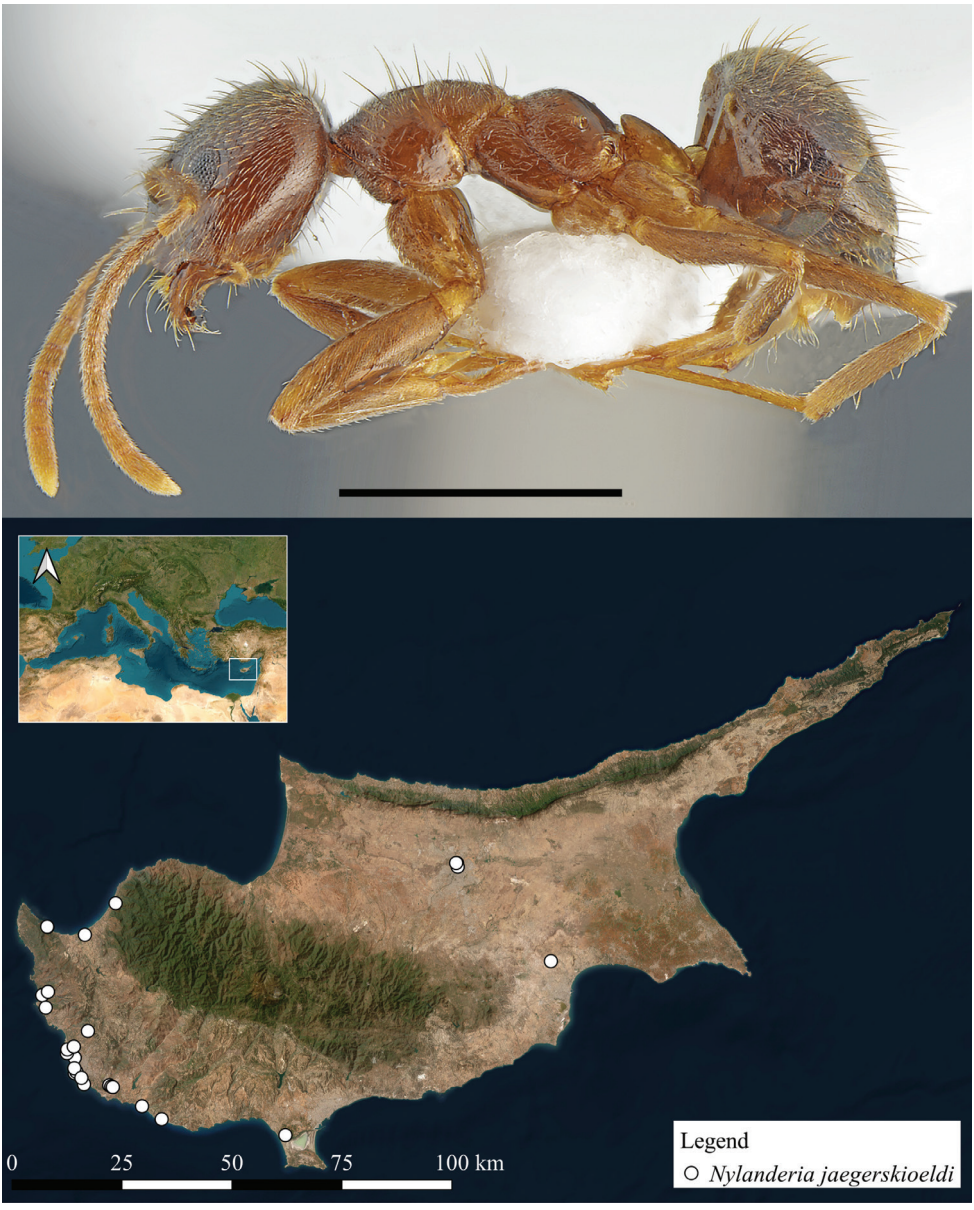

Figure 3. Habitus of *Nylanderia jaegerskioeldi* (Mayr, 1904) (specimen from Paphos, Baths of Aphrodite) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

impacts of P. *longicornis* on native biodiversity are necessary. *Paratrechina longicornis* is also known to tend honeydew producing Hemiptera such as aphids (Saddiqui et al. 2019). In Cyprus, it was collected from *Eucalyptus* foliage probably feeding on honeydew secreted from *Glycaspis brimblecombei* Moore, 1964. Such a behaviour could exacerbate the socio-economic impacts of the psyllid. Further research on the impacts

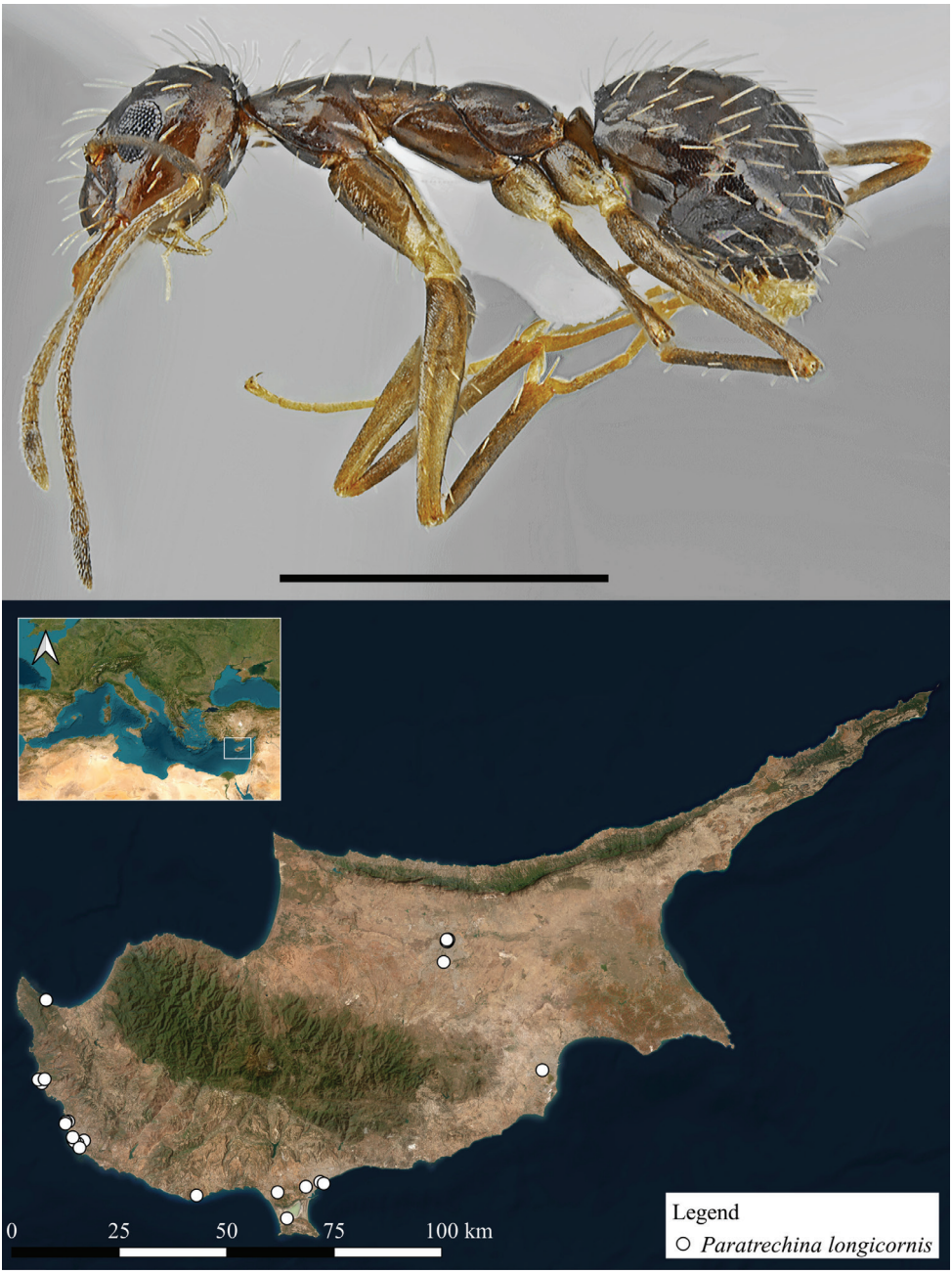

Figure 4. Habitus of *Paratrechina longicornis* (Latreille, 1802) (specimen from Paphos, Baths of Aphrodite) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

of the species as a household pest and its interactions with agricultural pests such as aphids or the alien cricket *Myrmecophilus americanus* Saussure, 1877 (Wetterer and Hugel 2014) could be prioritised.

Myrmicinae
Attini

***Pheidole fadli* Sharaf, 2007**
Fig. 5

Literature records. N/A.

Material examined. Suppl. material 1.

Origin. Egypt (Sino-Arabian biogeographic realm).

Habitat details. Only one specimen collected from a plant nursery in Paphos. Probably unintentionally introduced through the horticultural pathway in soil.

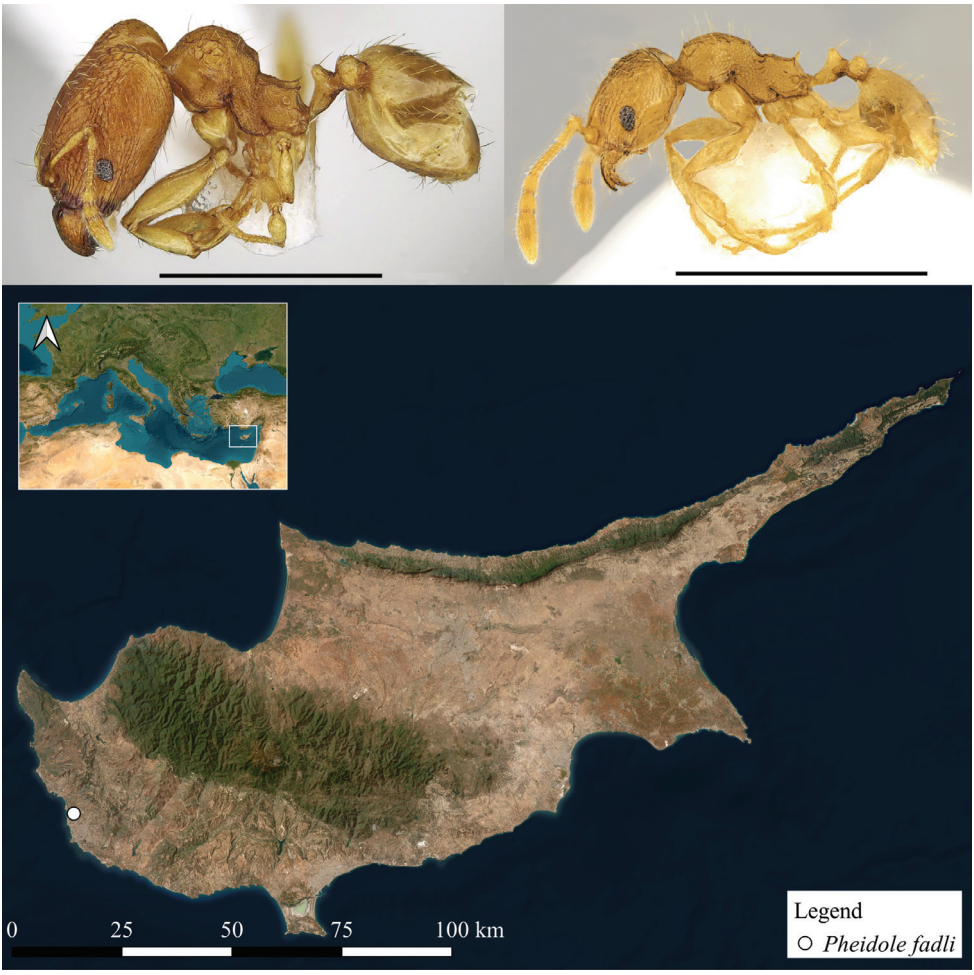

Figure 5. Habitus of *Pheidole fadli* Sharaf, 2007 major worker (left, from Egypt, Aswan, photographed by Michele Esposito, from www.antweb.org, CASENT0919803) and minor worker (right, from Paphos, Lemba) in lateral view (scale bar: 1 mm) and its known distribution in Cyprus below.

Degree of establishment. Unknown.

Notes. The species was first described in Fadl et al. (2007) from specimens collected near the river Nile and was considered to be endemic to Egypt. A single specimen was collected in Paphos from a plant nursery, under plastic sheets placed on the soil. It was probably introduced unintentionally in potted plants from Egypt but this is not confirmed. The high soil moisture and temperature in the glasshouse may have provided suitable microhabitats for the species.

***Pheidole indica* Mayr, 1879**
Fig. 6

Literature records. Salata et al. (2019).

Material examined. Suppl. material 1.

Origin. Indomalayan biogeographic realm.

Habitat details. Inhabiting urban habitats including parks, parking lots, pedestrian paths, plant nurseries, ports and parks as well as semi-natural habitats associated with humans such as sea and lake shores.

Degree of establishment. Established.

Notes. Synanthropic species collected from urban and semi-natural habitats in which there is human activity. In the Balearics, it [as *Ph. teneriffana*] has been observed to attack native *Tetramorium* cf. *caespitum* (Gómez and Espadaler 2006). Nevertheless, according to Sarnat et al. (2015), "*Pheidole indica* is not considered to be a major pest to either agriculture or native ecosystems", although "further studies are required to test its ecological and agricultural impact outside its native range".

***Wasmannia auropunctata* (Roger, 1863)**
Fig. 7

Literature records. Demetriou et al. (2022).

Material examined. Suppl. material 1.

Origin. Central and South America (Panamian and Neotropical biogeographic realms).

Habitat details. Exclusively associated with human presence. Specimens have been collected from plant nurseries, greenhouses, urban parks, parking lots and pedestrian paths near hotels and tourist sites.

Degree of establishment. Established.

Notes. In invaded territories, *W. auropunctata* has been found to negatively affect native biodiversity as well as human and animal health (Lubin 1984; Hayashi 1999; Wetterer et al. 1999; Roque-Albelo and Causton 1999; Nishida and Evenhuis 2000; Roque-Albelo et al. 2000; Wetterer and Porter 2003; Mbenoun-Masse et al. 2017; Kidon et al. 2022). Only recently detected in Cyprus (Demetriou et al. 2022),

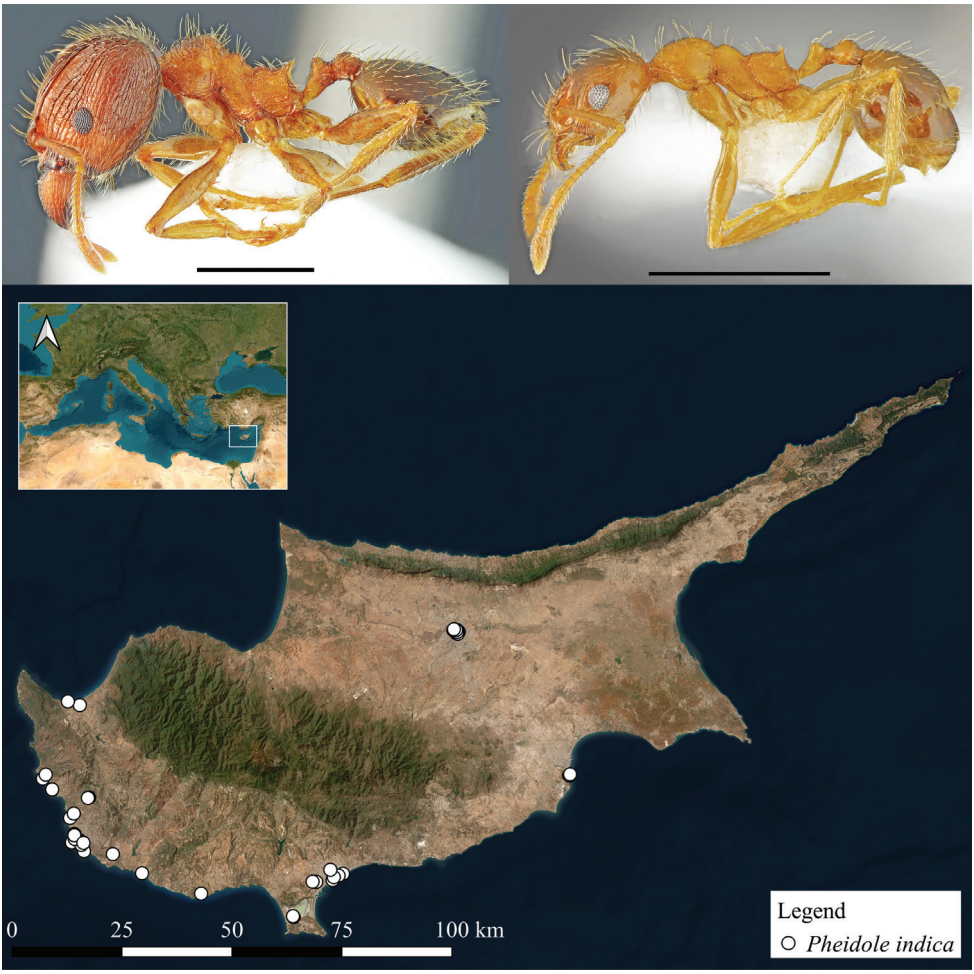

Figure 6. Habitus of *Pheidole indica* Mayr, 1879 major worker (left, from Limassol, Polemidia) and minor worker (right, Paphos, Agios Neofytos Monastery) in lateral view (scale bar: 1 mm) and its known distribution in Cyprus below.

W. auropunctata seems to be widely distributed in the Western part of the island (Paphos district). The abundance of the species seems to be variable, with only a few specimens collected from some sites and very high numbers from others. For example, in tourist sites, such as a hotel garden in Coral Bay and the Kato Paphos harbour, large numbers of the species were recovered while beating ornamental plants (*Hibiscus rosa-sinensis* and *Ficus microcarpa*), while sidewalks of a park in Mesogi, a hotel garden in Coral Bay and a hotel parking lot had very large colonies. More research is needed to comprehensively map the distribution of *W. auropunctata* in Cyprus and to assess interactions with native ants.

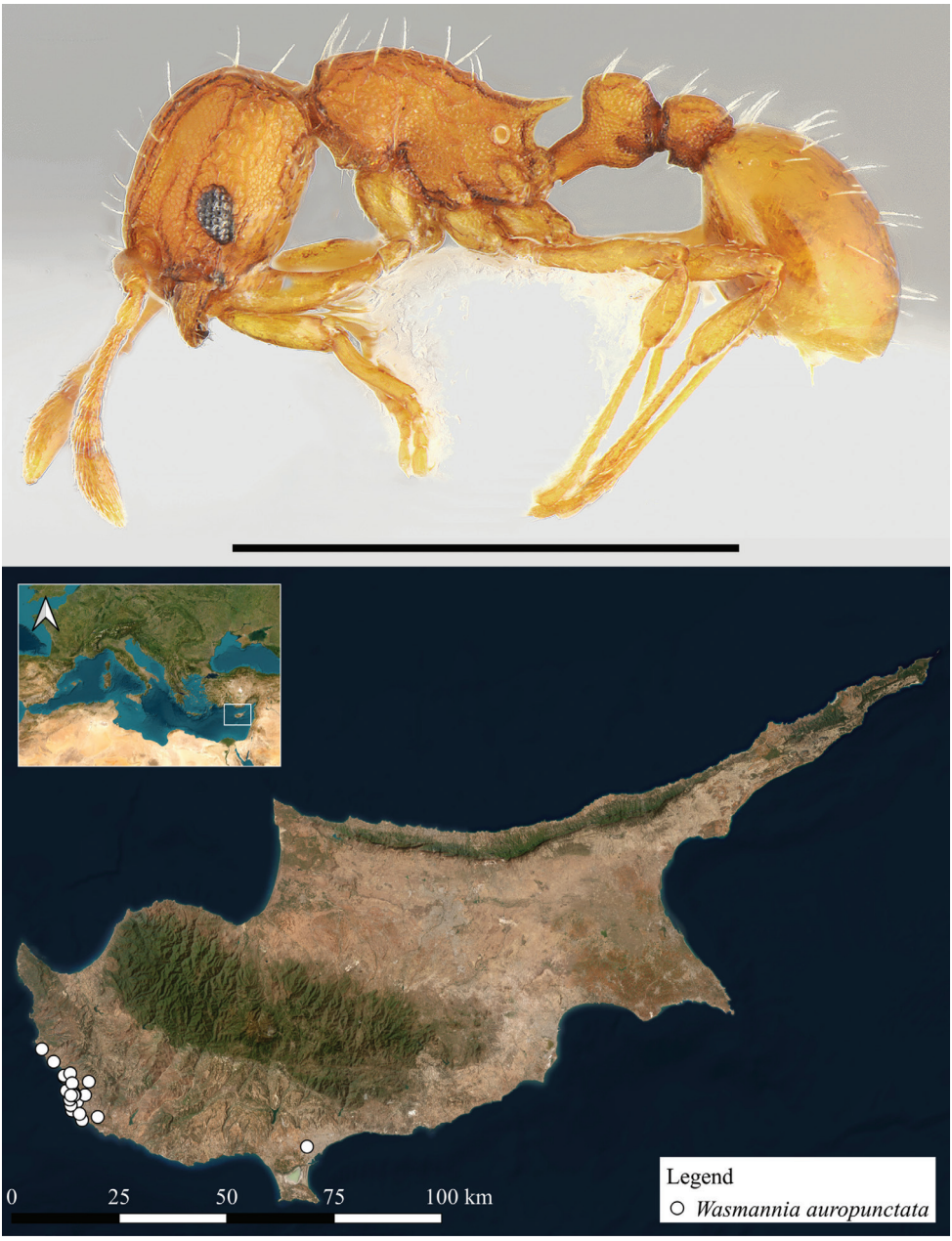

Figure 7. Habitus of *Wasmannia auropunctata* (Roger, 1863) (from Paphos, Kissonerga) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

Crematogastrini

***Cardiocondyla mauritanica* Forel, 1890**
Fig. 8

Literature records. Emery (1909).

Material examined. Suppl. material 1.

Origin. Saharo-Arabian biogeographic realm.

Habitat details. Found in urban (park, parking lot), agricultural (plant nursery) and natural habitats (dry river bank, reservoir).

Degree of establishment. Established.

Notes. *Cardiocondyla mauritanica* is known to prefer xerothermous, urban and semi-arid environments (Seifert 2003; Wetterer 2014b). According to its ecological preferences, in Cyprus it has been collected from the lowlands, in disturbed areas with evident human interference.

***Cardiocondyla obscurior* Wheeler, W.M., 1929**
Fig. 9

Literature records. N/A.

Material examined. Suppl. material 1.

Origin. Indomalayan biogeographic realm.

Habitat details. Collected from urban habitats in Paphos foraging on trees, shrubs as well as on the ground in gardens and parking lots.

Degree of establishment. Established.

Notes. Native to Indomalaya, *C. obscurior* has been recorded from Europe and the Mediterranean as an indoor introduced species in France, Germany and the Netherlands (Seifert 2003; Blatrix et al. 2018; Boer et al. 2018) as well as an established alien species in Egypt, Israel, Syria and Spain (Donisthorpe 1930; Mohamed et al. 2001; Seifert 2003; Sánchez-García and Espadaler 2015; Janicki et al. 2016; Trigos Peral and Reyes-López 2016; Espadaler and Ortiz de Zugasti 2019). In contrast to recent findings of a single specimen in Greece (Demetriou et al. 2023b), *C. obscurior* seems to be established on the island of Cyprus with specimens being collected both on trees, according to its arboreal habits (Espadaler and Ortiz de Zugasti 2019) and from the soil.

***Tetramorium bicarinatum* (Nylander, 1846)**
Fig. 10

Literature records. N/A.

Material examined. Suppl. material 1.

Origin. Indomalayan biogeographic realm.

Habitat details. Collected from two plant nurseries and a zoo in Paphos.

Degree of establishment. Indoor introduced.

Figure 8. Habitus of *Cardiocondyla mauritanica* Forel, 1890 (from Limassol, Molos) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

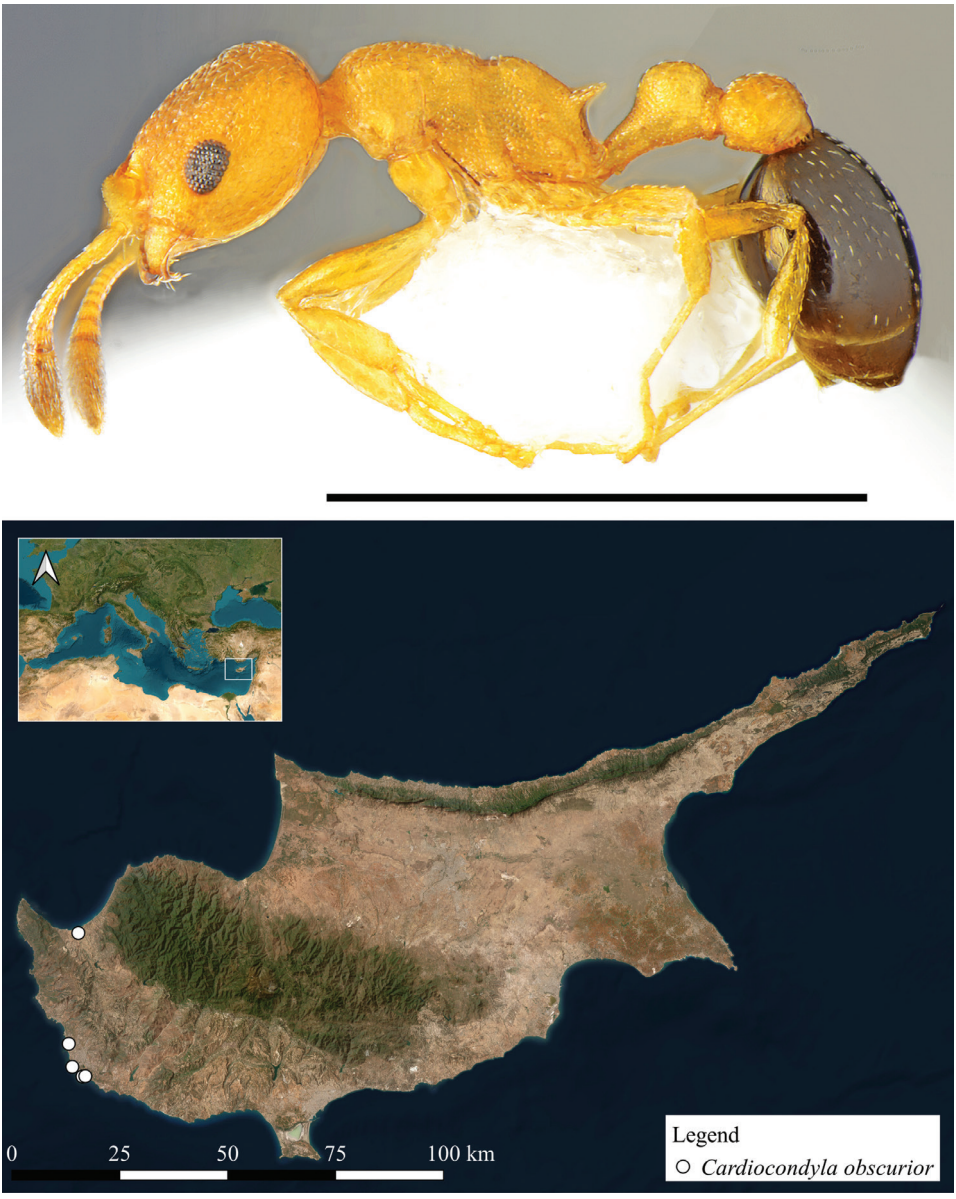

Figure 9. Habitus of *Cardiocondyla obscurior* Wheeler, W.M., 1929 (from Paphos, Kato Paphos) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

Notes. The distribution of this species on the island of Cyprus should be monitored. It is predicted to have socio-economic impacts on households or horticultural plants, through mutualistic relationships with aphids and scale-insects including *Aphis gossypii* Glover, 1877 (Saddiqui et al. 2019), an alien aphid species collected from a variety of arable and ornamental plants (Morris 1937; Georghiou 1977).

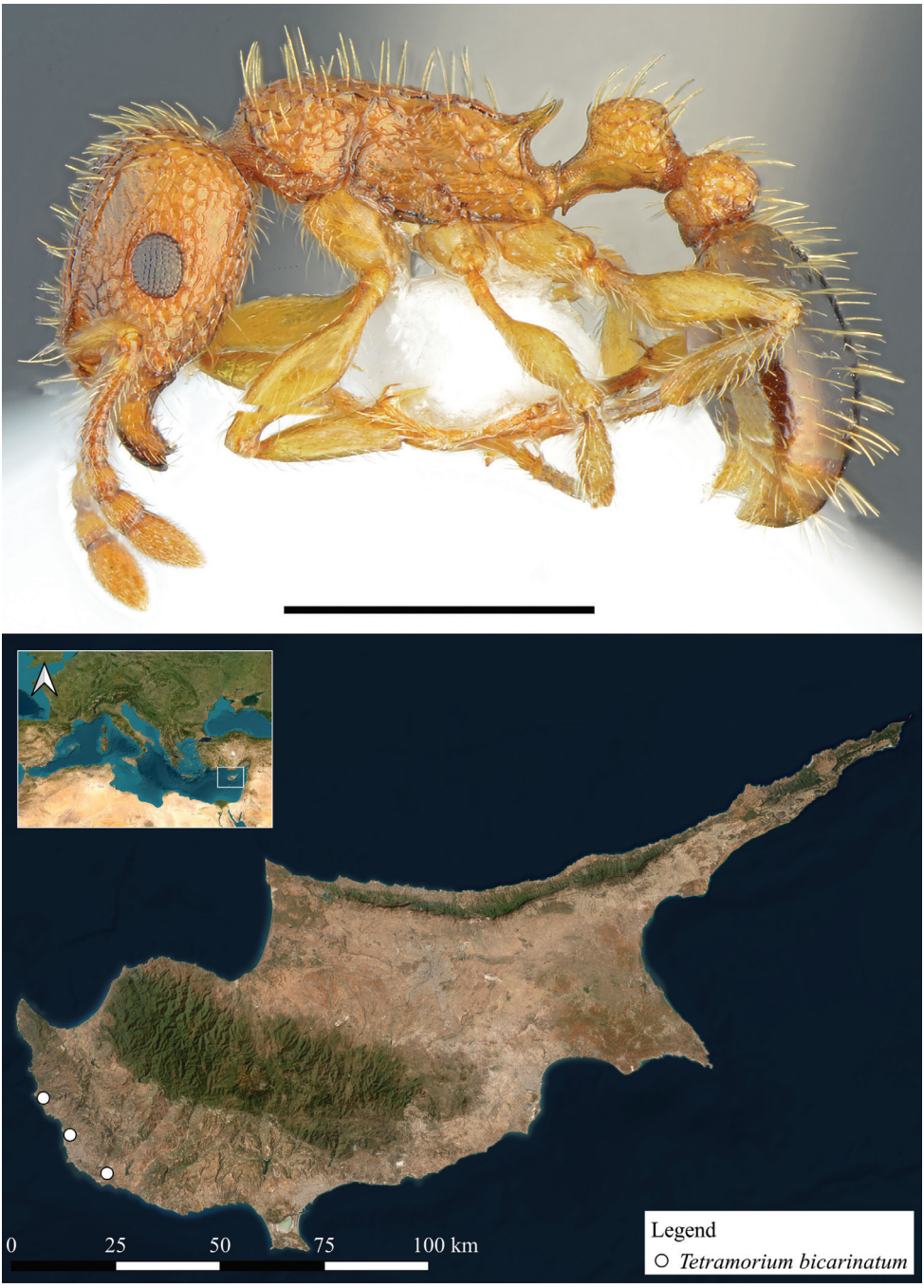

Figure 10. Habitus of *Tetramorium bicarinatum* (Nylander, 1846) (from Paphos, Paphos Zoo) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

***Tetramorium caldarium* (Roger, 1857)**
Fig. 11

Literature records. N/A.

Material examined. Suppl. material 1.

Origin. Afrotropical biogeographic realm.

Habitat details. Found only from a zoo.

Degree of establishment. Unknown.

Notes. A species that has been detected only from a few countries in the Mediterranean region, including France (Radchenko 2004), mainland Spain and the Balearic Islands (Reyes and Espadaler 2005; Gómez and Espadaler 2006) as well as Egypt (Donisthorpe 1942) and Morocco (Cagniant and Espadaler 1993; Cagniant 1997; Taheri and Reyes-López 2018) in Northern Africa. According to Bolton (1980), the species is "associated with man and living in hothouses, zoos, or other constantly heated buildings", although it has also been collected from urban habitats in gardens, terraces, and flowerpots (Cagniant 1997) being currently widespread in the cities and coasts of Morocco (Taheri and Reyes-López 2018). In Cyprus, the species has been collected only from a zoo, during ant collection on pavements and outdoors areas. Despite its worldwide distribution, no adverse ecological impacts have been recorded for the species (Wetterer and Hirta-Garcia 2015).

***Tetramorium immigrans* Santschi, 1927**
Fig. 12

Literature records. N/A.

Material examined. Suppl. material 1.

Origin. Central Asia and Europe (Palearctic biogeographic realm).

Habitat details. Found from only two collecting sites in Paphos district, a zoo and Kato Paphos area.

Degree of establishment. Established.

Notes. A member of the recently taxonomically revised *Tetramorium caespitum* complex, currently widespread in Europe and the Mediterranean that has been found in anthropogenic and natural habitats (Wagner et al. 2017; Demetriou et al. 2023b). The species has been found to hybridise and compete with native Mediterranean species (Wagner et al. 2017; Cordonnier et al. 2019; Schifani et al. 2022). Although the native and invaded range of *T. immigrans* needs further examination, its presence in only two urban areas and absence from sampled natural habitats leads us to assume that the species is alien to the island.

***Tetramorium lanuginosum* Mayr, 1870**
Fig. 13

Literature records. N/A.

Material examined. Suppl. material 1.

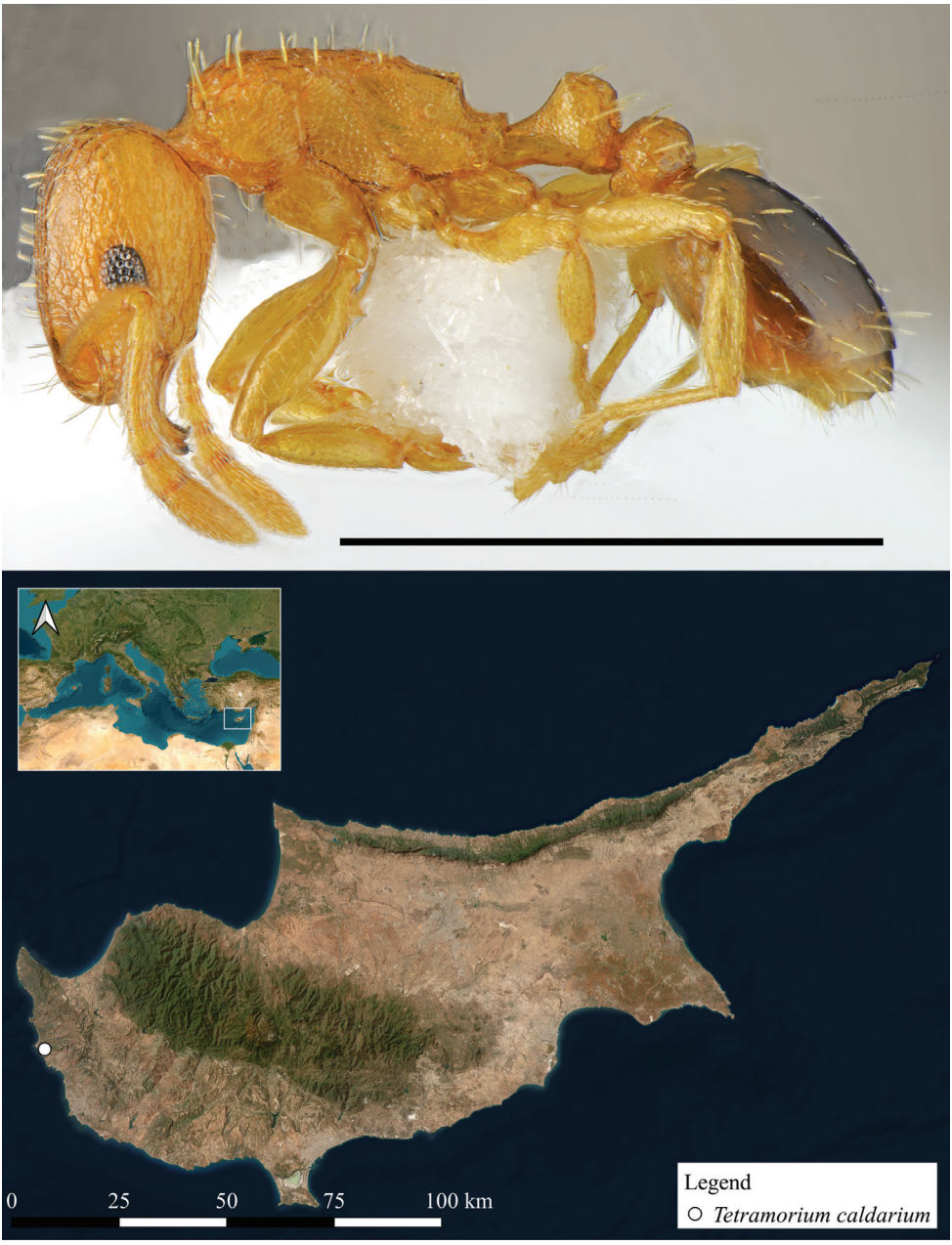

Figure 11. Habitus of *Tetramorium caldarium* (Roger, 1857) (from Paphos, Paphos Zoo) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

Origin. Subtropical East Asia (Indomalayan biogeographic realm).

Habitat details. Found in urban habitats including parking lots, urban green spaces with ornamental vegetation and a zoo.

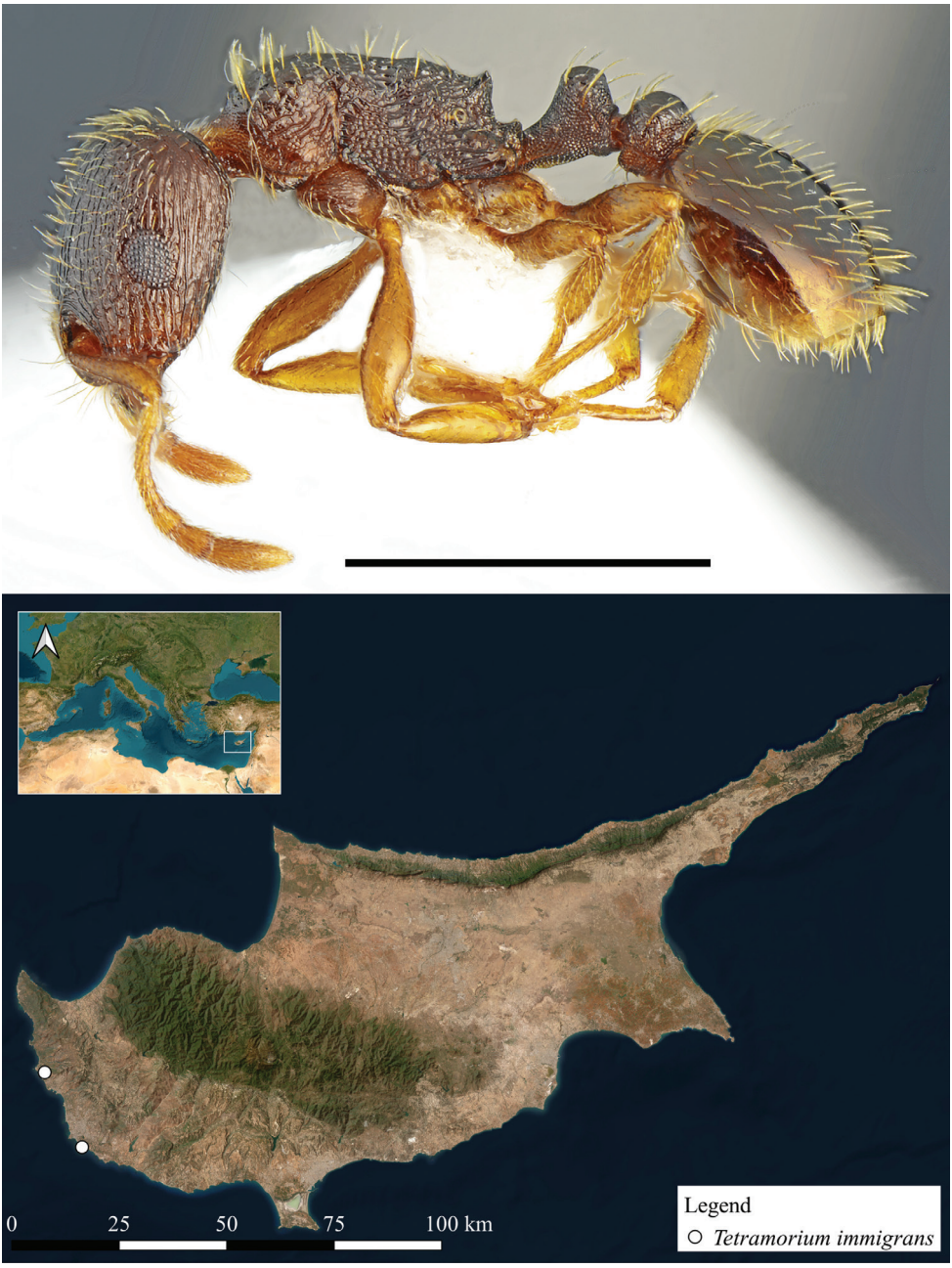

Figure 12. Habitus of *Tetramorium immigrans* Santschi, 1927 (from Paphos, Paphos Zoo) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

Degree of establishment. Established.

Notes. The species has been collected from neighbouring Israel and Lebanon since the last century and more recently from Egypt (Wetterer 2010a). In Spain, *T. lanuginosum* was

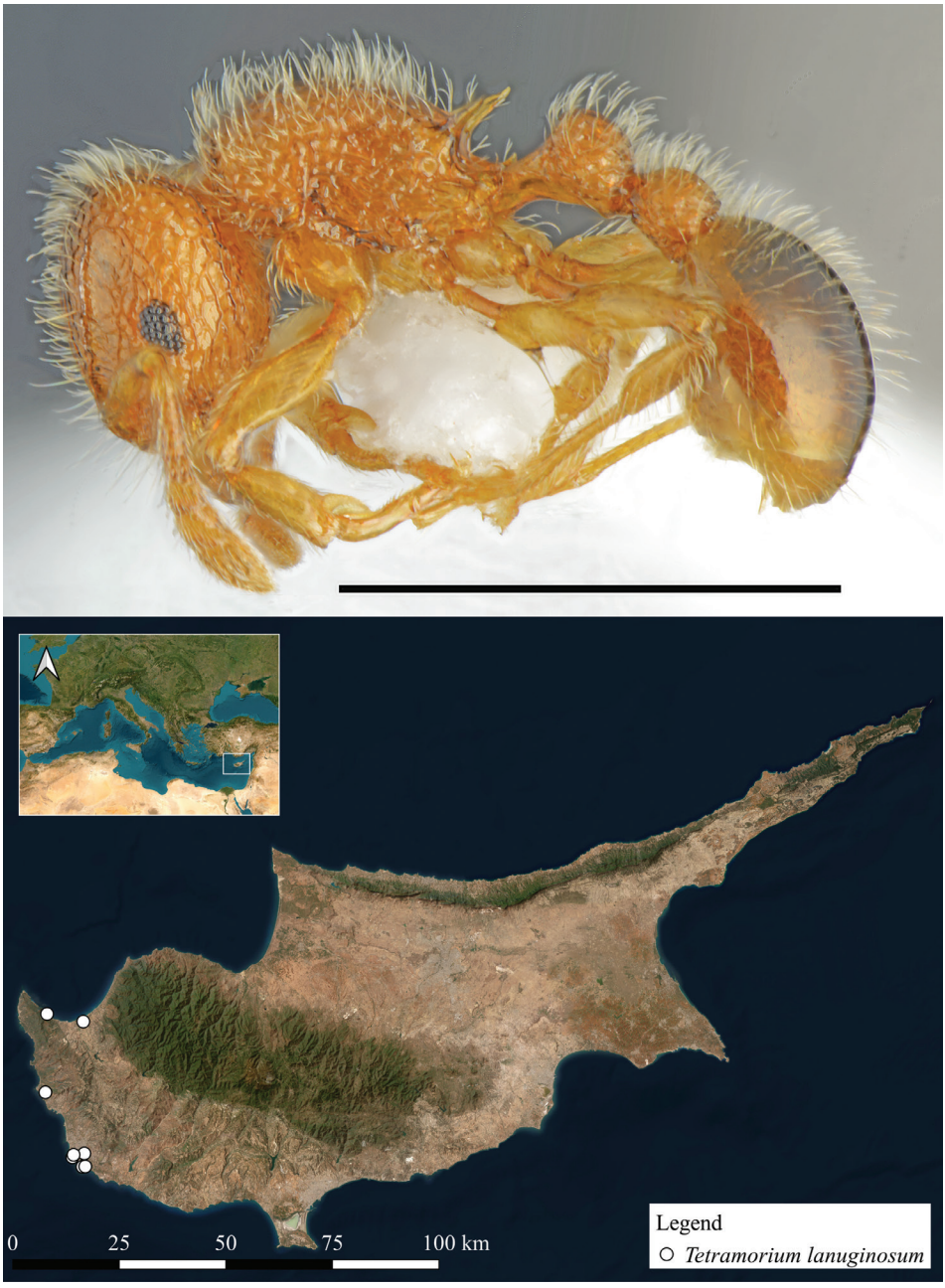

Figure 13. Habitus of *Tetramorium lanuginosum* Mayr, 1870 (from Paphos, Paphos Zoo) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

first recorded by Reyes and Espadaler (2005) and subsequently collected from a date palm grove where it presumably did not establish (Casiraghi et al. 2020). *Tetramorium lanuginosum* has been also recorded from urban habitats in Malta and Sicily (Schembri and Colling-

wood 1981; Schifani and Alicata 2018). In Cyprus it can be found in anthropogenic habitats, with two sites within the boundaries of the protected Akamas Peninsula (CY4000023 and CY4000010). Although the species has no recorded adverse environmental impacts, more research is necessary to establish its further spread into protected areas.

Solenopsidini

***Monomorium bicolor* Emery, 1877**
Fig. 14

Literature records. Salata and Borowiec (2015b); Salata et al. (2019).

Material examined. Suppl. material 1.

Origin. Africa, Arabian Peninsula, Levant and Turkey (Palearctic, Saharo-Arabian and Afrotropical biogeographic realms).

Habitat details. Widespread, found in all kinds of habitats.

Degree of establishment. Established.

Notes. The most common and widespread alien ant in Cyprus, reaching the highest altitudinal range and collected from 15 protected areas. Despite its large AOO and EOO, it has been only recently detected in Cyprus (Salata and Borowiec 2015b) and does not seem to have any adverse environmental impacts. Nevertheless, the alien or native status of this species in the Middle East and in Cyprus is rather problematic. *Monomorium bicolor* is believed to be native to the Afrotropics (Bolton 1987) although on AntMaps it is shown as native to the whole of Africa and Middle East except Greece and Cyprus. Despite its recent report from Cyprus, its distribution on the island may suggest either its unintentional introduction since ancient times (L. Borowiec pers. comm.) or indeed its native status. Molecular analyses on populations from Cyprus, the Middle East, Northern and Sub-Saharan Africa could help to unveil the true status of the species in the aforementioned regions.

***Solenopsis* sp_CYP139**
Fig. 15

Literature records. N/A.

Material examined. Suppl. material 1.

Origin. Unknown.

Habitat details. Collected from plant nurseries (indoors in crops under foil) and outdoor urban areas of Limassol and Paphos.

Degree of establishment. Established.

Notes. This unidentified species is well distinguished from all native species from Greece and Turkey; it is very small in size and has extremely small eyes (in the form of a black dot). We have decided to classify this morpho-species as alien due to its occurrence only within urban habitats and plant nurseries, which lead us to the hypothesis of an unintentional introduction via infested plant material. The species presumably

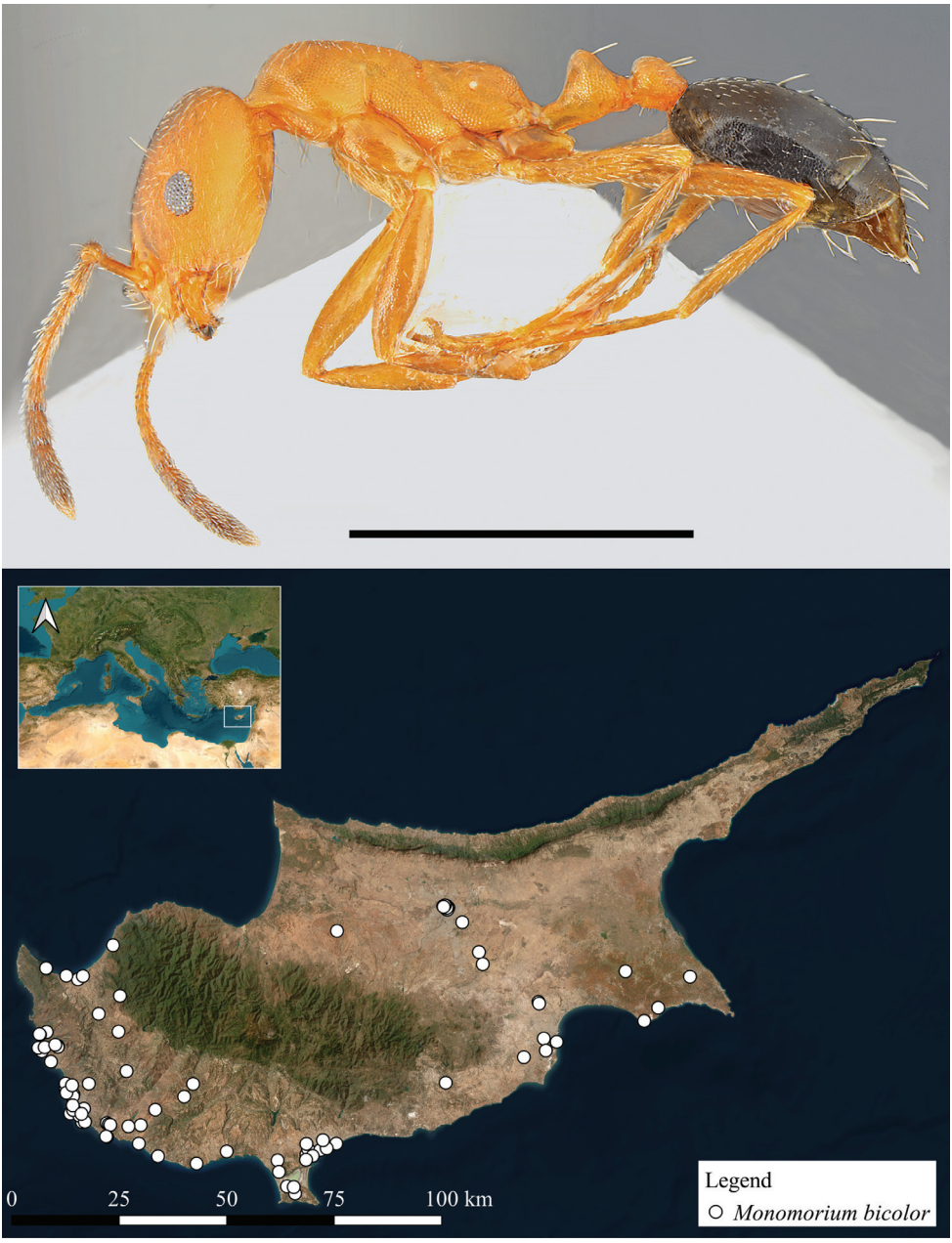

Figure 14. Habitus of *Monomorium bicolor* Emery, 1877 (from Paphos, Kato Paphos) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

belongs to an unidentified species of tropical/subtropical origin, which could be further investigated with the help of molecular tools. The description and morphometric data of this morphospecies can be found Suppl. material 4 for further examination and future comparisons.

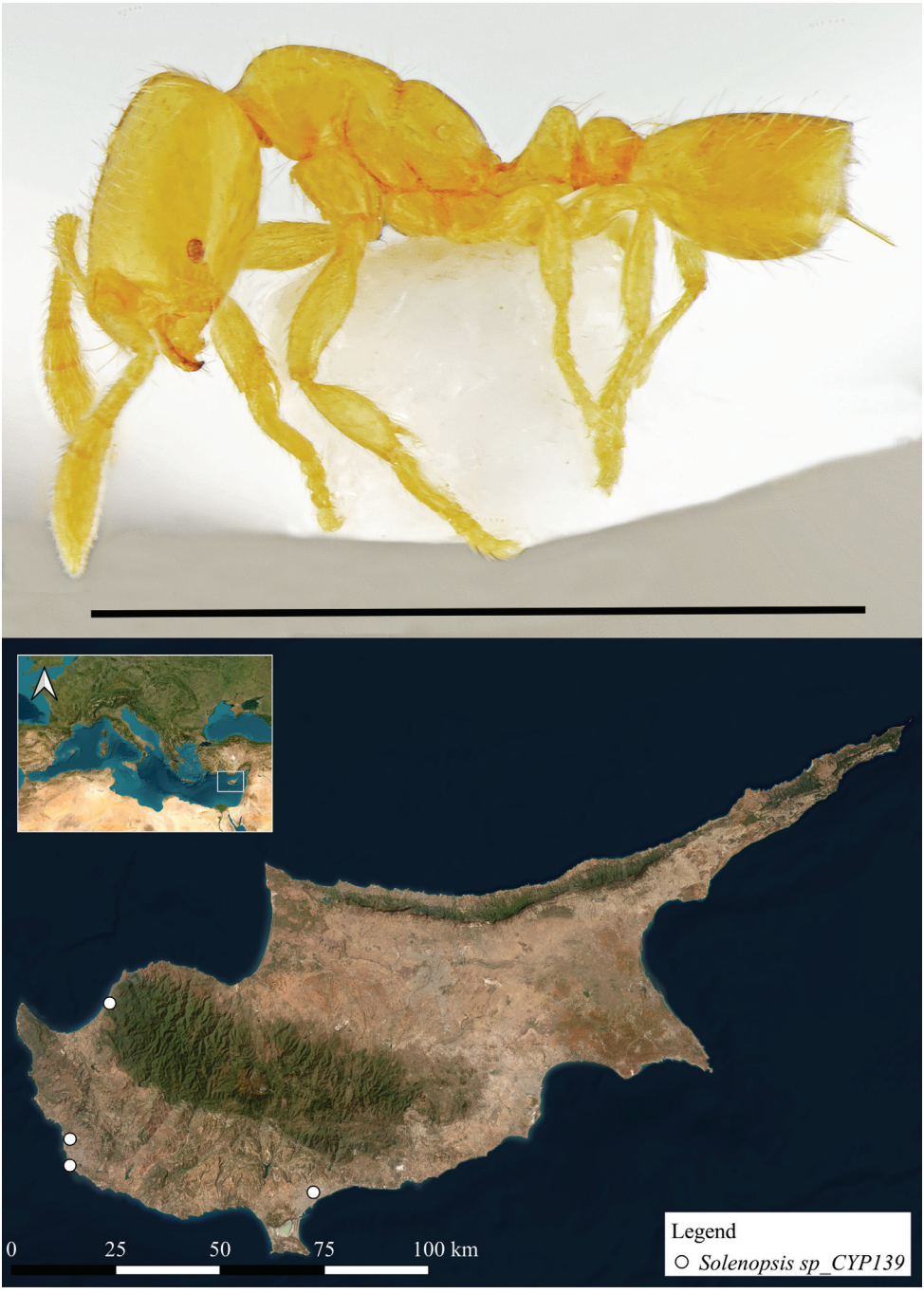

Figure 15. Habitus of *Solenopsis* sp_CYP139 (from Paphos, Lemba) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

***Trichomyrmex destructor* (Jerdon, 1851)**
Fig. 16

Literature records. Georghiou (1977); Wetterer (2009b).
Material examined. Suppl. material 1.
Origin. Indomalayan biogeographic realm.

Figure 16. Habitus of *Trichomyrmex destructor* (Jerdon, 1851) (from Limassol, Savvas Savva park) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

Habitat details. Urban habitats including houses, parking lots and paved roads.

Degree of establishment. Established.

Notes. Wetterer (2009b) cite "CAB 2000 in DAFF 2001" as a literature source for the presence of *T. destructor* in Cyprus. When checking CABI (2022) *T. destructor* was reported as present in Cyprus citing "CABI Data Mining (Undated)". Despite comments of Salata et al. (2019) excluding the species from their list, Demetriou et al. (2023a) decided to include it based on records of Georghiou (1977), which had previously been overlooked. In particular, Georghiou (1977) noted this species as "*Monomorium destructor* Jerd.", "from olives infested by *Dacus oleae*" in 1956 as well as in 1925 under the synonymic name "*M. gracillimum* Sm." "feeding of eggs of *Thaumatopoea wilkinsoni* (Lep., Notodontidae)". Upon collection of further material we confirm the presence of *T. destructor* on the island. The species was collected from five urban sites in Paphos and Limassol districts. *Trichomyrmex destructor* is known to be associated with electronic devices causing electrical damages as well as destroying stored household products and inflicting painful bites on humans (Wetterer 2009b). Negative socio-economic impacts in households or possible health risk could be monitored through citizen science initiatives assessing the socio-economic impacts of ants in households.

***Trichomyrmex mayri* (Forel, 1902)**

Fig. 17

Literature records. N/A.

Material examined. Suppl. material 1.

Origin. Indomalayan biogeographic realm [speculated by Bolton (1987)].

Habitat details. Both in urban (dirt roads, road sides and uncultivated green spaces) and natural habitats (dry meadow, pine forest, reservoir).

Degree of establishment. Established.

Notes. A species common in the Arabian Peninsula (Sharaf et al. 2013), which is believed to originate from Indomalaya (Bolton 1987). It has been recorded from neighbouring Egypt, Israel and Syria where it is considered alien (Bolton 1987). In Cyprus, it occupies a large EOO and altitudinal range, while it has been also recorded from three protected areas (CY2000004, CY2000013 and RAMSAR1375). Nevertheless, its potential environmental or socio-economic impacts are unknown both throughout its native and introduced range.

Ponerinae
Ponerini

***Hypoponera punctatissima* (Roger, 1859)**

Fig. 18

Literature records. N/A.

Material examined. Suppl. material 1.

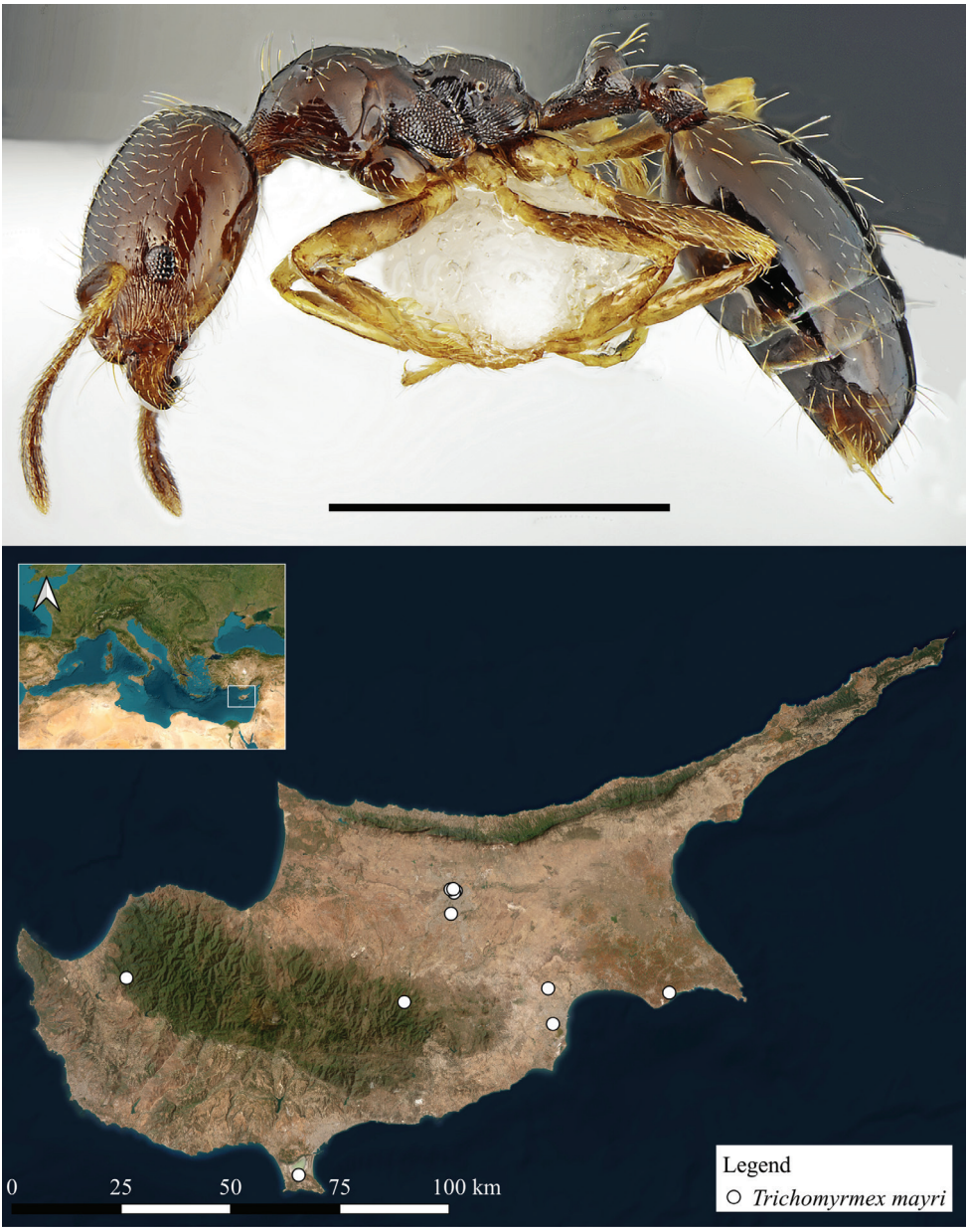

Figure 17. Habitus of *Trichomyrmex mayri* (Forel, 1902) (from Paphos, Lysos vic.) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

Origin. Probably Egypt and Sub-Saharan Africa (Saharo-Arabian and Afrotropical biogeographic realms).

Habitat details. Only one collection site corresponding to a plant nursery (indoors in crops under foil) in Paphos.

Degree of establishment. Unknown.

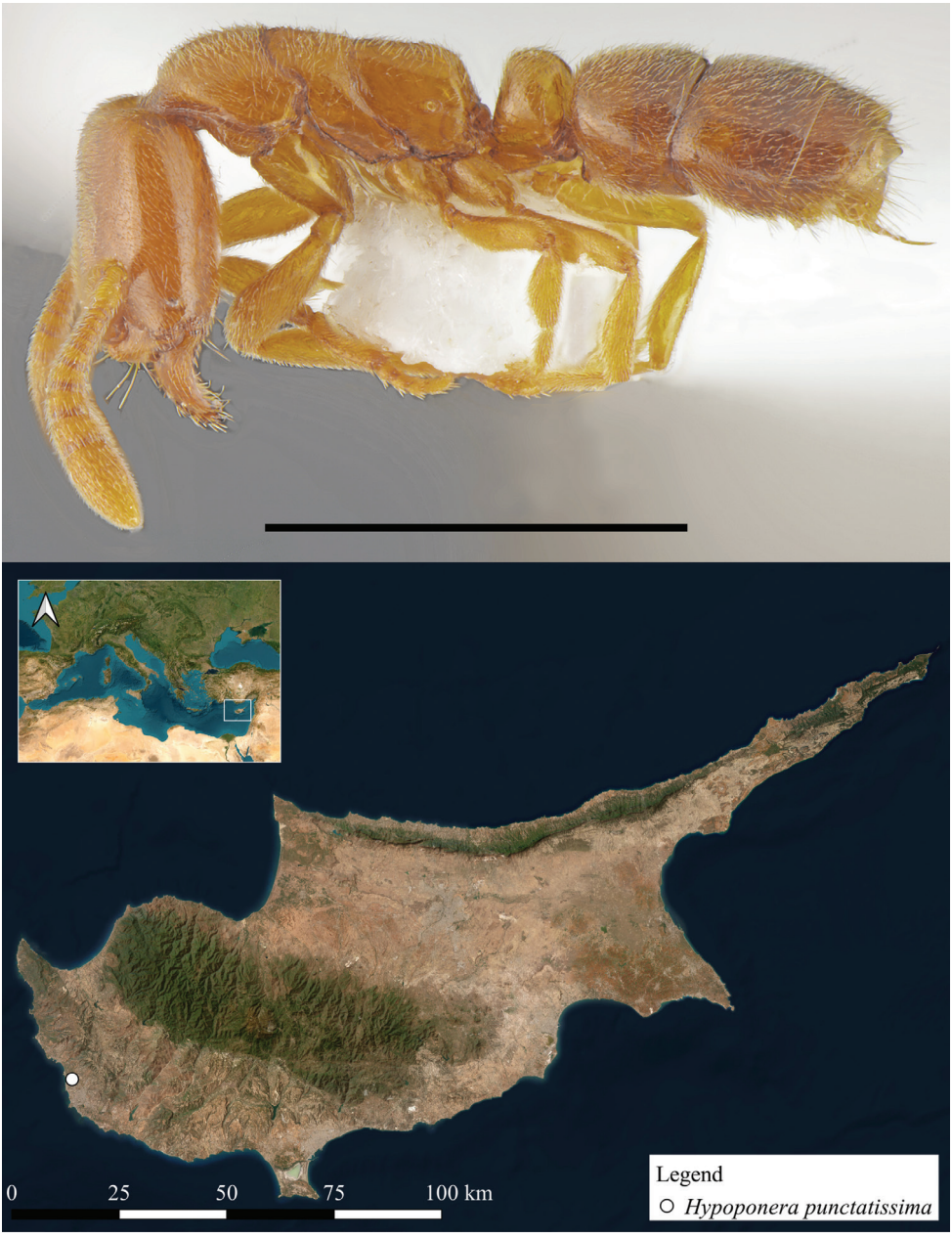

Figure 18. Habitus of *Hypoponera punctatissima* (Roger, 1859) (from Paphos, Lemba) in lateral view above (scale bar: 1 mm) and its known distribution in Cyprus below.

Notes. An alien species collected across Europe and the Mediterranean from both indoors and outdoors localities, including natural habitats (Atanassov and Dlusskij 1992; Czechowski et al. 2012; Borowiec and Salata 2022). Although its native range remains quite uncertain, its presence on the island is supported by only one specimen collected in a plant nursery. This may indicate its recent introduction to the island

through the horticultural or ornamental pathway, with further spread leading to its establishment in areas with sufficient humidity as observed in other European countries. Although *Hypoponera ergatandria* Forel, 1893 has been also noted as an alien species in Europe, the status of this species is uncertain, representing either a valid species or a junior synonym of *H. punctatissima*. As such, *H. ergatandria* is not included in the provided identification key and considered here as a junior synonym of *H. punctatissima* (Bolton and Fisher 2011; Seifert 2013; Lubertazzi 2019).

Species excluded from previous checklists

Cardiocondyla nuda (Mayr, 1866)

Notes. Although previously thought to be a widespread alien species, a revision of the group has concluded that *C. nuda* is geographically restricted in Oceania (Seifert et al. 2017). According to Seifert (2003), investigation of authentic material from the Palaearctic turned out to be *C. mauritanica*. Although the species is mentioned for Cyprus by Bernard (1956), these records also probably correspond to *C. mauritanica*.

Monomorium pharaonis (Linnaeus, 1758)

Notes. The only records of the species can be traced back to Wetterer (2010b) citing Radchenko (2004), a record corresponding to data in the Fauna Europaea database. Nevertheless, no specimens or scientific literature have been provided to support these records. The record of *M. pharaonis* in Fauna Europaea is probably erroneous as already shown for other ant species in the database, noted for example by Schifani and Alicata (2018) regarding Sicily or Demetriou et al. (2023b) for Greece. Although the presence of *M. pharaonis* on the island is highly possible, given its extended distribution throughout the world (Wetterer 2010b), we tentatively suggest the exclusion of the species from lists of alien species of Cyprus until further investigations provide adequate evidence. Citizen science approaches looking into the biodiversity and socio-economic impacts of ants in households could potentially uncover records of this synanthropic, indoors introduced species.

Monomorium subopacum (F. Smith, 1858)

Notes. As in the case of Greece (Demetriou et al. 2023b), following assumptions of Bolton (1987) and the native status of the species for neighbouring Mediterranean countries (AntWiki 2022), *M. subopacum* is considered native to Cyprus.

Nylanderia vividula (Nylander, 1846)

Notes. In Georghiou (1977) "*Paratrechina nitidula* Nyl." is mentioned as collected in 1935 and identified by H.S. Donisthorpe. Such a nomenclatural combination does not exist and probably corresponds to *Paratrechina vividula* (Nylander, 1846), currently an

obsolete combination of *N. vividula*. *Nylanderia vividula* has been reported as an alien species from neighbouring Egypt, Greece, Israel, Lebanon, and Turkey (Emery 1881, 1898; Donisthorpe 1950; Borowiec 2014). However, records from Greece are believed to correspond to *N. jaegerskioeldi* (Demetriou et al. 2023b) and no additional records have been uncovered from Turkey since Donisthorpe (1950). During our sampling in Cyprus we extensively collected only samples of *N. jaegerskioeldi*. *Nylanderia vividula*, a species native to the Nearctic biogeographic realm, might have been introduced to the island but failed to establish. Alternatively, records may correspond to *N. jaegerskioeldi*, a common species missing from Georghiou's (1977) list but already known from Cyprus since 1910 (Emery 1910). Further sampling and tracing material in historical collections may shed light on the presence and invasion history of *N. vividula* on Cyprus. For the time being, records from Cyprus remain doubtful and in need of verification.

***Solenopsis geminata* (Fabricius, 1804)**

Notes. The only record mentioning the presence of *S. geminata* in Cyprus can be traced to Collingwood et al. (1997), where the island is simply listed in the known distribution of the species. After 25 years of this mention no material has been uncovered. As in the case of Greece (Demetriou et al. 2023b), we expect that the presence and impacts of this invasive alien species would not go unnoticed. In the possible event of its past introduction to the island, any individuals or populations did not manage to establish. Furthermore, as horizon scanning exercises undertaken on the island (Peyton et al. 2019) did not assess *S. geminata*, due to the aforementioned dubious records, the possibility of the species reaching Cyprus, establishing viable populations and impacting native biodiversity, could be taken into consideration in the future.

***Hypoponera eduardi* (Forel, 1894)**

Notes. Although included in the list of invasive ants of Greece and Cyprus (Salata et al. 2019), upon re-examination the species is currently treated by the authors as native to Cyprus due to both its narrow ecological requirements (i.e. soil moisture, habitat types found) as well as its native status in neighbouring countries (Demetriou et al. 2023b).

Identification key to distinguish alien from native worker ants inhabiting Cyprus, with the support of male and queen characters

Key to subfamilies

[After Borowiec and Salata (2022), modified]

1 Pedicel with two distinct segments (petiole and postpetiole) (Suppl. material 3: figs S56, S58, S60) ..... **Myrmicinae**

– Pedicel with one segment (petiole) (Suppl. material 3: figs S3, S16, S20) **2**

2 Sting projected, first gastral segment separated from the second one by a distinct constriction (Suppl. material 3: figs S142, S144, S146, S148) **3**
– Sting not projected, first and second gastral segments not separated by a constriction (Suppl. material 3: figs S16, S18, S20, S22) **5**
3 Tergite of the second gastral segment much longer than its sternite, strongly arched, abdominal segments pointed downward .... **Proceratiinae** (only one native species)
– Tergite of the second gastral segment as long as its sternite, never arched, abdominal segments not pointed downward **4**
4 Petiole broadly attached to the first gastral segment, separated from it only by shallow constriction ..... **Amblyoponinae** (only one native species)
– Petiole narrowly attached to the first gastral segment, separated from gaster by sharp and deep constriction (Suppl. material 3: figs S142, S144, S146, S148) .... **Ponerinae**
5 Apex of gaster with circular nozzle-like acidopore, fringed with setae (Suppl. material 3: figs S18, S20, S22) ..... **Formicinae**
– Apex of gaster without acidopore and coronula only with transverse slit (Suppl. material 3: figs S1, S3, S5) ..... **Dolichoderinae**

Subfamily Dolichoderinae

[After Salata and Borowiec (2022), and Fisher and Bolton (2016), modified]

1 Petiole very reduced or vestigial, in profile very small and low, often invisible from above, covered under the first segment of the gaster (Suppl. material 3: figs S1, S3, S5, S7) **2**
– Petiole a well-developed scale, distinct in profile (Suppl. material 3: figs S14, S16).... **5**
2 Anterior margin of clypeus straight (Suppl. material 3: fig. S2); in dorsal view 5 gastral tergites visible, the fifth gastral tergite small but continues the line of the gaster and is not reflexed below the fourth; gastral tergites with numerous erect and thick setae (Suppl. material 3: fig. S1) ..... ***Technomyrmex*** (not reported from Cyprus but possible one alien outdoor or five alien indoor species known from Europe)
– Anterior margin of clypeus in the middle shallowly or deeply emarginate (Suppl. material 3: figs S4, S6, S8, S13); in dorsal view only 4 gastral tergites visible, the fifth gastral tergite reflexed below the fourth; gastral tergites without erect and thick setae (Suppl. material 3: figs S3, S5, S7, S12) **3**
3 Large species, mesosoma length in major workers above 1 mm; body uniformly brown to black (Suppl. material 3: figs S3, S5,S 7) anterior margin of clypeus with distinct median emargination (Suppl. material 3: figs S4, S6, S8)..... **4**
– Very small, mesosoma length always below 0.6 mm. Body bicoloured, head brown to black, mesosoma and anterior half or gaster with pale, whitish to whitish-brown areas (Suppl. material 3: fig. S12). Anterior margin of clypeus with very shallow median emargination (Suppl. material 3: fig. S13) .... ***Tapinoma melanocephalum*** (alien species not reported from Cyprus)

4 Parameres in male genitalia with broadly rounded apex (Suppl. material 3: fig. S10) ..... ***Tapinoma magnum*** (native to Western Europe but alien in Greece, not reported from Cyprus)
– Parameres in male genitalia with narrow or distinctly angulate apex (Suppl. material 3: figs S9, S11) ..... ***Tapinoma*** (two native species)
5 Propodeum in profile not or only slightly surpassed by promesonotum (Suppl. material 3: fig. S14) mandibular denticles not strongly heterodont (Suppl. material 3: fig. S15) .....***Bothriomyrmex*** (one native species)
– Propodeum in profile distinctly surpassed by promesonotum (Suppl. material 3: fig. S16) mandibular denticles strongly heterodont, with 5–6 larger dents dispersed over the masticatory border and 11–15 clearly smaller denticles present in interspaces (Suppl. material 3: fig. S17)..... .....***Linepithema humile*** (alien species not reported from Cyprus)

Subfamily Formicinae

[After Borowiec and Salata (2022), modified]

1 Antennae 11-segmented.....**2**
– Antennae 12-segmented.....**5**
– Antennae 9-segmented..... .....***Brachymyrmex patagonicus*** (alien species not recorded from Cyprus)
2 Propodeum unarmed, rounded in profile, dorsal margin of petiole not emarginate (Suppl. material 3: figs S20, S22, S28).....**3**
– Propodeum bispinose or bituberculate, dorsal margin of petiole emarginated (Suppl. material 3: figs S18) ..... ***Lepisiota*** (at least three native species)
3 Very small ants, legs and antennae short, hind femora not extending behind apex of gaster (Suppl. material 3: figs S22–S25) **4**
– Moderately large ants with very elongate legs and antennae, hind femora distinctly extending behind the apex of gaster (Suppl. material 3: figs S20, S21) ....***Anoplolepis gracilipes*** (alien species not reported from Cyprus)
4 Body yellowish-brown to dark brown, if mostly yellow then first gastral tergite without dark spots in posterolateral corners (Suppl. material 3: figs S24, S25) ... ***Plagiolepis*** (at least three native species and their two workerless social parasite species)
– Body mostly yellow, only posterolateral corners of first gastral tergite and apex of gaster with brown spots (Suppl. material 3: figs S22, S23) ....***Plagiolepis alluaudi*** (alien indoor species not reported from Cyprus)
5 Antennal insertions placed distinctly behind clypeal margin (Suppl. material 3: figs S27, S29, S31, S33).....**6**
– Antennal insertions placed close to clypeal margin (Suppl. material 3: figs S41, S43, S45, S47, S49) **10**

6 Frontal carinae straight, slightly converging to the front in major workers, head truncate anteriorly, plug-like (Suppl. material 3: figs S26, S27) ..... ***Colobopsis*** (one native species)

– Frontal carinae arched, distinctly converging to the front in major workers head not modified (Suppl. material 3: figs S31, S33, S37) **7**

7 Dorsal profile of mesosoma with deep impression between mesonotum and propodeum; propodeum always abruptly falling down to its caudal slope (Suppl. material 3: fig. S28)..... ***Camponotus*** **subgen.** ***Myrmentoma***, part (two native species)

– Dorsal profile of mesosoma continuously convex or with only shallow impression between mesonotum and propodeum (Suppl. material 3: figs S32, S34, S36, S38) **8**

8 Anterior margin of clypeus forms regular arch, without any protrusion (Suppl. material 3: figs S31, S33, S35) **9**

– Anterior margin of clypeus forms a lobiform protrusion extending beyond anterior margin of gena (Suppl. material 3: figs S37, S39) ..... ***Camponotus*** **subgen.** ***Tanaemyrmex***, part (five native species)

9 Body completely black; dorsum of propodeum flat or slightly convex (Suppl. material 3: figs S32–S35) ..... ***Camponotus*** **subgen.** ***Myrmentoma*****, part** (two native species)

– Body colouration various, head, mesosoma and femora partly reddish, partly reddish-brown to brown; propodeum with dorsal concavity (Suppl. material 3: figs S30, S31) ..... ***Camponotus*** **cf.** ***vitiosus*** (alien species)

10 Propodeal spiracle round to oval; legs short to moderately long (Suppl. material 3: figs S42, S44, S46), HTL/CW < 1.50 ..... **11**

– Propodeal spiracle elongate; legs very long Suppl. material 3: fig. S40), HTL/CW > 1.50 ..... ***Cataglyphis*** (two native species)

11 Eyes situated at or in front of the midlength of the sides of head (Suppl. material 3: figs S43, S45) **12**

– Eyes situated distinctly behind the midlength of the sides of head (Suppl. material 3: figs S41, S47) **13**

12 Mandible unsculptured, with 6–7 teeth; scape short, less than 1.5 times length of head, body stout (Suppl. material 3: fig. S43)..... ***Nylanderia jaegerskioeldi*** (alien species)

– Mandible with longitudinal striation and 5 teeth; scape long, more than 1.5 times length of head, body elongate (Suppl. material 3: fig. S47)..... ***Paratrechina longicornis*** (alien species)

13 Hind coxa widely separated; ortificie of propodeal spiracle circular or broadly oval; mesosoma rather short and high, usually densely pubescent; propodeum approximately two times shorter than high (Suppl. material 3: figs S48, S50, S52). Size usually smaller, total length 2.5–5.0 mm..... **14**

– Hind coxa close together; ortificie of propodeal spiracle elongate to slit-like; mesosoma rather long and slender, usually sparsely pubescent (Suppl. material 3: fig. S46); propodeum approximately as long as high (Suppl. material 3: fig. S46). Size larger, total length 4.5–9.0 mm..... ***Formica*** (one native species)

14 Pubescence on the whole body present but moderate to dense; antennal scapi lacking erect setae; pubescence of clypeus sparse, surface of the clypeus well visible (Suppl. material 3: figs S48, S49); mean number of mandibular dents < 8 ..... ***Lasius neglectus*** (alien species not reported from Cyprus)

– Characters combination different (Suppl. material 3: figs S50–S53)..... ***Lasius*** (two native species)

Subfamily Myrmicinae

[After Salata et a. (2020), Borowiec and Salata (2022), Bolton (1980, 2000) and Seifert (2023), modified]

1 Postpetiole attached to dorsum of first gaster segment, petiole without node (Suppl. material 3: figs S54, S55) ..... ***Crematogaster*** (five native species)

– Postpetiole attached to anterior part of first gaster segment, petiole with node (Suppl. material 3: figs S56, S58, S60) **2**

2 Antennae 10- or 11-segmented **3**

– Antennae 12-segmented..... **9**

– Antennae 4 to 6-segmented..... ***Strumigenys*** (no species recorded from Cyprus. If dorsal alitrunk and first gastral segment without erect hair then *S. membranifera* – alien species)

3 Antennae 11-segmented; two prominent propodeal spines (Suppl. material 3: figs S56, S58) **4**

– Antennae 10-segmented; no propodeal spines (Suppl. material 3: figs S60, S62, S64, S66, S68, S70) **5**

4 Eyes big, longitudinal, narrowing downwards, anterior margin of eye situated very close to insertion of mandible (Suppl. material 3: figs S56, S57); head without antennal scrobes. Body colour black ..... ***Oxyopomyrmex*** (one native species)

– Eyes moderate, elonagte oval, situated in distance from insertion of mandible; head with antennal scrobes; body colour yellow to rusty (Suppl. material 3: figs S58, S59) ..... ***Wasmannia auropunctata*** (alien species)

5 Body colour pale, yellow, occipital margin of head straight or shallowly emarginate; length of mesosoma in major workers below 1 mm (Suppl. material 3: figs S62–S65) **6**

– Body colour orange-red to black, if yellow then head of large majors with deeply emarginate occipital margin; length of mesosoma in major workers distinctly above 1 mm (Suppl. material 3: figs S66–S71) **7**

6 Larger species, in major workers, length of mesosoma up to 0.7 mm or small species (length of mesosoma < 0.55 mm) with elongated head (head length/width ratio 1.3–1.4) (Suppl. material 3: figs S62, S63)..... ***Solenopsis*** (two native species)

– Small species (ML < 0.55 mm), head stouter (head length/width ratio < than 1.3) (Suppl. material 3: figs S64, S65) ..... ***Solenopsis* sp_CYP139** (one unidentified alien indoor species)

7 Body yellow to reddish-brown, sometimes with mixed yellow and brown, only occasionally dark brown; clypeus with or without a median tooth (Suppl. material 3: figs S66–S69) **8**

– Body brown to black with an orange tergal maculation on the first gastral tergite; clypeus always with a median tooth (Suppl. material 3: figs S70, S71) .... ***Solenopsis richteri*** (alien species not reported from Cyprus)

8 Median tooth on clypeus absent; mandibles of major workers with three teeth; occipital margin of head in major workers deeply emarginate; colour variable, from yellow to reddish-brown, occasionally dark brown (Suppl. material 3: figs S66–S67) ..... ***Solenopsis geminata*** (alien species not reported from Cyprus)

– Median tooth on clypeus always present; mandibles of major workers with four teeth; occipital margin of head in major workers shallowly emarginate; colour uniformly orange/red to rusty (Suppl. material 3: figs S68–S69) .... ***Solenopsis invicta*** (alien species not reported from Cyprus)

9 Ventrolateral margins of head without longitudinal carina; petiole usually with well-marked peduncle and node (Suppl. material 3: figs S72, S78, S84)..... **10**

– Ventrolateral margins of head with longitudinal carina; petiole low, without peduncle, gable-like (Suppl. material 3: figs S60, S61)..... ***Myrmecina*** (one native species)

10 Posterior edge of clypeus raised into sharp ridge in front of antennal insertions (Suppl. material 3: figs S73, S75, S77, S79) **11**

– Posterior edge of clypeus not raised into sharp ridge in front of antennal insertions (Suppl. material 3: figs S95, S97, S101) **22**

11 Frontal carinae long, projecting to or behind mid-length of eyes; antennal scrobes present; head in occipital and lateral parts usually with strong reticulate sculpture, never with smooth and shiny areas (Suppl. material 3: figs S73, S75, S77, S79, S81) **12**

– Frontal carinae short, never projecting behind mid-length of eyes; antennal scrobes absent; head usually only with longitudinal sculpture or with smooth and shiny areas (Suppl. material 3: figs S83, S85, S87, S89, S91, S93)..... **17**

12 Propodeum with long spines, longer than width of eye (Suppl. material 3: figs S72, S76, S80) **13**

– Propodeum with short spines, shorter than width of eye (Suppl. material 3: figs S74, S78) **15**

13 Dorsum of mesosoma in profile flat to slightly convex with sparse long erect setae (Suppl. material 3: figs S72, S76) **14**

– Dorsum of mesosoma in profile strongly convex with extremely dense long erect setae (Suppl. material 3: figs S80, S81)... ***Tetramorium lanuginosum*** (alien species)

14 Mandibles finely striated; gaster always darker coloured than head and mesosoma; erect setae between frontal carinae shorter than diameter of eye (Suppl. material 3: figs S72, S73) ..... ***Tetramorium bicarinatum*** (alien species)

– Mandibles smooth and shiny, only with piliferous pits; gaster the same colour as head and mesosoma; erect setae between frontal carinae mostly longer than diameter of eye (Suppl. material 3: figs S76, S77) .... ***Tetramorium insolens*** (alien species not reported from Cyprus)

15 Sides of head immediately behind eyes with a single stout projecting hair, directed anteriorly at an angle of about 45 ..... ***Tetramorium delagoense*** (alien species not recorded for Cyprus)

– Sides of head immediately behind eyes without such a hair, either hairless or with a number of minute decumbent to appressed hairs **16**

16 Frontal carinae strongly developed throughout their length, running unbroken almost to occipital margin; surface of head between frontal carinae strongly granular or reticulate-punctated, appears matt; antennal scrobes well-marked (Suppl. material 3: figs S78, S79) ..... ***Tetramorium simillimum*** (alien species not reported from Cyprus)

– Frontal carinae well developed only to the level of midlength of eyes, behind which they become weak, broken, or gradually fade out posteriorly; surface of head between frontal carinae only finely micropunctated, appears quite shiny; antennal scrobe very shallow, barely marked (Suppl. material 3: figs S74, S75) ..... ***Tetramorium caldarium*** (alien species)

17 Dorsum of petiole and postpetiole node with strong rugose sculpture, without smooth areas (Suppl. material 3: figs S82, S84) ..... ***Tetramorium chefketi*** **and** ***flavidulum*** **groups (four native species)**

– At least dorsum of petiole with smooth area (Suppl. material 3: figs S86, S88, S90, S92) **18**

18 Head with complete sculpture of longitudinal rugae **19**

– Head partly with smooth areas ..... ***Tetramorium semilaeve*** **group** (two native species)

19 Gyne with strongly transverse postpetiole at least 2.5 × as wide as long ..... ***Tetramorium ferox*** **group** (one native species)

– Gyne with not modified postpetiole, at most 1.7 × as wide as long (*Tetramorium caespitum* group; proper species identification needs a complex morphometric procedure and examination of male genitalia) **20**

20 Male genitalia: in ventral view one or two corners visible on ventral paramere lobe; in posterior view no distinct emargination between paramere lobes **21**

– Male genitalia: in ventral view no corner but rounded ends on ventral paramere lobe; in posterior view distinct division of ventral and dorsal lobe by deep emargination between paramere lobes ..... ***Tetramorium staerckei*** (native species) [Note: separation of members of the *caespitum* group requires combining morphometric data and studies on male genitalia. For more details see keys and photographs in Wagner et al. (2017).]

21 Male genitalia: in ventro-posterior view ventral paramere lobe with two corners > 87 μm apart. Worker: generally larger species: CS (arithmetic mean of head length and head width) = 834 ± 56. Usually in anthropogenically influenced, vegetation-free, and even concreted habitats (Suppl. material 3: figs S88, S89).... ***Tetramorium immigrans*** (alien species)

– Male genitalia: In ventro-posterior view ventral paramere lobe has one corner or two corners, < 87 μm apart. Worker: generally smaller species: CS (arithmetic mean of head length and head width) = 717 ± 52. In both anthropogenic and

natural habitats (Suppl. material 3: figs S90, S91) ..... ***Tetramorium indocile*** (native species)

22 Postpetiole ventrally without tooth or spine (Suppl. material 3: fig. S94) **23**

– Postpetiole ventrally with tooth or spine (Suppl. material 3: fig. S96) ..... ***Temnothorax*** **of the former** ***muellerianus*** **group (formerly in the genus** ***Chalepoxenus*****)** (one native social parasite in nests of *Temnothorax*)

23 Dorsum of head and mesosoma without standing hairs; postpetiole usually strongly widened, much wider than petiole; propodeum with short, sharp or obtuse denticles (Suppl. material 3: figs S98–S105) **24**

– Dorsum of head and mesosoma with at least sparse, conspicuous standing hairs; postpetiole not strongly widened, only somewhat wider than petiole or even subequal to it; propodeum with spines, denticles, or unarmed (Suppl. material 3: figs S106–S141) **29**

24 Very small species, CW < 420 mm ..... ***Cardiocondyla minutior*** (alien species not recorded from Cyprus)

– Larger species, CW > 420 mm **25**

25 Minute species with CS (arithmetic mean of head length and head width) < 470; head, mesosoma and petiolar segments yellowish-red, red or reddish-brown (Suppl. material 3: figs S98–S101) **26**

– Larger species with CS (arithmetic mean of head length and head width) > 490; head, mesosoma and petiolar segments from brown to black, if mesosoma reddish then head and petiolar segments darker coloured than mesosoma (Suppl. material 3: figs S102–S105) **28**

26 Anterior margin of postpetiole deeply emarginate, in anterolateral view with prominent anterolateral corners (Suppl. material 3: figs S100, S101) **27**

– Anterior margin of postpetiole feebly emarginate, in anterolateral view with obtuse anterolateral corners (Suppl. material 3: figs S98, S99) ..... ***Cardiocondyla emeryi*** (alien species not reported from Cyprus)

27 1st gastral segment in a majority of samples with absent or weakly developed blackish pigmentation ..... ***Cardiocondyla wroughtonii*** (alien species not reported from Cyprus)

– 1st gastral segment in a majority of samples with strongly developed blackish pigmentation ..... ***Cardiocondyla obscurior*** (alien species)

28 Postpetiole wide, kidney-shaped; metanotal groove deep; body predominantly or completely black (Suppl. material 3: figs S104, S105) ..... ***Cardiocondyla nigra*** (native species)

– Postpetiole moderately wide, oval; metanotal groove shallow; body usually bicoloured with mesosoma paler coloured than head and gaster (Suppl. material 3: figs S102, S103) ..... ***Cardiocondyla mauritanica*** (alien species)

29 Median portion of clypeus sharply raised and delineated by a pair of lateral longitudinal carinae (Suppl. material 3: figs S107, S109, S113, S115) **30**

– Median portion of clypeus not raised, evenly convex or somewhat flattened, without carinae or with single central longitudinal carina Suppl. material 3: figs S123, S125, S139, S141) **38**

30 Propodeum with short sharp teeth; eyes of workers very small, with less than 20 ommatidia; anterior clypeal margin with two long medial setae; head and mesosoma with strong reticulate and/or rugose sculpture (Suppl. material 3: figs S106, S107) ..... ***Stenamma*** (one native species)

– Propodeum rounded or at most slightly angled; eyes of workers bigger, with more than 20 ommatidia; anterior clypeal margin with a single long medial seta; head and mesosoma with fine microreticulate or microgranulate sculpture (Suppl. material 3: figs S108–S119) **31**

31 Monomorphic species, the largest workers only slightly larger than small workers; antennal scapi long and slim, reaching behind occipital margin of head (Suppl. material 3: figs S108–S113) **32**

– Polymorphic species, major workers with distinctly larger and wider head than in minor workers; antennal scapi short and stout, not reaching to occipital margin of head (Suppl. material 3: figs S114–S119) **36**

32 First gastral tergite bicoloured; at least partially light-coloured at its basal part (Suppl. material 3: figs S110, S111) **33**

– First gastral tergite dark (brown to black) and uniformly coloured (Suppl. material 3: figs S108, S109, S112, S113) **34**

33 2/3 of the first gastral tergite (abdominal segment 4) light-coloured; mesosoma dorsally with erect setae (Suppl. material 3: figs S110, S111) ..... ***Monomorium pharaonis*** (indoor introduced)

– 1/4 of the first gastral tergite (abdominal segment 4) light-coloured; mesosoma dorsally lacking erect setae ..... ***Monomorium sahlbergi*** (alien species not recorded from Cyprus)

34 Whole body uniformly dark coloured, reddish-brown to black, sometimes head darker than mesosoma, and mesosoma brighter than gaster (Suppl. material 3: figs S112, S113) **35**

– Head and mesosoma uniformly coloured, from orange to brick-red, gaster black (Suppl. material 3: figs S108, S109) ..... ***Monomorium bicolor*** (alien species)

35 Body matt and strongly sculptured; body reddish-brown to brown, sometimes head darker than mesosoma, and mesosoma brighter than gaster, but then never with uniformly colouration (Suppl. material 3: figs S112, S113) ..... ***Monomorium subopacum*** (native species)

– Body smooth and shiny, body uniformly blackish-brown to black ..... ***Monomorium carbonarium*** (alien species not recorded from Cyprus)

36 Propodeal spiracle vertically slit-shaped or elliptical; anterior clypeal margin with a pair of well-developed strong teeth (Suppl. material 3: figs S118, S119) ..... ***Trichomyrmex perplexus*** (native species)

– Propodeal spiracle circular or subcircular; anterior clypeal margin without teeth (Suppl. material 3: figs S114–S117) **37**

37 Body predominantly dark brown to black (Suppl. material 3: figs S116, S117) ... ***Trichomyrmex mayri*** (alien species)

– Body predominantly yellow (Suppl. material 3: figs S114, S115) ..... ***Trichomyrmex destructor*** (alien species)

38 Apical club 3-segmented (Suppl. material 3: figs S94, S95, S120–S135); smaller species (1.5 mm) **39**

– Apical club barely marked or 4-segmented (Suppl. material 3: figs S136–S141); larger species (ML > 2.2 mm in the largest workers) ..... ***Aphaenogaster*** **(four native species);** ***Messor*** **(three native species)**

39 Workers dimorphic, head of major workers very large, wider than mesosoma length. Mesosoma of minor workers with deep metanotal groove and antennal scapus longer than head length (Suppl. material 3: figs S120–S135) **40**

– Workers monomorphic; head of workers always shorter than mesosoma length; mesosoma of minor workers without or with shallow metanotal groove (Suppl. material 3: figs S94, S95), if metanotal groove distinct then antennal scapus always shorter than head length (Suppl. material 3: figs S96, S97) .... ***Temnothorax*** (12 native species)

40 Major workers: head longitudinally striated from clypeus to occiput; occipital lobes mostly with strong longitudinal or reticulate sculpture. Minor workers: mesosoma with distinct microreticulate sculpture, matt or with pronotum mostly smooth and shiny and mesonotum and propodeum with microreticulate sculpture but with shiny background; mesosoma with deep promesonotal groove (Suppl. material 3: figs S120–S127) **41**

– Major workers: head longitudinally striated from clypeus to the middle of head's length; occipital lobes smooth and shiny. Minor workers: mesosoma with pronotum mostly smooth and shiny and mesonotum and propodeum with microreticulate sculpture and shiny background; mesosoma without promesonotal groove (Suppl. material 3: figs S128–S133) **42**

41 Very small, length of mesosoma in major workers below 1 mm, in minor workers below 0.6 mm. Major workers: occipital lobes of head and anterolateral corners of pronotum with reticulate sculpture. Minor workers: head and mesosoma mostly with microreticulate sculpture, matt; mesosoma with shallow promesonotal groove (Suppl. material 3: figs S120–S123) ..... ***Pheidole fadli*** (indoors introduced)

– Larger, length of mesosoma in major workers above 1 mm, in minor workers above 0.6 mm. Major workers: occipital lobes of head with longitudinal sculpture and anterolateral corners of pronotum with reticulate sculpture. Minor workers: head and pronotum mostly smooth and shiny, mesosoma with deep promesonotal groove (Suppl. material 3: figs S124–S127) .... ***Pheidole indica*** (alien species)

42 Major and minor workers: propodeal spines minute, not longer than basal width, often in form of small tubercle; postpetiole in profile without conspicuous ventral convexity (Suppl. material 3: figs S128–S131) ..... ***Pheidole koshewnikovi*** (native species)

– Major and minor workers: propodeal spines prominent, usually as long as or longer than basal width; postpetiole in profile with conspicuous ventral convexity (Suppl. material 3: figs S132, S133) ..... ***Pheidole megacephala*** (alien species not reported from Cyprus)

Subfamily Ponerinae

[After Borowiec and Salata (2022) and Schmidt and Shattuck (2014), modified]

1 Mandibles with more than 8 dents and denticles, the 1–3 apical dents often somewhat stronger and the following 8–13 dents small to minute; mid and hind tibiae each with one pectinate spur (Suppl. material 3: figs S144–S149) **2**

– Mandibles with 6–7 strong dents of approximately equal size; mid and hind tibiae each with two spurs, median spur large and pectinate, lateral spur much smaller and not pectinate (Suppl. material 3: figs S142, S143) ..... ***Cryptopone*** (one native species)

2 Ventral apex of the metatibia with a single spur, which is pectinate **4**

– Ventral apex of the metatibia with both a large pectinate spur and a smaller simple spur **3**

3 Propodeal spiracle slit-shaped ..... ***Parvaponera darwinii*** (alien species not recorded from Cyprus)

– Propodeal spiracle round or ovoid ..... ***Brachyponera chinensis*** (alien species not recorded from Cyprus)

4 Petiolar base in profile with two small, sharp dents or angles and anteriorly with a circular translucent "window" (Suppl. material 3: figs S144, S145) ..... ***Ponera*** (one native species)

– Petiolar base in profile form a simple rounded lobe, without a translucent "window"(Suppl. material 3: figs S146–S149) **5**

5 Scape reaching to hind margin of head, scape length/head width ratio > 0.88; petiole in profile significantly higher and narrower; mesopleuron completely covered with carinulate sculpture (Suppl. material 3: figs S146, S147) ..... ***Hypoponera eduardi*** (native species)

– Scape not reaching to hind margin of head, scape length/head width ratio < 0.88; petiole in profile significantly lower and thicker; mesopleuron smooth (Suppl. material 3: figs S148, S149) ..... ***Hypoponera punctatissima*** (alien species)

Discussion

Land cover and protected areas

The number of known alien insect species in Cyprus has increased dramatically during the last decade (Demetriou et al. 2023a); there has been a steep increase in the number of recorded ants in part due to increased sampling intensity (Tables 1, 2). According to our analysis of CLC occupied by alien ants in Cyprus, the majority of species (90%) have been collected from anthropogenic habitats including artificial surfaces and agricultural land, with limited spread to forest and semi-natural areas or inland waters (Fig. 1). These data are in accordance with other similar observations, reporting al-

ien insects, including ants, mostly dominating anthropogenic habitats (Espadaler and Bernal 2003; Lopez-Vaamonde et al. 2010; Schifani 2019; Rosas-Mejía et al. 2021; Demetriou et al. 2023b). Regarding the second level of CLC types, within artificial surfaces more than half of the habitats (54%) correspond to "urban fabric", followed by "artificial, non-agricultural vegetated areas" (43%). Within agricultural land, "heterogeneous agricultural areas" dominate occupied habitats with a percentage of 69% of obtained records. Lastly, regarding forest and semi-natural areas, half of the occurrence records were classified as "shrub and/or herbaceous vegetation associations" (52%), followed by "forests" (33%) and "open spaces with little or no vegetation" (15%) (Suppl. material 1). Nevertheless, looking in greater detail into these forest and semi-natural areas and comparing these classifications with the notes taken on the habitat during the surveys, some correspond to traffic islands, roadsides, urban habitats and/or other areas with evident human pressure and modifications. This comes to show that the spread of alien ants into natural habitat types is perhaps limited and that their spread is probably favoured by anthropogenic habitat heterogeneity (Elton 1958; Hobbs and Huenneke 1992; Melbourne et al. 2007).

The NATURA 2000 and RAMSAR wetland networks also seem not to be impervious to biological invasions of ants, with seven species being present in a total of 20 protected areas (Suppl. material 2). Many records were situated around the edges of protected areas, as already reported by Liu et al. (2020), with the most noticeable case in Cyprus being that of *W. auropunctata*, collected just outside the protected areas of Faros Kato Paphou (CY4000013), Chersonisos Akama (CY4000010) and Ekboles Potamon Ezousas, Xerou, kai Diarizou (CY4000018) in Paphos. The alien ant fauna of the island both within protected areas and surrounding areas (Holenstein et al. 2021), should be further monitored to increase understanding of potential adverse effects on native biodiversity and protected habitat types. The Akamas Peninsula (CY4000010 and CY4000023) is of particular importance because of increasing pressure from urban developments which may increase the number and spread of alien species. Four alien species, *M. bicolor*, *N. jaegerskioeldi*, *P. longicornis* and *T. lanuginosum* have already been identified from the region, although no adverse effects have been reported. Although protected areas have been reported as refuges for native species against invasive alien species (Gallardo et al. 2017), the spread and establishment of species such as *W. auropunctata* should be monitored further.

Establishment status and introduction pathways

Twelve out of 17 species are considered to be established with self-sustaining populations on the island; one is considered as an introduction to indoors because it is confined to plant nurseries and the zoo (i.e. *T. bicarinatum*). For four species, *C. cf. vitiosus*, *H. punctatissima*, *P. fadli* and *T. caldarium*, the establishment status is currently unknown because only single records/specimens have been found. These species may represent recent introductions that will fail to establish but ongoing monitoring

is recommended. It is important to mention that the greenhouse in which *P. fadli* was detected, was destroyed and reconstructed (paved) a few months after the specimen's collection (Demetriou pers. obs.).

Although introduction pathways of alien ants in Cyprus are largely unknown, plant nurseries seem to play a crucial role in the movement of alien ants (Jucker et al. 2008; Pospischil 2011; Blatrix et al. 2018). As shown in our study, six alien ant species were collected from plant nurseries and greenhouses with *P. fadli* and *H. punctatissima* known only from such localities. This shows that alien ants can be moved outside their native range in the soil of potted plants, as hypothesised for *W. auropunctata* (Vonshak et al. 2010; Demetriou et al. 2022), potentially bypassing phytosanitary inspections and border controls (Rabitsch 2011; Wong et al. 2023). The identification key aims to support detection and monitoring activities. Quarantine measures or chemical treatment could be implemented for imported plant material to mitigate further spread of invasive alien species such as *S. geminata*, *S. invicta*, *S. richteri*, and *W. auropunctata* (Rabitsch 2022a, b).

Impacts

There is a lack of information on the environmental and socio-economic impacts of alien ants inhabiting Cyprus, although some invasive alien species have been scored as high through global impact assessments such as *W. auropunctata*, *P. longicornis*, *T. bicarinatum*, and *T. destructor* (Salata et al. 2019; Demetriou et al. 2022; Gruber et al. 2022; present study). Furthermore, according to Salata et al. (2019) aggressive behaviour towards native ant species has been observed by *N. jaegerskioeldi* but such observations are not supported by quantified analyses suggesting the need for further studies. These species should be considered for prioritisation on lists with further ongoing research on their impacts. As an example *W. auropunctata* has been listed both as one of the world's worst invasive alien species (GISD 2023) and as an invasive alien species of Union Concern (EU 1143/2014; EU 2022/1203). Currently, no other native species have been found to occur in sites heavily infested by *W. auropunctata* and for the moment no spread in natural habitats has been observed (Demetriou pers. obs.).

Wasmannia auropunctata has the potential to threaten human and animal health because it can sting and in rare cases cause anaphylactic shocks with the potential to harm both wild and domesticated animals (Wetterer and Porter 2003; Kidon et al. 2022). Infestations of electronic devices by *T. destructor* also pose a potentially life-threatening socio-economic impact of ants on the island. Citizen science is being considered as an approach by the authors to assess the socio-economic impacts of ants in Cyprus and particularly their impacts in households. Such an initiative could also be used to enhance understanding of the presence of other alien species, verify past records of *M. pharaonis*, raise awareness of the impacts of alien ants as well as provide adequate data to perform risk assessments under EICAT and SEICAT protocols (Hawkins et al. 2015; Bacher et al. 2018).

Conclusions

A total of 17 alien ant species have been documented in Cyprus, with nine representing new records for the island. Most species have been predominantly found in urban and agricultural habitats although some observations have been also made in semi-natural and natural habitats including protected areas. All species are largely synanthropic and are distributed in the island's lowlands, with the majority (14 out of 17) being detected within the last decade and considered to be established (12 out of 17) on the island.

Although introduction pathways of alien insects in Cyprus are largely unknown (Demetriou et al. 2023a), the CBD pathway category "Transport – Contaminant: 3.1. Contaminant nursery material" (CBD 2014), is proposed as one of the main introduction pathways of alien ants to the island. Potted ornamental plants seem to facilitate the introduction and spread of nests such as in the case of *W. auropunctata* in Israel (Vonshak and Ionescu-Hirsch 2009).

The identification key aims to support phytosanitary inspections and border controls in order to provide early detection and management of alien ants. Future studies could incorporate molecular methods to assess the biological invasion history and introduction pathways of alien ants to the island. Online, accessible, and more user-friendly identification guides could further enhance monitoring efforts.

Regarding the impacts of alien ants in Cyprus, further monitoring through citizen science initiatives and structured surveys could be insightful particularly for studying the spread of alien ants and their interactions within ecosystems. Data on possible and observed impacts could raise awareness and inform local policy and management actions mitigating the impacts through containment and eradication campaigns.

Acknowledgements

We are thankful to the anonymous reviewers and Subject Editor Dr Wolfgang Rabitsch for their corrections to the manuscript. Lech Borowiec and Sebastian Salata thank the University of Wroclaw for supporting collecting trips to Cyprus. Lech Borowiec thanks Dr Jolanta Świętojańska (University of Wrocław) for her assistance during his first collecting field trip to Cyprus in 2012. We would also like to thank the UK Government through Darwin Plus (DPLUS0124 and DPLUS200), for funding this project and material surveys of Jakovos Demetriou.

References

Agosti D, Collingwood CA (1987) A provisional list of the Balkan ants (Hym. Formicidae) and a key to the worker caste. I. Synonymic list. Mitteilungen der Schweizerische Entomologische Gesellschaft 60: 51–62.

Angulo E, Hoffmann BD, Ballesteros-Mejia L, Taheri A, Balzani P, Bang A, Renault D, Cordonnier M, Bellard C, Diagne C, Ahmed DA, Watari Y, Courchamp F (2022) Economic costs of invasive alien ants worldwide. Biological Invasions 24(7): 2041–2060. https://doi.org/10.1007/s10530-022-02791-w

AntWiki (2022) AntWiki. https://www.antwiki.org/wiki/Welcome_to_AntWiki [accessed 22/11/2022]

Atanassov N, Dlusskij G (1992) Hymenoptera, Formicidae. In: Vasilev I (Ed.) Fauna Bulgarica. 22. Bulgarian Academy of Sciences, Sofia, 310 pp. [In Bulgarian]

Bacher S, Blackburn TM, Essl F, Genovesi P, Heikkilä J, Jeschke JM, Jones G, Keller R, Kenis M, Kueffer C, Martinou AF, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roy HE, Saul C-W, Scalera R, Vilà M, Wilson JRU, Kumschick S (2018) Socio-economic impact classification of alien taxa (SEICAT). Methods in Ecology and Evolution 9(1): 159–168. https://doi.org/10.1111/2041-210X.12844

Bachman S, Moat J, Hill A, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: Geospatial Conservation Assessment Tool. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Bernard F (1956) Révision des fourmis paléarctiques du genre *Cardiocondyla* Emery. Bulletin de la Société Histoire Naturelle de l'Afrique du Nord 47: 299–306.

Bibby CJ, Crosby MJ, Heath MF, Johnson TH, Long TH, Sattersfield AJ, Thirgood SJ (1992) Putting Biodiversity on the Map: Global Priorities for Conservation. International Council for Bird Preservation, Cambridge, U.K.

Blatrix R, Colin T, Wegnez P, Galkowski C, Geniez P (2018) Introduced ants (Hymenoptera: Formicidae) of mainland France and Belgium, with a focus on greenhouses. Annales de la Société Entomologique de France 54(4): 293–308. https://doi.org/10.1080/00379271.2018.1490927

Boer P, Noordijk J, Heijerman T, Verhoogt K, van Vugt R (2018) *Cardiocondyla obscurior* in the Hortus botanicus Leiden (Hymenoptera: Formicidae). Entomologische Berichten 78(1): 10–15.

Bolton B (1980) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Ethiopian zoogeographical region. Bulletin of the British Museum (Natural History). Entomology 40: 193–384.

Bolton B (1987) A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). Bulletin of the British Museum (Natural History). Entomology 54(3): 263–452.

Bolton B (2000) The ant tribe Dacetini. Memoirs of the American Entomological Institute 65: 1–1028.

Bolton B, Fisher BL (2011) Taxonomy of Afrotropical and West Palaearctic ants of the ponerine genus *Hypoponera* Santschi (Hymenoptera: Formicidae). Zootaxa 2843(1): 1–118. https://doi.org/10.11646/zootaxa.2843.1.1

Borowiec L (2014) Catalogue of ants of Europe, the Mediterranean Basin and adjacent regions (Hymenoptera: Formicidae). Genus 25(1–2): 1–340.

Borowiec L, Salata S (2022) A monographic review of ants of Greece (Hymenoptera: Formicidae). Vol. 1. Introduction and review of all subfamilies except the subfamily Myrmicinae. Natural History Monographs of the Upper Silesian Museum 1: 1–775.

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwellsmith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie JC, Watson R (2010) Global biodiversity: Indicators of recent declines. Science 328(5982): 1164–1168. https://doi.org/10.1126/science.1187512

CABI (2022) *Monomorium destructor* (Singapore ant). https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.34581 [accessed 22/11/2022]

Cagniant H (1997) Le genre *Tetramorium* au Maroc (Hymenoptera: Formicidae): clé et catalogue des espèces. Annales de la Société entomologique de France (N.S.) 33: 89–100. https://doi.org/10.1080/21686351.1997.12279181

Cagniant H, Espadaler X (1993) Liste des espèces de fourmis du Maroc. Actes des Colloques Insectes Sociaux 8: 89–93. https://doi.org/10.4000/books.editionsmsh.39003

Casiraghi A, Espadaler X, Pérez Hidalgo N, Gómez K (2020) Two additions to the Iberian myrmecofauna: *Crematogaster inermis* Mayr, 1862, a newly established, tree-nesting species, and *Trichomyrmex mayri* (Forel, 1902), an emerging exotic species temporarily nesting in Spain (Hymenoptera, Formicidae). Journal of Hymenoptera Research 78: 57–68. https://doi.org/10.3897/jhr.78.51858

CBD (2014) Convention on Biological Diversity. Pathways of introduction of invasive species, their prioritization and management. https://www.cbd.int/doc/meetings/sbstta/sbstta-18/official/sbstta-18-09-add1-en.pdf

Cheikh Albassatneh M, Escudero M, Monnet A-C, Arroyo J, Bacchetta G, Bagnoli F, Dimopoulos P, Hampe A, Leriche A, Médail F, Nikolic T, Ponger L, Vendramin GG, Fady B (2021) Spatial patterns of genus-level phylogenetic endemism in the tree flora of Mediterranean Europe. Diversity & Distributions 27(5): 913–928. https://doi.org/10.1111/ddi.13241

Collingwood CA, Tigar BJ, Agosti D (1997) Introduced ants in the United Arab Emirates. Journal of Arid Environments 37(3): 505–512. https://doi.org/10.1006/jare.1997.0309

Cordonnier M, Gayet T, Escarguel G, Kaufmann B (2019) From hybridization to introgression between two closely related sympatric ant species. Journal of Zoological Systematics and Evolutionary Research 57(4): 778–788. https://doi.org/10.1111/jzs.12297

Czechowski W, Radchenko A, Czechowska W, Vepsäläinen K (2012) The ants (Hymenoptera: Formicidae) of Poland with reference to the myrmecofauna of Europe (Fauna Poloniae n.s. 4). Natura Optima Dux Foundation, Warsaw, 1–496.

Demetriou J, Georgiadis C, Roy HE, Martinou AF, Borowiec L, Salata S (2022) One of the world's worst invasive alien species *Wasmannia auropunctata* (Hymenoptera: Formicidae) detected in Cyprus. Sociobiology 69(4): e8536. https://doi.org/10.13102/sociobiology.v69i4.8536

Demetriou J, Radea C, Peyton J, Groom Q, Roques A, Rabitsch W, Seraphides N, Arianoutsou M, Roy HE, Martinou AF (2023a) The Alien to Cyprus Entomofauna (ACE) database: A review of the current status of alien insects (Arthropoda, Insecta) including an updated

species checklist, discussion on impacts and recommendations for informing management. NeoBiota 83: 11–42. https://doi.org/10.3897/neobiota.83.96823

Demetriou J, Georgiadis C, Koutsoukos E, Borowiec L, Salata S (2023b) Alien ants (Hymenoptera: Formicidae) on a quest to conquer Greece: a review including an updated species checklist and guidance for future research. NeoBiota 86: 81–122. https://doi.org/10.3897/neobiota.86.98157

Donisthorpe H (1930) *Cardiocondyla bicolor*, sp. n. (Hymenoptera, Formicidae), a species of myrmecine ant new to science. Annals & Magazine of Natural History 10(6): 366. https://doi.org/10.1080/00222933008673226

Donisthorpe H (1942) The Formicidae (Hym.) of the Armstrong College expedition to the Siwa Oasis. Annals & Magazine of Natural History 9(11): 26–33. https://doi.org/10.1080/03745481.1942.9755460

Donisthorpe H (1950) A first instalment of the ants of Turkey. Annals & Magazine of Natural History 3(12): 1057–1067. https://doi.org/10.1080/00222935008654119

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London, UK. https://doi.org/10.1007/978-1-4899-7214-9

Emery C (1881) Viaggio ad Assab nel Mar Rosso dei Signori G. Doria ed O. Beccari con il R. Avviso "Esploratore" dal 16 novembre 1879 al 26 febbraio 1880. I. Formiche. Annali del Museo Civico di Storia Naturale 16: 525–535.

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

Emery C (1909) Beiträge zur Monographie der Formiciden des paläarktischen Faunengebietes. (Hym.) Teil VI. Deutsche Entomologische Zeitschrift 1909: 19–37. https://doi.org/10.1002/mmnd.48019090105

Emery C (1910) Beiträge zur Monographie der Formiciden des paläarktischen Faunengebietes. (Hym.) Teil X. Deutsche Entomologische Zeitschrift 1910: 127–132. https://doi.org/10.1002/mmnd.4801910201

Espadaler X, Bernal V (2003) Exotic ants in the Canary Islands (Hymenoptera, Formicidae). Vieraea 31: 1–7.

Espadaler X, Ortiz de Zugasti N (2019) *Cardiocondyla obscurior* Wheeler, 1929 (Hymenoptera: Formicidae) in Catalonia (NE Spain), with comments on exotic ant species. Butlleti de la Institucio Catalana d'Historia Natural 83: 153–156.

Essl F, Bacher S, Genovesi P, Hulme PE, Jeschke JM, Katsanevakis S, Kowarik I, Kühn I, Pyšek P, Rabitsch W, Schindler S, van Kleunen M, Vilà M, Wilson JRU, Richardson DM (2018) Which taxa are alien? Criteria, applications, and uncertainties. Bioscience 68(7): 496–509. https://doi.org/10.1093/biosci/biy057

Fadl H, Bakr RF, Badawy RM (2007) Six new species of ants (Insecta: Hymenoptera: Formicidae) from Egypt. Proceedings of the 2nd International Conference of the Entomological Society of Egypt 2: 235–249.

Fisher BL, Bolton B (2016) Ants of the world. Ants of Africa and Madagascar. A guide to the genera. University of California Press, Berkeley, 1–503. [+ ix plates] https://doi.org/10.1525/9780520962996

Gallardo B, Aldridge DC, González-Moreno P, Pergl J, Pizarro M, Pyšek P, Thuiller W, Yesson C, Vilà M (2017) Protected areas offer refuge from invasive species spreading under climate change. Global Change Biology 23(12): 5331–5343. https://doi.org/10.1111/gcb.13798

Georghiou GP (1977) The insects and mites of Cyprus. With emphasis on species of economic importance to agriculture, forestry, man and domestic animals. Benaki Phytopathological Institute, Kiphissia, Athens, Greece, 347 pp.

Georgiadis C, Leonidou K, Tsipouridou C, Legakis A (2017) Ants of Cyprus. Agricultural University of Athens, Athens, Greece, Conference: 17th National Entomological Congress, Agricultural University of Athens, Athens, Greece https://doi.org/10.13140/RG.2.2.19289.01123

GISD (2023) Global Invasive Species Database. http://www.iucngisd.org/gisd/100_worst.php [accessed on 23-01-2023]

Gómez K, Espadaler X (2006) Exotic ants (Hymenoptera: Formicidae) in the Balearic Islands. Myrmecologische Nachrichten 8: 225–233.

Gotzek D, Martinez S (2021) First record of the red imported fire ant, *Solenopsis invicta* Buren, from Hispaniola. BioInvasions Records 10(3): 567–576. https://doi.org/10.3391/bir.2021.10.3.06

Gruber MAM, Santoro D, Cooling M, Lester PJ, Hoffmann BD, Boser C, Lach L (2022) A global review of socioeconomic and environmental impacts of ants reveals new insights for risk assessment. Ecological Applications 32(4): e2577. https://doi.org/10.1002/eap.2577

Guénard B, Dunn RR (2012) A checklist of the ants of China. Zootaxa 3558(1): 1–77. https://doi.org/10.11646/zootaxa.3558.1.1

Guénard B, Weiser M, Gomez K, Narula N, Economo EP (2017) The Global Ant Biodiversity Informatics (GABI) database: A synthesis of ant species geographic distributions. Myrmecological News 24: 83–89.

Hadjisterkotis E, Masala B (1995) Vertebrate extinction in Mediterranean islets: An example from Cyprus. Biogeographia 18: 691–699. https://doi.org/10.21426/B618110414

Hand R, Hadjikyriakou GN, Christodoulou CS [Eds] (2011) [continuously updated] Flora of Cyprus – a dynamic checklist. http://www.flora-of-cyprus.eu/

Hand R, Hadjikyriakou GN, Christodoulou CS (2019) Updated numbers of the vascular flora of Cyprus including the endemism rate. Cypricola 13: 1–6.

Hawkins CL, Bacher S, Essl F, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Vilà M, Wilson RJU, Genovesi P, Blackburn TM (2015) Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT). Diversity & Distributions 21(11): 1360–1363. https://doi.org/10.1111/ddi.12379

Hayashi AM (1999) Attack of the fire ants. Scientific American 280(2): 26–28. https://doi.org/10.1038/scientificamerican0299-26b

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion – implications for conservations. Conservation Biology 6(3): 324–337. https://doi.org/10.1046/j.1523-1739.1992.06030324.x

Holenstein K, Simonson WD, Blackburn TM, Charpentier A (2021) Non-native species surrounding protected areas influence the community of non-native species within them. Frontiers in Ecology and Evolution 8: 625137. https://doi.org/10.3389/fevo.2020.625137

Holt BG, Lessard J-P, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre P-H, Graham CH, Graves GR, Jønsson KA, Nogués-Bravo D, Wang Z, Whittaker RJ, Fjeldså J, Rahbek C (2013) An update of Wallace's zoogeographic regions of the world. Science 339(6115): 74–78. https://doi.org/10.1126/science.1228282

Ionescu-Hirsch A (2009) An annotated list of *Camponotus* of Israel (Hymenoptera: Formicidae), with a key and descriptions of new species. Israel Journal of Entomology 39: 57–98.

IPBES (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, 1–1148. https://doi.org/10.5281/zenodo.3831673

IUCN (2001) IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK, 30 pp.

Janicki J, Narula N, Ziegler M, Guénard B, Economo EP (2016) Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. Ecological Informatics 32: 185–193. https://doi.org/10.1016/j.ecoinf.2016.02.006

Jucker C, Rigato F, Regalin R (2008) Exotic ant records from Italy (Hymenoptera, Formicidae). Bollettino di Zoologia Agraria e di Bachicoltura 40(1): 99–107.

Kidon M, Klein Y, Weinberg T (2022) Little fire ant (*Wasmannia auropunctata*) in Israel – from nuisance to life-threatening. Harefuah 161(4): 207–209.

Kim G, Lyu D (2012) Distribution of ants (Insecta, Hymenoptera) in Chiaksan Mountain, prov. Gangweon, Korea. Journal of Korean Nature 5(2): 127–129. https://doi.org/10.7229/jkn.2012.5.2.127

Kiran K, Karaman C (2020) Additions to the ant fauna of Turkey (Hymenoptera, Formicidae). Zoosystema 42(18): 285–329. https://doi.org/10.5252/zoosystema2020v42a18

Leclerc C, Courchamp F, Bellard C (2018) Insular threat associations within taxa worldwide. Scientific Reports 8(1): 6393. https://doi.org/10.1038/s41598-018-24733-0

Liu X, Blackburn TM, Song T, Wang X, Huang C, Li Y (2020) Animal invaders threaten protected areas worldwide. Nature Communications 11(1): 2892. https://doi.org/10.1038/s41467-020-16719-2

Lopez-Vaamonde C, Glavendekić M, Paiva MR (2010) Invaded habitats. BioRisk 4(1): 45–50. https://doi.org/10.3897/biorisk.4.66

Lubertazzi D (2019) The ants of Hispaniola. Bulletin of the Museum of Comparative Zoology 162(2): 59–210. https://doi.org/10.3099/MCZ-43.1

Lubin Y (1984) Changes in the native fauna of the Galapagos Islands following invasion by the little fire ant *Wasmannia auropunctata*. Biological Journal of the Linnean Society. Linnean Society of London 21(1–2): 229–242. https://doi.org/10.1111/j.1095-8312.1984.tb02064.x

Mbenoun-Masse PS, Tindo M, Kenne M, Tadu Z, Mony R, Djieto-Lordon C (2017) Impact of the invasive ant *Wasmannia auropunctata* (Formicidae: Myrmicinae) on local ant diversity in southern Cameroon. African Journal of Ecology 55(4): 423–432. https://doi.org/10.1111/aje.12366

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H

(2007) Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? Ecology Letters 10(1): 77–94. https://doi.org/10.1111/j.1461-0248.2006.00987.x

Mohamed S, Zalat S, Fadl H, Gadalla S, Sharaf M (2001) Taxonomy of ant species (Hymenoptera: Formicidae) collected by pitfall traps from Sinai and Delta region, Egypt. Egyptian Journal of Natural History 3: 40–61. https://doi.org/10.4314/ejnh.v3i1.30001

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the United States of America 98(10): 5446–5451. https://doi.org/10.1073/pnas.091093398

Morris HM (1937) Injurious insects of Cyprus. Agricultural Department of Cyprus. Bulletin 4(Ent. Ser.): 1–21.

Myers N, Mittermeier R, Mittermeier C, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772): 853–858. https://doi.org/10.1038/35002501

Nishida GM, Evenhuis NL (2000) Arthropod pests of conservation significance in the Pacific: A preliminary assessment of selected groups. In: Sherley G (Ed.) Invasive Species in the Pacific: A Technical Review and Draft Regional Strategy. South Pacific Regional Environment Programme, Samoa, 154–142.

Obregón Romero R, Reyes López J (2012) Nuevas aportaciones sobre hormigas exóticas para Portugal continental (Hymenoptera: Formicidae). Boletin de la Asociacion Espanola de Entomologia 36: 279–284.

Park S-H, Hosoishi S, Ogata K (2014) Long-term impacts of Argentine ant invasion of urban parks in Hiroshima, Japan. Journal of Ecology and Environment 37(3): 123–129. https://doi.org/10.5141/ecoenv.2014.015

Pawluk F, Borowiec L, Salata S (2022a) First record of *Plagiolepis alluaudi* Emery, 1894 (Hymenoptera: Formicidae) from Poland. Annals of the Upper Silesian Museum in Bytom Entomology 31(6): 1–5. https://doi.org/10.5281/zenodo.6522444

Pawluk F, Borowiec L, Salata S (2022b) *Technomyrmex vitiensis* Mann, 1921 (Hymenoptera: Formicidae) – a new exotic ant species in Poland. Annals of the Upper Silesian Museum in Bytom Entomology 31(11): 1–5. https://doi.org/10.5281/zenodo.7346624

Peyton J, Martinou AF, Pescott OL, Demetriou M, Adriaens T, Arianoutsou M, Bazos I, Bean CW, Booy O, Botham M, Britton JR, Cervia JL, Charilaou P, Chartosia N, Dean HJ, Delipetrou P, Dimitriou AC, Dörflinger G, Fawcett J, Fyttis G, Galanidis A, Galil B, Hadjikyriakou T, Hadjistylli M, Ieronymidou C, Jimenez C, Karachle P, Kassinis N, Kerametsidis G, Kirschel ANG, Kleitou P, Kleitou D, Manolaki P, Michailidis N, Mountford JO, Nikolaou C, Papatheodoulou A, Payiatas G, Ribeiro F, Rorke SL, Samuel Y, Savvides P, Schafer SM, Tarkan AS, Silva-Rocha I, Top N, Tricarico E, Turvey K, Tziortzis I, Tzirkalli E, Verreycken H, Winfield IJ, Zenetos A, Roy HE (2019) Horizon scanning for invasive alien species with the potential to threaten biodiversity and human health on a Mediterranean island. Biological Invasions 21(6): 2107–2125. https://doi.org/10.1007/s10530-019-01961-7

Pospischil R (2011) The role of tropical greenhouses for introduction and establishment of foreign ant species (Hymenoptera: Formicidae) in Central Europe. In: Robinson WH, de Carvalho Campos AE (Eds) Proceedings of the Seventh International Conference on Urban Pests; 2011 Aug 7–10; Ouro Preto, Brazil, Instituto Biológico, São Paulo, 59–66.

Rabitsch W (2011) The hitchhiker's guide to alien ant invasions. BioControl 56(4): 551–572. https://doi.org/10.1007/s10526-011-9370-x

Rabitsch W (2022a) The management of Fire Ants (*Solenopsis geminata*, *Solenopsis invicta*, *Solenopsis richteri*) – Information on measures and related costs in relation to species on the Union list. Technical note prepared by IUCN for the European Commission.

Rabitsch W (2022b) The management of the Little Fire Ant (*Wasmannia auropunctata*) – Information on measures and related costs in relation to species on the Union list. Technical note prepared by IUCN for the European Commission.

Radchenko A (2004) Formicidae. – Fauna Europaea version 1.1. http://www.faunaeur.org [retrieved on 20 November 2007]

Reaser J, Meyerson L, Cronk Q, de Poorter M, Elgrege L, Green E, Kairo M, Latasi P, Mack RN, Mauremooto J, O'Down D, Orapa W, Sastroutomo S, Saunders A, Shine C, Thrainsson S, Vaiutu L (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. Environmental Conservation 34(2): 98–111. https://doi.org/10.1017/S0376892907003815

Reyes J, Espadaler X (2005) Tres nuevas especies foráneas de hormigas para la Península Ibérica (Hymenoptera: Formicidae). Boletin de la SEA 36: 263–265.

Reyes-López J-L, Taheri A (2018) First checklist of ants (Hymenoptera, Formicidae) of urban green areas in Cádiz (Andalusia, Spain). Boletin de la Asociacion Espanola de Entomologia 42(3): 217–223.

Roque-Albelo L, Causton C (1999) El Niño and the introduced insects in the Galápagos Islands: Different dispersal strategies, similar effects. Noticias de Galápagos 60: 30–36.

Roque-Albelo L, Causton CE, Mieles A (2000) The ants of Marchena Island, twelve years after the introduction of the little fire ant, *Wasmannia auropunctata*. Noticias de Galápagos 61: 17–20.

Rosas-Mejía M, Guénard B, Aguilar-Méndez MJ, Ghilardi A, Vásquez-Bolaños M, Economo EP, Janda M (2021) Alien ants (Hymenoptera: Formicidae) in Mexico: the first database of records. Biological Invasions 23(6): 1669–1680. https://doi.org/10.1007/s10530-020-02423-1

Russell JC, Meyer JY, Holmes ND, Pagad S (2017) Invasive alien species on islands: Impacts, distribution, interactions and management. Environmental Conservation 44(4): 359–370. https://doi.org/10.1017/S0376892917000297

Saddiqui JA, Li J, Zou X, Bodlah I, Huang X (2019) Meta-analysis of the global diversity and spatial patterns of aphid-ant mutualistic relationships. Applied Ecology and Environmental Research 17(3): 5471–5524. https://doi.org/10.15666/aeer/1703_54715524

Salata S, Borowiec L (2015a) A taxonomic revision of the genus *Oxyopomyrmex* André, 1881 (Hymenoptera: Formicidae). Zootaxa 4025(1): 1–66. https://doi.org/10.11646/zootaxa.4025.1.1

Salata S, Borowiec L (2015b) Redescription of *Crematogaster cypria* Santschi, 1930, new status, with description of two new related species from Greece and Turkey (Hymenoptera, Formicidae). ZooKeys 505: 59–77. https://doi.org/10.3897/zookeys.505.9566

Salata S, Georgiadis C, Borowiec L (2019) Invasive ant species (Hymenoptera: Formicidae) of Greece and Cyprus. North-Western Journal of Zoology 15(1): 13–23.

Salata S, Borowiec L, Trichas A (2020) Review of ants (Hymenoptera: Formicidae) of Crete, with keys to species determination and zoogeographical remarks. Monographs of the Upper Silesian Museum 12: 1–300. https://doi.org/10.5281/zenodo.3738001

Salata S, Demetriou J, Georgiadis C, Borowiec L (2023a) The ant genus *Cataglyphis* Förster (Hymenoptera: Formicidae) in Cyprus. Zootaxa 5264(3): 301–322. https://doi.org/10.11646/zootaxa.5264.3.1

Salata S, Demetriou J, Georgiadis C, Borowiec L (2023b) *Camponotus* Mayr, 1861 (Hymenoptera: Formicidae) of Cyprus: generic synopsis and description of a new species. Asian Myrmecology 16: 016007.

Sánchez-García D, Espadaler X (2015) *Cardiocondyla obscurior* Wheeler, 1929 (Hymenoptera, Formicidae) in Spain. Iberomyrmex 7: 7–9.

Santschi F (1930) Trois notes myrmécologiques. Bulletin et annales de la Société royale belge d'entomologie 70: 263–270.

Santschi F (1934) Contribution aux *Solenopsis* paléarctiques. Revue Suisse de Zoologie 41: 565–592. https://doi.org/10.5962/bhl.part.146021

Santschi F (1937) Contribution à l'étude des *Crematogaster* paléarctiques. Mémoires de la Société vaudoise des sciences naturelles 5: 295–317.

Sarnat EM, Fischer G, Guénard B, Economo EP (2015) Introduced *Pheidole* of the world: Taxonomy, biology and distribution. ZooKeys 543: 1–109. https://doi.org/10.3897/zookeys.543.6050

Schembri SP, Collingwood CA (1981) A revision of the myrmecofauna of the Maltese Islands (Hymenoptera, Formicidae). Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova) 83: 417–442.

Schifani E (2019) Exotic ants (Hymenoptera, Formicidae) invading Mediterranean Europe: A brief summary over about 200 years of documented introductions. Sociobiology 66(2): 198–208. https://doi.org/10.13102/sociobiology.v66i2.4331

Schifani E, Alicata A (2018) Exploring the myrmecofauna of Sicily: Thirty-two new ant species recorded, including six new to Italy and many new aliens (Hymenoptera, Formicidae). Polskie Pismo Entomologiczne 87(4): 323–348. https://doi.org/10.2478/pjen-2018-0023

Schifani E, Castracani C, Giannetti D, Spotti FA, Mori A, Grasso DA (2022) Tool use in pavement battles between ants: First report of *Tetramorium immigrans* (Hymenoptera, Formicidae) using soil-dropping as an interference strategy. Insectes Sociaux 69(4): 355–359. https://doi.org/10.1007/s00040-022-00876-2

Schmidt CA, Shattuck SO (2014) The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. Zootaxa 3817: 1–242. https://doi.org/10.11646/zootaxa.3817.1.1

Seifert B (2003) The ant genus *Cardiocondyla* (Insecta: Hymenoptera: Formicidae) – a taxonomic revision of the *C. elegans*, *C. bulgarica*, *C. batesii*, *C. nuda*, *C. shuckardi*, *C. stambuloffii*, *C. wroughtonii*, *C. emeryi*, and *C. minutior* species groups. Annalen des Naturhistorischen Museums in Wien. B, Botanik. Zoologie 104: 203–338.

Seifert B (2013) *Hypoponera ergatandria* (Forel, 1893) – a cosmopolitan tramp species different from *H. punctatissima* (Roger, 1859) (Hymenoptera: Formicidae). Soil Organisms 85(3): 189–201.

Seifert B (2018) The ants of Central and North Europe Lutra Verlags- und Vertriebsgesellschaft, Taur, 408 pp.

Seifert B (2020) A taxonomic revision of the Palaearctic members of the subgenus *Lasius* s.str. (Hymenoptera, Formicidae). Soil Organisms 92(1): 15–86. https://doi.org/10.25674%2Fso92iss1pp15

Seifert B (2023) A revision of the Palaearctic species of the ant genus *Cardiocondyla* Emery 1869 (Hymenoptera: Formicidae). Zootaxa 5274(1): 1–64. https://doi.org/10.11646/zootaxa.5274.1.1

Seifert B, Okita I, Heinze J (2017) A taxonomic revision of the *Cardiocondyla nuda* group (Hymenoptera: Formicidae). Zootaxa 4290(2): 324–356. https://doi.org/10.11646/zootaxa.4290.2.4

Sharaf MR, Abdel-Dayem MS, Al Dhafer HM, Aldawood SA (2013) The ants (Hymenoptera: Formicidae) of Rawdhat Khorim Nature Preserve, Saudi Arabia, with description of a new species of the genus *Tetramorium* Mayr. Zootaxa 3709(6): 565–580. https://doi.org/10.11646/zootaxa.3709.6.6

Sharaf MR, Salman S, Al Dhafer HM, Akbar SA, Abdel-Dayem MS, Aldawood AS (2016) Taxonomy and distribution of the genus *Trichomyrmex* Mayr, 1865 (Hymenoptera: Formicidae) in the Arabian Peninsula, with the description of two new species. European Journal of Taxonomy 246(246): 1–36. https://doi.org/10.5852/ejt.2016.246

Taheri A, Reyes-López J (2018) Exotic ants (Hymenoptera: Formicidae) in Morocco: checklist, comments and new faunistic data. Transactions of the American Entomological Society 144(1): 99–107. https://doi.org/10.3157/061.144.0104

Trigos Peral G, Reyes-López JL (2016) Quite a cosmopolitan neighborhood: A new record of *Cardiocondyla obscurior* Wheeler, 1929 together with *Cardiocondyla mauritanica* Forel, 1890 and *Linepithema humile* (Mayr, 1868) (Hymenoptera, Formicidae). Boletin de la Asociacion Espanola de Entomologia 40(3–4): 503–506.

Tseng S-P, Darras H, Hsu P-W, Yoshimura T, Lee C-Y, Wetterer JK, Keller L, Scotty Yang C-C (2022) Genetic analysis reveals the putative native range and widespread double-clonal reproduction in the invasive longhorn crazy ant. Molecular Ecology 32(5): 1020–1033. https://doi.org/10.1111/mec.16827

Varnava AI, Roberts SPM, Michez D, Ascher JS, Petanidou T, Dimitriou S, Devalez J, Pittara M, Stavrinides MC (2020) The wild bees (Hymenoptera, Apoidea) of the island of Cyprus. ZooKeys 924: 1–114. https://doi.org/10.3897/zookeys.924.38328

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

Vonshak M, Dayan T, Ionescu-Hirsh A, Freidberg A, Hefetz A (2010) The little fire ant *Wasmannia auropunctata*: A new invasive species in the Middle East and its impact on the local arthropod fauna. Biological Invasions 12(6): 1825–1837. https://doi.org/10.1007/s10530-009-9593-2

Wagner HC, Arthofer W, Seifert B, Muster C, Steiner FM, Schlick-Steiner BC (2017) Light at the end of the tunnel: Integrative taxonomy delimits cryptic species in the *Tetramorium caespitum* complex (Hymenoptera: Formicidae). Myrmecological News 25: 95–129. https://doi.org/10.25849/myrmecol.news_025:095

Wetterer JK (2009a) Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (Hymenoptera: Formicidae). Myrmecological News 12: 23–33.
Wetterer JK (2009b) Worldwide spread of the destroyer ant, *Monomorium destructor* (Hymenoptera: Formicidae). Myrmecological News 12: 97–108.
Wetterer JK (2010a) Worldwide spread of the wooly ant, *Tetramorium lanuginosum* (Hymenoptera: Formicidae). Myrmecological News 13: 81–88.
Wetterer JK (2010b) Worldwide spread of the pharaoh ant, *Monomorium pharaonis* (Hymenoptera: Formicidae). Myrmecological News 13: 115–129.
Wetterer JK (2014a) Worldwide spread of Alluaud's little yellow ant, *Plagiolepis alluaudi* (Hymenoptera: Formicidae). Myrmecological News 19: 1–7.
Wetterer JK (2014b) Worldwide spread of the Moorish sneaking ant, *Cardiocondyla mauritanica* (Hymenoptera: Formicidae). Sociobiology 59(3): 985–997. https://doi.org/10.13102/sociobiology.v59i3.561
Wetterer JK (2020) First Baltic record of *Plagiolepis alluaudi* (Hymenoptera: Formicidae), a tropical ant found in an Estonian greenhouse. Entomologist's Monthly Magazine 2(2): 127–128. https://doi.org/10.31184/M00138908.1562.4036
Wetterer JK, Hirta-Garcia F (2015) Worldwide spread of *Tetramorium caldarium* (Hymenoptera: Formicidae). Myrmecological News 21: 93–99.
Wetterer JK, Hugel S (2014) First North American records of the Old World ant cricket *Myrmecophilus americanus* (Orthoptera, Myrmecophilidae). The Florida Entomologist 97(1): 126–129. https://doi.org/10.1653/024.097.0117
Wetterer JK, Porter SD (2003) The little fire ant, *Wasmannia auropunctata*: Distribution, impact and control. Sociobiology 44: 1–41.
Wetterer JK, Walsh PD, White LJT (1999) *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae), a highly destructive tramp ant, in wildlife refuges of Gabon, West Africa. African Entomology 7: 292–294.
Wong MKL, Economo EP, Guénard B (2023) The global spread and invasion capacities of alien ants. Current Biology 33(3): 1–6. https://doi.org/10.1016/j.cub.2022.12.020

Supplementary material 1

Georeferenced records of alien ant species in Cyprus

Authors: Jakovos Demetriou, Christos Georgiadis, Angeliki F. Martinou, Helen E. Roy, James K. Wetterer, Lech Borowiec, Evan P. Economo, Kostas A. Triantis, Sebastian Salata

Data type: csv

Link: https://doi.org/10.3897/neobiota.88.106750.suppl1

Supplementary material 2

Alien ant species in protected NATURA 2000 and RAMSAR areas

Authors: Jakovos Demetriou, Christos Georgiadis, Angeliki F. Martinou, Helen E. Roy, James K. Wetterer, Lech Borowiec, Evan P. Economo, Kostas A. Triantis, Sebastian Salata

Data type: xlsx

Link: https://doi.org/10.3897/neobiota.88.106750.suppl2

Supplementary material 3

Plates including morphological characteristics used in the identification key to distinguish alien from native worker ants inhabiting Cyprus

Authors: Jakovos Demetriou, Christos Georgiadis, Angeliki F. Martinou, Helen E. Roy, James K. Wetterer, Lech Borowiec, Evan P. Economo, Kostas A. Triantis, Sebastian Salata

Data type: zip

Link: https://doi.org/10.3897/neobiota.88.106750.suppl3

Supplementary material 4

Description of *Solenopsis* CYP139 and morphometric data for future comparisons

Authors: Jakovos Demetriou, Christos Georgiadis, Angeliki F. Martinou, Helen E. Roy, James K. Wetterer, Lech Borowiec, Evan P. Economo, Kostas A. Triantis, Sebastian Salata

Data type: pdf

Link: https://doi.org/10.3897/neobiota.88.106750.suppl4