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Schifani, Enrico
Scupola, Antonio
Alicata, Antonio

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Morphology, ecology, and biogeography of *Myrmecina sicula*
André, 1882, rediscovered after 140 years
(Hymenoptera, Formicidae)

ENRICO SCHIFANI^{1,*}, ANTONIO SCUPOLA², ANTONIO ALICATA³

¹*Department of Chemistry, Life Sciences and Environmental Sustainability (SCVSA), University of Parma, Parco Area delle Scienze 11/A, I-43124 Parma (Italy) - <http://orcid.org/0000-0003-0684-6229>*

²*Museo civico di Storia Naturale di Verona, Lungadige Porta Vittoria 9, I-37129 Verona (Italy)*

³*Department of Biological, Geological and Environmental Sciences (DBGES), University of Catania, Via Androne 81, I-95124 Catania (Italy)*

**corresponding author: enrsc8@gmail.com*

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SUMMARY

The ant genus *Myrmecina*, whose diversity is mostly concentrated in SE-Asia and Oceania, counts four W-Palaearctic species. The extremely euryecious and well-studied *Myrmecina graminicola* occurs from Iberia to the Caucasus and from the Maghreb to Scandinavia, while three little-known species (*M. atlantis*, *M. melonii* and *M. sicula*) coexist with *M. graminicola* in their narrow Maghrebian, Sardinian and Sicilian ranges, respectively. *Myrmecina sicula* has been described about 140 years ago from a single site and two specimens only. Their unique morphology suggested the validity of this taxon ever since, but no additional specimens were found in the following century. We present the results of decades of sampling efforts across Sicily, resulting in the collection of *M. graminicola* from 70 sites and *M. sicula* from 13 sites. We confirm *M. sicula* unique morphological identity and report on the marked distributional and ecological differences between the two species. *Myrmecina graminicola* is widespread and inhabits diverse, mainly forested habitats from lowland to high mountain sites, while *M. sicula* was found in a very narrow region of old carbonate platform between NW-Sicily and the Egadi Islands, mostly in sparsely vegetated sites at mid to low-altitude. Reviewing their common morphological and biogeographic traits, we propose to consider *M. atlantis*, *M. melonii* and *M. sicula* as a distinct *M. sicula* complex, whose identity and history deserves further investigation through molecular analyses.

INTRODUCTION

The genus *Myrmecina* Curtis, 1829 is part of the myrmicine ant tribe Crematogastrini Forel, 1893 (Ward et al. 2015) and belongs to the *Myrmecina* genus-group, an isolated lineage that arose about 62 Mya and includes the living genera *Acanthomyrmex* Emery, 1893, *Dilobocondyla* Santschi, 1910, *Perissomyrmex* Smith, M.R., 1947 and *Pristomyrmex* Mayr, 1947 (Blaimer et al. 2018), and the fossil genus *Thanacomymex* Chény, Wang & Perrichot, 2019 (Chény et al. 2019). The first three of these genera have only few species (Antcat 2020), and are entirely limited to Southeastern Asia or cross the Wallace line into Australasia (Antmaps 2020). On the other hand, *Myrmecina* and *Pristomyrmex* count more taxa and possess a wider geographic distribution, but most of their diversity is still concentrated in the Indomalayan and Australasian realms. *Myrmecina* is thought to be about 22-25 Mya (Blaimer et al. 2018), it is the largest genus group currently counting about 100 living species (Antcat 2020; Okido et al. 2020), and has the widest distribution range of the five, encompassing the whole Holarctic realm (Antmaps 2020). Its diversity is mostly concentrated in SE Asia (Okido et al. 2020).

Uncommonly collected, *Myrmecina* ants generally form small-sized colonies, nest in the soil or in decaying wood, and forage on the leaf litter (Satria & Yamane 2019). Their biology is usually little-known, but at least some oriental species are thought to be specialized predators of oribatid mites (Masuko 1994), while some others are host of myrmecophilous mites of the same group (Aoki et al. 1994; Ito & Takaku 1994; Ito & Aoki 2003). Queen polymorphism is a peculiar biological trait of many species of *Myrmecina*, and attracted significant attention due to its ability to enable different colony structures (Ohkawara et al. 1993; Ito 1996; Murakami et al. 2000; 2002; Buschinger & Schreiber 2002; Buschinger et al. 2003; Buschinger 2005; Miyazaki et al. 2005; Steiner et al. 2006; Satria & Yamane 2019). Moreover,

M. graminicola (Latreille, 1802) has recently attracted attention being the first ant among the very few animals known to escape from danger by actively curling itself into a ball and rolling away (Grasso et al. 2020).

In the W-Palearctic, the genus is very easily recognizable morphologically (Seifert 2018) and only four species occur according to the latest revision (Rigato 1999; Fig. 1): *M. atlantis* Santschi, 1939, *M. graminicola*, *M. melonii* Rigato, 1999 and *M. sicula* André, 1882. Of these species, *M. graminicola* is widely distributed in the region (Rigato 1999; Seifert 2018; Fig. 1). It appears morphologically somewhat similar to several other Holarctic species, such as the E-Palearctic *M. nipponica* Wheeler, W.M., 1906 and *M. sinensis* Wheeler, 1921 or even the Indomalayan *M. butteli* Forel, 1913 and the Australian *M. rugosa* Forel, 1902. To a lesser degree, it also resembles Nearctic species, such as *M. americana* Emery, 1895 or *M. harrisoni* Brown, 1967, which are not characterized by enlarged scapes. Steiner et al. (2006) offered a limited phylogeny including species close to *M. graminicola*, but the evolutive relationships within the genus are far from being understood. While the biology of *M. graminicola* was the subject of several studies (e.g. Donisthorpe 1927; Buschinger & Schreiber 2002; Buschinger et al. 2003; Buschinger 2003; 2005; Seifert 2018; Grasso et al. 2020), little to no information is available on the remaining West-Palearctic taxa. They exhibit morphological similarities (Rigato 1999) and are characterized by small distribution ranges overlapping with that of *M. graminicola*: *M. atlantis* is only known from a small area around the border between Algeria and Tunisia, while *M. melonii* and *M. sicula* are exclusively known from their type localities, respectively in S-Sardinia and NW-Sicily (Fig. 1).

The type material of *M. sicula* consists of two workers collected by Teodosio De Stefani near the Sicilian locality of Partinico (near Palermo, NW-Sicily) at an unknown time (De Stefani 1889; Rigato 1999). De Stefani,

who noted how this species was rarer than *M. graminicola* (De Stefani 1889), sent these two specimens to Ernst André, leading to its first formal description as *Myrmecina latreillei* var. *sicula* (André 1882). André sent back one of specimens to De Stefani, who donated it to Carlo Emery, and, on this basis, Emery raised the taxon described by André to species rank (Emery 1916a). Today, the two specimens are respectively stored in the Muséum National d'Histoire Naturelle (Paris, France) (Lectotypus) and the Museo Civico di Storia Naturale “Giacomo Doria” (Genoa, Italy) (Paralectotypus) (Rigato 1999). Two specimens are a very small amount to delimit intraspecific variation or to certainly exclude rare cases of developmental defects. Nonetheless, their morphology appeared so remarkably unique that the status of *M. sicula* as a *bona species* was confirmed when the W Palearctic species of the genus were reviewed, even if no additional material could be studied (Rigato 1999). In addition to the two workers, De Stefani (1889) had also offered a very brief description of a single male, later mentioned by Emery (1916b). However, this male specimen was studied exclusively by De Stefani (Emery 1916a; 1916b) and is currently considered lost (Rigato 1999). The same unfortunate fate occurred to the vast majority of De Stefani’s collection (Bruno Massa pers. comm.). The Sicilian ant fauna has been overlooked for several decades (Schifani & Alicata 2018); so that, in addition to the cryptic habits of *Myrmecina* spp., an insufficient investigation on the Sicilian ant fauna may contribute to explain the absence of any further record of *M. sicula* after its initial description. On the other hand, *M. graminicola* is currently reported from only seven localities on the island (De Stefani 1885; Emery 1916; Baroni Urbani 1964; Rigato 1999).

New extensive collecting efforts across Sicily and circum-Sicilian islands enabled us to recover several new records of *Myrmecina* spp. for the region, enabling us to depict a first detailed picture of *M. graminicola* and *M.*

sicula Sicilian distribution and ecology. At the same time, the collection of several new specimens of *M. sicula* also allowed a better understanding of its morphological identity and the variation of its diagnostic characters, so far only known on the basis of two workers.



Figure 1. Approximate distribution of *Myrmecina* species inhabiting the W-Palearctic: *Myrmecina graminicola* and the three species of the *M. sicula* complex whose distribution overlaps with the first. Data from Rigato (1999), AntMaps (2020), and this paper.

MATERIALS AND METHODS

Data were collected by the authors throughout independent researches from 1987 to 2020 and with the aid of several additional collectors. The study area includes the whole Sicily and the circumsicilian islands. Different sampling methods were employed and the following abbreviations are used to refer to them: direct sampling, pitfall traps (widely used to sample terri-colous ants – see Agosti et al. 2000, in our case filled with a non-attractive solution of water and salt and kept in place for 1 month), subterranean sampling devices (SSD, similar to pitfall traps in their functioning but aimed at a deeper soil fauna – see Mammola et al. 2016, in our case filled with chicken meat as an attractant and kept in place for 2 months), and soil sifting. The collected material was mainly stored in the authors’ personal collections and kept either under ethanol or pinned. Additional specimens were discovered at the Milan Natural History Museum. The T. De Stefani collection was also investigated at the Doderlain Zoological Museum of Palermo University and

at the Regional Natural History Museum of Terrasini.

Statistical analyses were carried out by using the software R 3.6.3 and R Studio Desktop 1.3.1073 (R Core Team 2020).

Specimens were studied under stereoscopic microscopes and photos were taken using a Canon 1300D reflex and MP-E 65mm f/2.8 1–5× Macro Photo lens. The software Helicon Focus (www.heliconsoft.com/heliconsoft-products/helicon-focus) was used to fuse images taken at different focal planes into single images with greater depth of field. Measurements were obtained with the aim of providing only a baseline morphometric description of *Myrmecina sicula* and were taken by using photos of the specimens and the software ImageJ (Schneider et al. 2012). Morphometric nomenclature follows Seifert (2018), and the following 13 characters and 2 indices were recorded (measurements are given in μm):

CL - cephalic length, measured as the maximum distance between the occipital margin of the head to the lowermost margin of the clypeus (i.e. the central clypeal dent), head in full face view; CW - cephalic width, measured as the maximum width of the head, including the eyes, head in full face view; CS: arithmetic mean between CL and CW; EL - eye length, the longest diameter of the compound eye (including unpigmented marginal ommatidia); EW - eye width, the shortest diameter of the compound eye (including unpigmented marginal ommatidia); EYE: arithmetic mean between EL and EW; ML - mesosoma length, measured as the maximum diagonal between the point where the pronotum meets the cervical shield and the posterior basal angle of the propodeal lobe, lateral profile view of the specimen; MW - mesosoma width, calculated as the maximum width of the pronotum, dorsal view of the specimen; PpH – maximum petiole height, specimen in lateral view; PpW – maximum width of the petiole,

specimen in dorsal view; PpH – maximum postpetiole height, specimen in lateral view; PpW – maximum width of the postpetiole, specimen in dorsal view; SL - scape length, measured as the maximum length of the scapus but excluding the basal constriction or neck that occurs just distal of the condylar bulb; SPST - distance between the center of the propodeal spiracle and the distalmost tip of the propodeal spine, lateral profile view of the specimen; SPWI - distance between the distalmost tips of the two propodeal spines, dorsal profile of the specimen.

Throughout the text, descriptive statistical values are given as mean \pm standard deviation and accompanied by the minimum and maximum in square brackets. Coordinates of occurrence points were recovered whenever it was possible to do so with reasonable accuracy (error radius: ≤ 15 m).

RESULTS

Distribution and ecology

A total of 844 *Myrmecina* specimens were recovered from 146 samples, 83 sites and 101 sampling dates, from 1987 to 2020, through the participation of 13 collectors. A detailed list of all collecting localities, their main ecological characteristics, collected specimens, collecting dates and methodologies, collectors' names and collections where the material is kept is available as a supplementary material to this article. About 35% of the samples were taken from pitfall traps, 29% from soil sifting, 20% by direct sampling and 16% by the use of MSS traps. *Myrmecina graminicola* was collected 129 times, for a total of 70 sites, 795 workers and 5 queens, while *M. sicula* was collected 17 times, for a total of 13 sites and 44 workers.

Myrmecina graminicola sites (N=63) are widespread through Sicily from the coast to the interior (distance from the sea in km: 15 ± 12 [2, 44]), while those of *Myrmecina sicula* (N=12) are concentrated in an area of approximately 200 km² and significantly closer

to the coast (distance from the sea in km: 4 ± 3 [0, 9]; $t_{73} = 3.42$, $p = 0.001$) (Fig. 2, 3). Altitudinal ranges of the two species in Sicily are also clearly different according to our sampling data (in meters a.s.l.: *M. graminicola* = 657 ± 350 [70, 1575], *M. sicula* = 323 ± 209 [15, 660]; $t_{73} = 3.28$, $p = 0.001$, see Fig. 3) and so are the habitat in which the two were more often collected (Fig. 4).

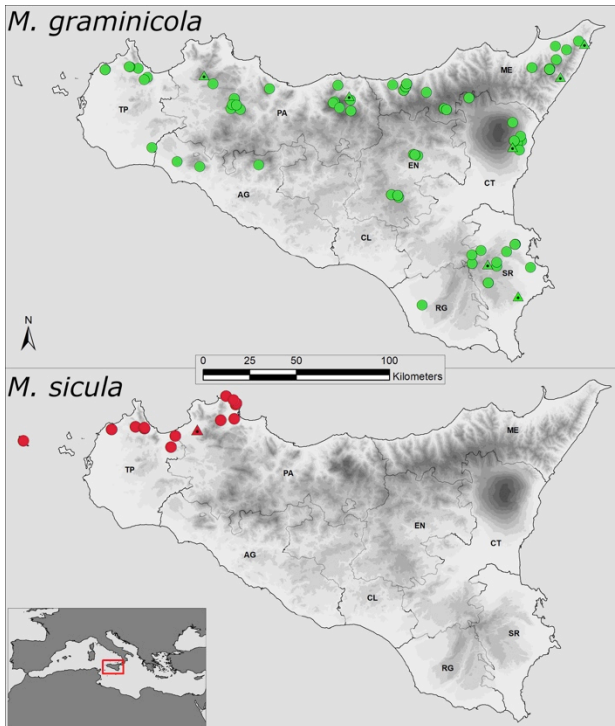


Figure 2. Distribution data of *M. graminicola* and *M. sicula* in the study area. Dots represent new occurrence points, while triangles represent literature data. Administrative provinces are indicated by their abbreviations. The inset shows the position of the study area in the Mediterranean basin.

Morphology

Morphology of *M. sicula* specimens that we examined showed the main characters observable in the type specimens (Fig. 5; Rigato 1999): the smooth mesosomal dorsum of and the characteristic shape of its scapi as

defined in Rigato (1999) are confirmed as steady, consistent characters in all examined specimens.

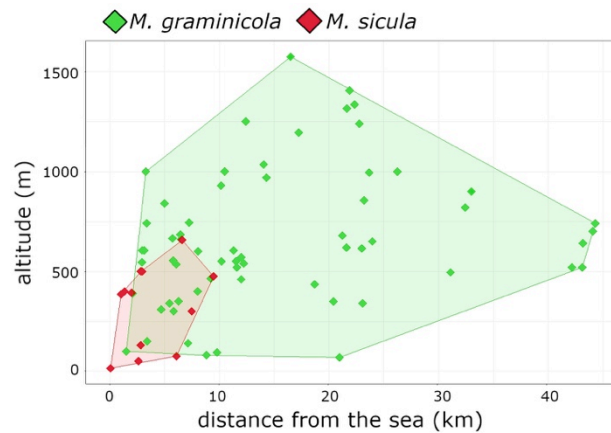


Figure 3. Altitudinal distribution and distance from the sea of our collecting sites of *Myrmecina graminicola* and *Myrmecina sicula*.

Morphometric values of *M. sicula* are the following (6 workers from 4 sites): CL = 694 ± 14 [677, 709]; CW = 664 ± 14 [650, 690]; CS = 679 ± 11 [669, 697]; EL: 78 ± 5 [74, 86]; EW = 67 ± 9 [60, 85]; EYE = 73 ± 6 [69, 84]; ML = 857 ± 34 [816, 899]; MW = 439 ± 13 [424, 462]; PeH = 213 ± 6 [203, 219]; PeW = 191 ± 9 [178, 202]; PpH = 232 ± 11 [214, 245]; PpW = 234 ± 12 [216, 248]; SL = 583 ± 15 [565, 606]; SPWI = 179 ± 22 [139, 204]; SPST = 185 ± 10 [175, 203]; CL/CW = 1.04 ± 0.02 [1.02, 1.07]; EYE/CS = 0.11 ± 0.01 [0.10, 0.12]; ML/CS = 1.26 ± 0.03 [0.21, 0.31]; MW/CS = 0.65 ± 0.02 [0.62, 0.68]; PeH/CS = 0.31 ± 0.01 [0.30, 0.33]; PeW/CS = 0.28 ± 0.01 [0.26, 0.29]; PpH/CS = 0.34 ± 0.01 [0.26, 0.29]; PpW/CS = 0.34 ± 0.02 [0.32, 0.37]; SL/CS = 0.57 ± 0.01 [0.55, 0.58]; SPWI/CS = 0.26 ± 0.03 [0.20, 0.30]; SPST/CS = 0.27 ± 0.02 [0.26, 0.30].

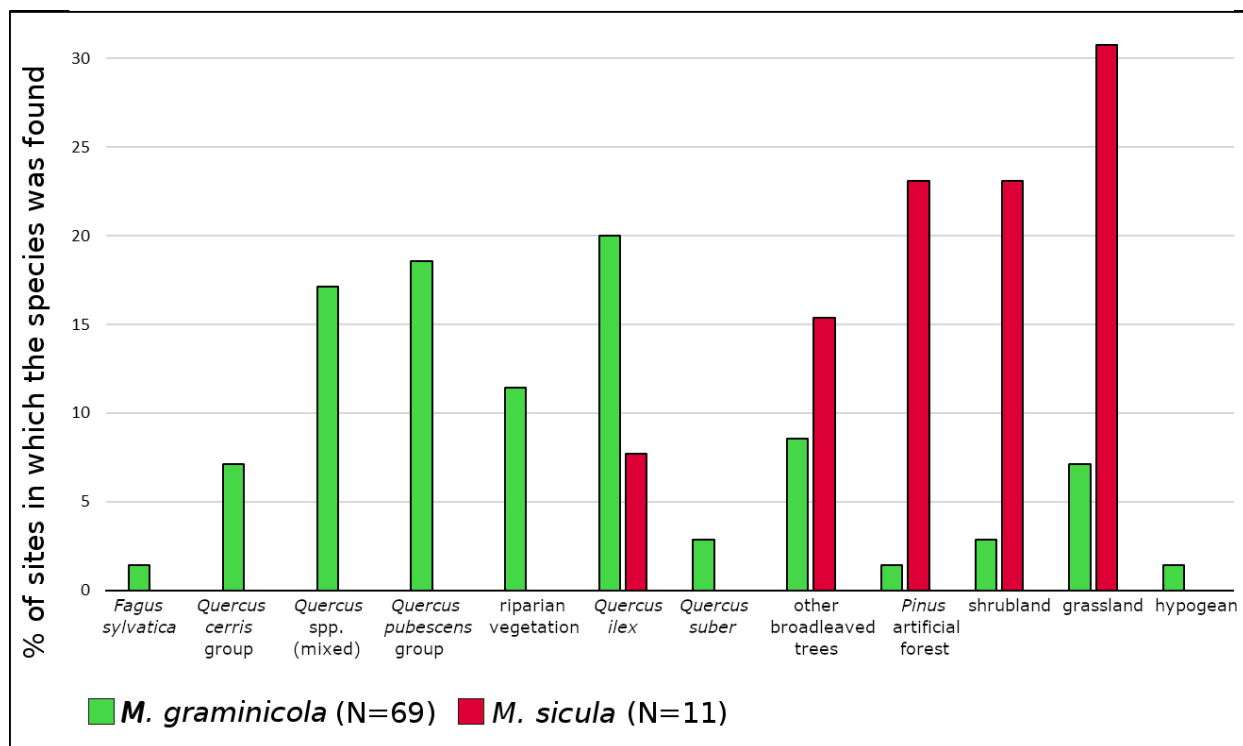


Figure 4. Ecological characteristics of our collecting sites of *Myrmecina graminicola* and *Myrmecina sicula*.

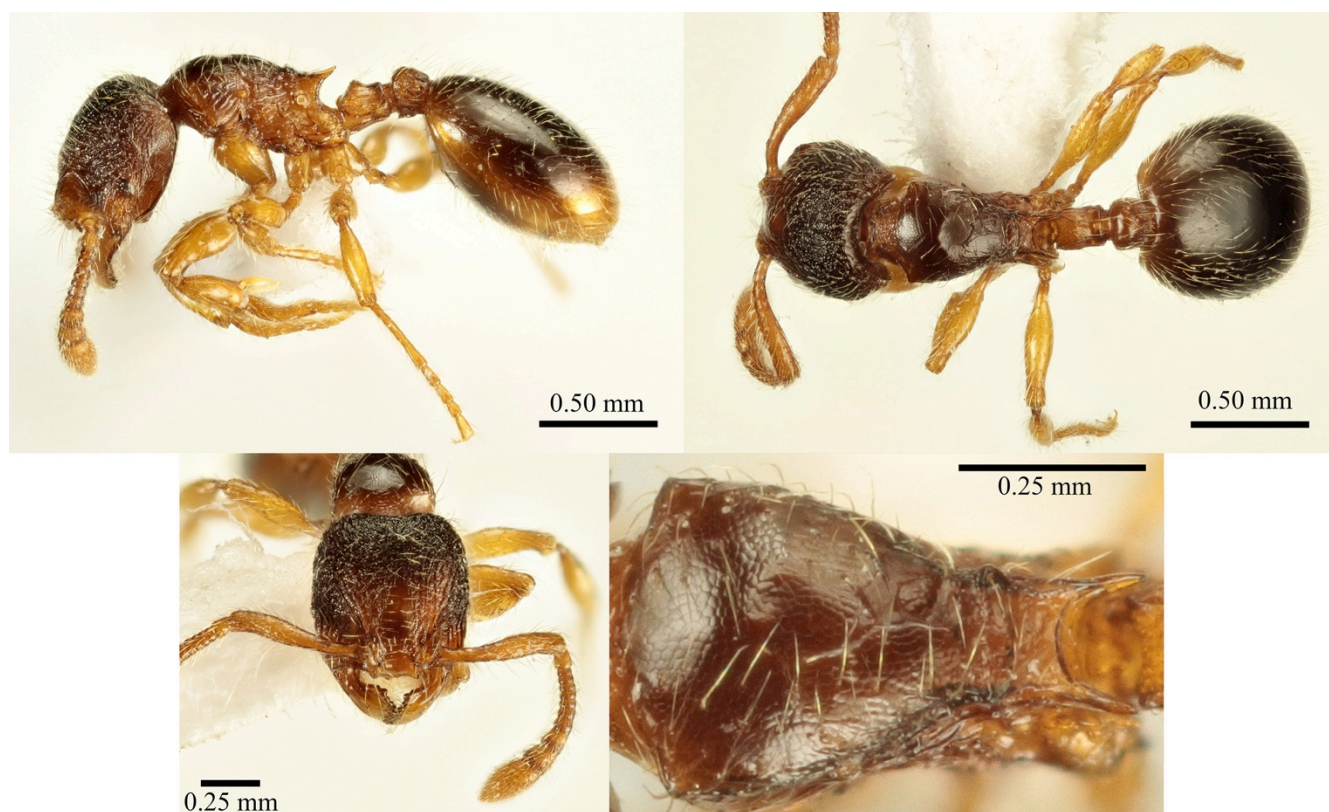


Figure 5. *Myrmecina sicula* worker from Monte Pellegrino (PA). Above: lateral view (left) and dorsal view (right). Below: head view (left), detail of the smooth dorsal mesosomal surface (right).

DISCUSSION

We are reasonably sure that the occurrence data we present are at least close to represent the entirety of all unpublished *Myrmecina* records from Sicily, and our extensive survey appears to be considerable as a good coverage of the genus distribution on the island. On the other hand, the recovery of an abundant number of *M. sicula* workers allowed a more precise morphological characterization of this species, which substantially confirmed all the previously known morphological characteristics as reliable traits. Males and queens, however, are still to be found and properly described, and our attempts to search again for the missing male described by De Stefani proved unsuccessful.

Even at sites in which it was repeatedly found, *M. sicula* is confirmed to be a relatively difficult species to find. Its colonies seem to be very small, and workers probably seldom (or only nocturnally) exhibiting strictly epigeal foraging: they were collected in low numbers within soil crevices, between grass roots, under stones, under moss or within the leaf litter. In addition, these ants seem to disappear underground during a long portion of the year, namely during the dry periods of spring, summer and autumn. Underground aestivation is typical of many species that inhabit the same areas (e.g. *Aphaenogaster pallida* (Nylander, 1849), *A. sicula* Emery, 1908, *Solenopsis latrosicula* Emery, 1915) and is also reported for *M. melonii* (Rigato 1999). Such biological traits partly explain the previous lack of records (Espadaler & López-Soria 1991). *Myrmecina sicula* differs markedly from *M. graminicola* in its ecological preferences: it occupies exclusively low to mid-altitude and often sparsely vegetated sites close to the coast, while *M. graminicola* was mostly found within the leaf litter of shady oak forests or sometimes wet meadows, covering about the entire Sicilian territory in terms of both altitudinal range and spatial distribution, and inhabiting very diverse geological contexts. On the other hand, the

distribution range of *M. sicula* is remarkably small: all collecting sites are concentrated in a small North-Western portion of Sicily and in the nearby Egadi Archipelago, forming a geologically relatively uniform area characterized by old carbonate formations (Basilone 2012). Such short-range condition is unfrequently witnessed in Mediterranean ants, and may represent an element of fragility to be taken into account for conservation (e.g. Talavera et al. 2015). As the reproductive and dispersal strategies of *M. sicula* remain unknown at this time, it is possible to speculate that these may have contributed to confine this taxon to such a small area: low dispersal range and dependent colony foundation are associated traits in *M. nipponica* (Cronin et al. 2020).

From a biogeographical perspective, North-Western Sicily is an area of significant interest: it hosts an early-Pleistocene fossil assemblage testifying an old admixture of African and European influences (Masini & Sarà 1998), and it is a well-recognized geobotanic district hosting a high number of endemics (Brullo et al. 1995; 2012; 2013; Raimondo & Domina 2006; Ilardi et al. 2014). This area also hosts a significant number of endemic invertebrates. Among them, one of the most interesting cases is represented by the distribution of the gastropod genus *Erctella* of pre-Messinian origin (Colomba et al. 2011), while among arthropods some examples are provided by *Acinipe galvagnii* Cusimano & Massa 1977 (Orthoptera, Pamphagidae) and *Pseudoapterogyna* spp. (Coleoptera, Melolonthidae) with Maghrebian relatives and by a *Temnothorax* ant species under description (Sparacio 2014; Massa & Fontana 2020; authors' unpublished data). In Sicily, the ant *Aphaenogaster sardoa* Mayr, 1853, elsewhere present in the Maghreb and in Sardinia, is exclusive to this area (Baroni Urbani 1971; authors' unpublished data). Finally, regarding the presence of *M. sicula* in the island of Marettimo, it is worth mentioning that unlike the other islands of the Egadi archipelago, no land connection between Marettimo and Sicily

occurred during the Last Glacial Maximum (Lo Presti et al. 2019).

However, to evaluate the biogeography of *M. sicula* at a broader geographic scale, it appears necessary to take into account the distribution of *M. atlantis* and *M. melonii*. Due to their strong biogeographical and morphological similarities, the three taxa most likely represent a monophyletic lineage well-separate from the other Palearctic *Myrmecina*. In light of the following evidence, we propose to provisionally name this putative lineage as the *M. sicula* species complex, coherently with the widely established practice of using species groups or complexes in ants to define morphologically and biogeographically consistent groups whenever exhaustive phylogenetic data are not yet available:

- As stated by Rigato (1999), these three species are morphologically closely related: in particular, the shape of the scapi in *M. atlantis*, *M. melonii* and *M. sicula* is similar and immediately recognizable as strongly different from *M. graminicola* (Fig. 6). Brownish pigmentation, reduced number of dorsal striae and slender head shape also appear as shared characters (Fig. 6).

- The distribution ranges of *M. atlantis*, *M. melonii* and *M. sicula* are similarly narrow and geographically very close to each other, occupying a relatively small area made of coastal land regions at the center of the Mediterranean basin (Fig. 1). The sea is the only element that makes them strictly allopatric taxa, while they are all sympatric with *M. graminicola* and geographically extremely isolated from any other *Myrmecina* species: the closest Palearctic species are found in China, India or far Eastern Russia. In turn, *M. graminicola* spreads at least from Iberia to the Caucasus and from the Maghreb to Scandinavia without any notable intraspecific variation (Seifert 2018; Fig. 1; for a detailed database of existing distribution records across its range see AntMaps – Janicki et al. 2016; Guénard et al. 2017).

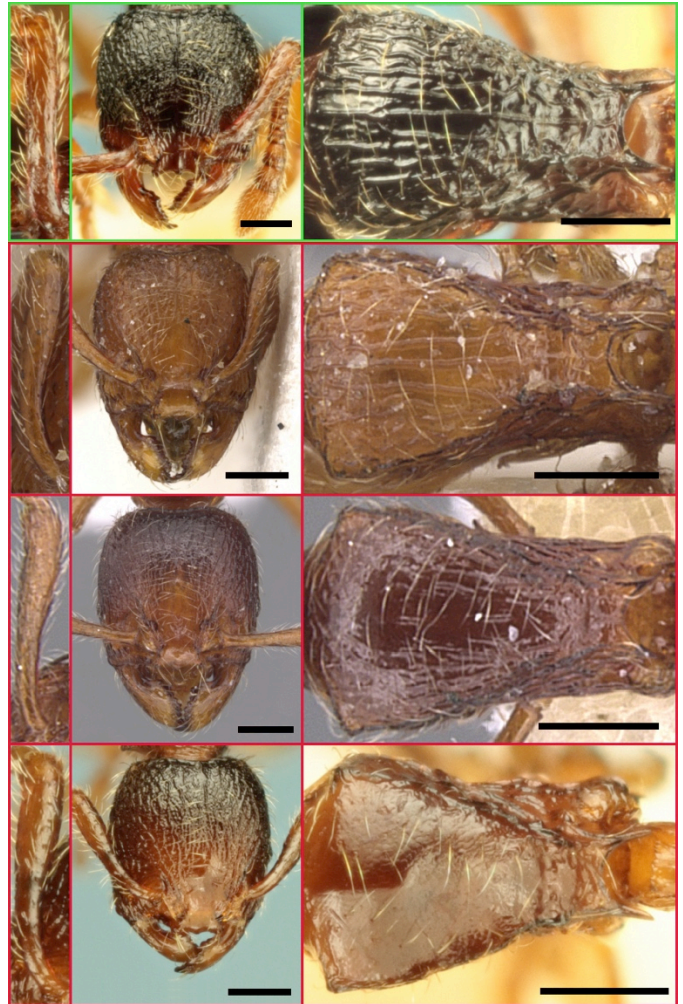


Figure 6. From left to right, scapus, head and dorsal mesosoma view of the W-Palearctic *Myrmecina* species. From above: *M. graminicola* (Sicily, Bosco della Ficuzza, ESPI); *M. atlantis* (Algeria, syntypus - AntWeb CASENT0913027, photo by Will Ericson); *M. melonii* (Sardinia, holotypus – AntWeb CASENT0904563, photo by Will Ericson); *M. sicula* (Sicily, Monte Petroso, ESPI). Scale bars: 0.25 mm.

Typical allopatric speciation time in ants is estimated to be 2-5 Mya (Schär et al. 2018). The existing molecular evidence on other organisms shows that distributions spreading across the Eastern Maghreb, Sardinia and Sicily may be a product of very different colonization processes occurred in remarkably different geological moments (e.g. < 25 Mya in *Tudorella* spp. gastropods according to Pfeiffer et al. 2010; < 0.6 Mya in *Chalcides* spp. skinks according to Stöck et al. 2016), thus offering no

univocal suggestion to interpret the *M. sicula* complex case. While only *A. sardoa* and *M. melonii* are elements of similarity between the ant faunas of Sicily and Sardinia, Siculo-Maghrebian elements are numerous (Alicata & Schifani 2019). Considering the complexity of the biogeography of the area, once available, molecular data will be of great help to understand its history, which may prove to be an important step to understand the timing and pattern of *Myrmecina* dispersion from SE-Asia into the W-Palaearctic.

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