



## RESEARCH ARTICLE - ANTS

## Morphology and Phenology of Sexualls and New Distribution Data on the Blind Mediterranean Ant *Hypoponera abeillei* (Hymenoptera, Formicidae)

ENRICO SCHIFANI<sup>1</sup>, ANTONIO SCUPOLA<sup>2</sup>, MATTIA MENCHETTI<sup>3</sup>, ERIKA BAZZATO<sup>4</sup>, XAVIER ESPADALER<sup>5</sup>

1 - Department of Chemistry, Life Sciences & Environmental Sustainability, University of Parma, Parma, Italy

2 - Museo civico di Storia Naturale di Verona, Verona, Italy

3 - Institut de Biologia Evolutiva (CSIC-UPF), Barcelona, Spain

4 - Department of Life and Environmental Sciences, University of Cagliari, Cagliari, Italy

5 - CREAF, Universitat Autònoma de Barcelona, Barcelona, Spain

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#### Corresponding author

Enrico Schifani

Department of Chemistry, Life Sciences & Environmental Sustainability, University of Parma, Parco Area delle Scienze 11/a, 43124 Parma, Italy.

E-Mail: enrico.schifani@unipr.it

### Abstract

*Hypoponera abeillei* is the sole member of the otherwise exclusively Afrotropical *abeillei* group to occur in the West-Palaearctic. Since its description about 140 years ago, it has remained little-known. Workers of this species are thought to entirely lack eyes. On the other hand, the male caste was described from 4 Tunisian specimens in 1921, and queens remain undescribed. We present an updated description of the male caste based on 62 specimens and a description of the queen caste. The *H. abeillei* material we examined comes from Italy, Spain, and Malta and comprises 11 new distribution records, including the first findings in the islands of Mallorca, Malta, and Sardinia. We provide a first phenological overview of the species' nuptial flights. Our data show that *H. abeillei* sexualls fly during the summer, mostly in August. We demonstrate that they can easily be distinguished from all the other *Hypoponera* species inhabiting the Mediterranean region based on their morphology. The remarkable diversity of Mediterranean *Hypoponera* males and queens suggest that sexualls may have a role in future attempts to understand relationships within this genus. Yet, the number of species in which sexual castes are documented is still extremely reduced.

### Introduction

The ponerine ant genus *Hypoponera* Santschi, 1938, counts over 150 valid species spread across all continents (Bolton, 2021). The diversity of ants from the subfamily Ponerinae (47 genera and over 1,250 species, Bolton, 2021) is mostly concentrated in the tropics. The Mediterranean region counts five genera and ten species only. Half belong to *Hypoponera* and the rest to the genera *Anochetus* Mayr, 1861, *Cryptopone* Emery, 1893, *Emeryopone* Forel, 1912 and *Ponera* Latreille, 1804 (Borowiec, 2014). The following *Hypoponera* species are known in the Mediterranean basin:

i) *H. abeillei* (André, 1881), considered to be the sole member of the *abeillei* group living outside the Afrotropics (Bolton & Fisher, 2011); ii) *H. eduardi* (Forel, 1894), *H. ergatandria* (Forel, 1893), *H. punctatissima* (Roger, 1859), and *H. ragusai* (Emery, 1894), all belonging to the cosmopolitan *punctatissima* group (Bolton & Fisher, 2011). At least *H. ergatandria* and *H. punctatissima* are introduced species in the Mediterranean region, while the status of *H. eduardi* is still disputed (Bolton & Fisher, 2011; Seifert, 2013; Schifani, 2019). Moreover, Bolton & Fisher (2011) suggested that *H. abeillei* may be a species of Afrotropical origins hitherto not detected south of the Sahara Desert.



Identification of *Hypoconera* species in the West-Palaearctic was historically often inaccurate (Bolton & Fisher, 2011). However, *H. abeillei*, which is also the type species of its genus, belongs to a different species-group compared to all other Mediterranean congeneric species. The recognition of its workers is considered easy due to many unique characters (e.g., lack of eyes; Bolton & Fisher, 2011). While ecological, biological, or morphological data on this species are still very scarce, the worker caste's lack of eyes is a rare functional trait suggesting an even more cryptic endogean specialization than sympatric congeners (also see Ortuño et al., 2014).

*Hypoconera abeillei* was originally described based on two workers collected near Ajaccio, Corsica (France) (André, 1881). It was then recorded from Israel (Vonshak & Ionescu-Hirsch, 2009), Italy (Mantero, 1908; Baroni Urbani, 1962; Mei, 1995), Oman (Sharaf et al., 2018), Portugal (Boieiro et al., 2002; 2009), Saudi Arabia (Collingwood, 1985), Spain (Espadaler & López-Soria, 1991; Espadaler, 1997; Espadaler & Colón, 2011; Espadaler et al., 2013; Albert & Arcos, 2015; García et al., 2020), and Tunisia (Santschi, 1910; 1921). Since Bolton & Fisher (2011) only studied the two type specimens from Corsica in their revision, the credibility of this alleged distribution is uncertain. At least some records have been discovered to be based on misidentifications of other species: *H. camerunensis* (Santschi, 1914) in the Afrotropics, *H. gibbinota* (Forel, 1912) in the United Kingdom (Bolton & Fisher, 2011). Interestingly, according to existing distribution data, the western Mediterranean populations appear disjunct from those of the Arabian Peninsula and Israel. The only photograph of a specimen from this eastern distribution range was published by Sharaf et al. (2018) and referred to an Omani worker. Some of its morphological characteristics appear discordant with the *typus*: it possesses eyes. Its head is characterized by a long median impression on the dorsum (reaching the midlength of the vertex, similar to *H. ergatandria*, *H. punctatissima*, or *H. ragusai*). It is also notable that the description of Saudi specimens offered by Collingwood (1985) suggests a morphology relatively similar to the species from the *punctatissima* group and does not mention the absence of eyes. Considering these elements, it may be possible that what has been considered *H. abeillei* in the eastern Mediterranean and Arabian Peninsula belongs to a different species.

However, while the morphological identity of *H. abeillei* workers has been re-assessed by Bolton & Fisher (2011), the reproductive castes have remained little known so far. Santschi (1921) described the male caste from four Tunisian specimens. However, according to Bolton & Fisher (2011), they were unassociated with the other castes, making their identity as *H. abeillei* doubtful. The queen caste has never been described, and information on flight phenology has never been published.

We fill these gaps by offering a new male description and a first queen description alongside a phenological overview of

the sexual castes of *H. abeillei* and new distribution data. This work is possible thanks to the combined efforts of the authors, which independently collected males, queens, and workers of *H. abeillei* during the last 25 years. Our work focused on the W-Mediterranean populations without reviewing the status of the disjunct E-Mediterranean and Arabian populations.

## Materials and Methods

We examined the following *H. abeillei* specimens: 62 males, 15 queens, and four workers. They were collected between 1987 and 2020 in Italy, Malta, and Spain and are kept in the authors' collections (see supplementary material, Fig 1). We recorded 12 morphometric characters for our queen and male specimens. Their acronyms, as well as most character definitions, follow Seifert (2018), while the petiole length definition follows Bolton & Fisher (2011) (also see Fig 2). All measurements are presented in  $\mu\text{m}$ . The list and description of morphometric characters are provided below.

CL: cephalic length, measured as the maximum distance between the posterior margin of the head to the anterior margin of the clypeus. Head in full-face view.

CW: cephalic width, measured as the maximum width of the head, right above the eyes. Head in full-face view.

PoOC: post-ocular distance, measured as the distance between the occipital margin of the head and the central point of the imaginary horizontal line of the CW measurement. Head in full-face view.

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).

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.

MH: mesosoma height, longest section line directed perpendicular to the straight dorsal profile line of the mesosoma from the lowest part of the mesopleuron.

ML: mesosoma length, measured as the maximum diagonal line 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.

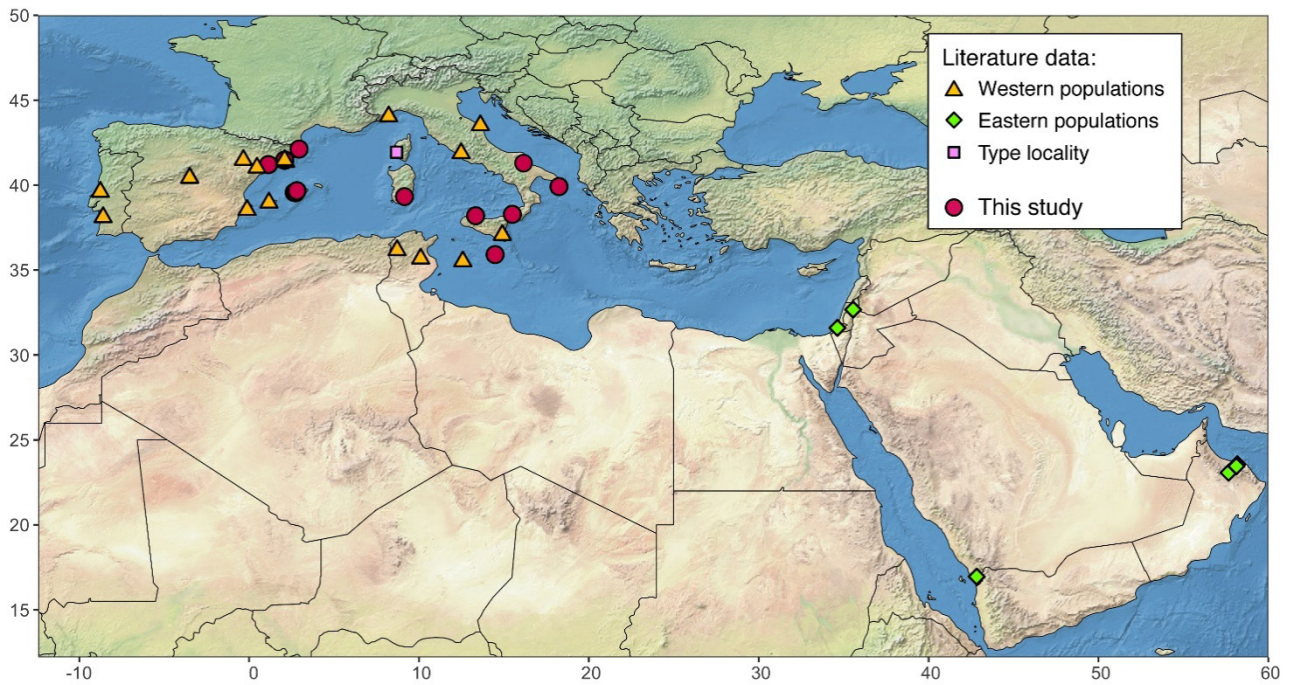
MW: mesosoma width, calculated as the maximum width of the pronotum. Dorsal view of the specimen.

PeH: petiole height, maximum height of the petiole, measured in lateral view.

PeL: petiole length, the maximum length of the petiole node, measured in a straight horizontal line from immediately above the dorsal base of the anterior petiolar tubercle to the posterior margin.

PeW: petiolar width, the maximum width of the petiole, measured in dorsal view.

CS: Cephalic size, calculated as the arithmetic mean between CL and CW.



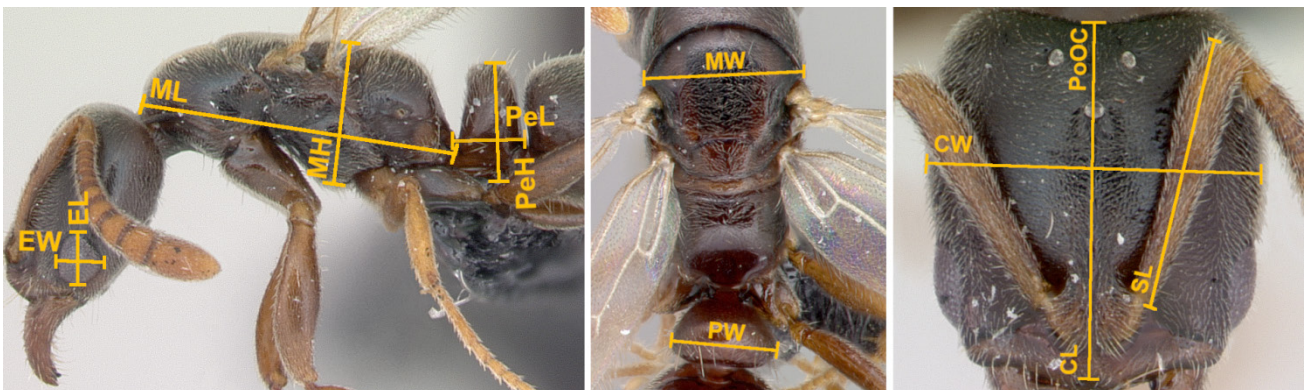
**Fig 1.** Distribution of *Hypoponera abeillei*.

We took measurements using micrometers and stereomicroscopes (Leica Wild M3B and Nikon SMZ 6) with up to 60x magnification (X. Espadaler, A. Scupola). We took pictures with a Carl Zeiss Stemi 2000-C stereomicroscope at magnification 2.25x equipped with a CMEX PRO-5 DC.5000p digital camera and ImageFocus 4 software (M. Menchetti) and at 5x magnification using Canon MP-E 65mm f/2.8 1–5x macro lens analyzed with the software ImageJ (Schneider et al., 2012) (E. Schifani). In addition, we took measurements on three queens and five males of *H. eduardi* and seven queens of *H. punctatissima* for comparison (see supplementary material). In some cases, measurements were made directly on AntWeb pictures (antweb.org) using ImageJ. Relevant taxonomic descriptions of the Mediterranean *Hypoponera* were consulted (Roger, 1859; Forel, 1874; Emery, 1895; Santschi, 1907; 1908; Bolton & Fisher, 2011; Seifert,

2013; 2018). Graphs were obtained using software R and R Studio and the package ggplot2 (R Core Team, 2021; Rstudio Team, 2021; Wickham, 2016).

## Results

**Specimen identification.** Like Santschi (1921), we did not find males or queens associated with workers of the same colony, yet identify the studied male and queen specimens as *H. abeillei* for the following reasons: *i*) a very strong similarity between the queen specimens and *H. abeillei* workers, paired with equally strong dissimilarity from any other Mediterranean *Hypoponera* (see below); *ii*) males were found associated with these queens multiple times; *iii*) areas where males and queens were collected were extensively searched, but rarely were *H. abeillei* workers found, in one case within



**Fig 2.** Morphometric measurements taken on *Hypoponera* queens and males in this study. AntWeb photographs of *H. punctatissima* queens (CASENT0173128 and CASENT0087461, by April Nobile and Erin Prado respectively).

few km from the sites where sexuals were found (Fig 3). In particular, at least two morphological characters strongly link queens we determined as *H. abeillei* to the worker caste. First, the absence of a well-marked longitudinal line at the center of the head connects the frons to the median ocellus in queens of those Mediterranean species whose workers have the same line reaching the posterior margin of the head (*H. ergatandria*, *H. punctatissima*, *H. ragusai*). It is shorter but still well-visible in both queens and workers of *H. eduardi*, and workers of *H. abeillei* are the only ones that lack it. Second, a comparatively more elongated head with subparallel

lateral margins converging frontad: the heads of queens and workers of *H. eduardi*, *H. ergatandria*, *H. punctatissima*, and *H. ragusai* are wider near eye level, and their lateral margins are strongly convex in most cases. In contrast, in workers of *H. abeillei*, these margins are almost entirely parallel. In addition to these similarities between queens of *H. abeillei* and *H. abeillei* type and non-type worker specimens, we provide detailed descriptions of other remarkable differences separating these queens and the associated males from the other Mediterranean *Hypoponera* species, further reinforcing our identification hypothesis.



**Fig 3.** *Hypoponera abeillei* worker from Catalonia (Spain). Scale bars: 0.5 mm (left) and 1 mm (right).

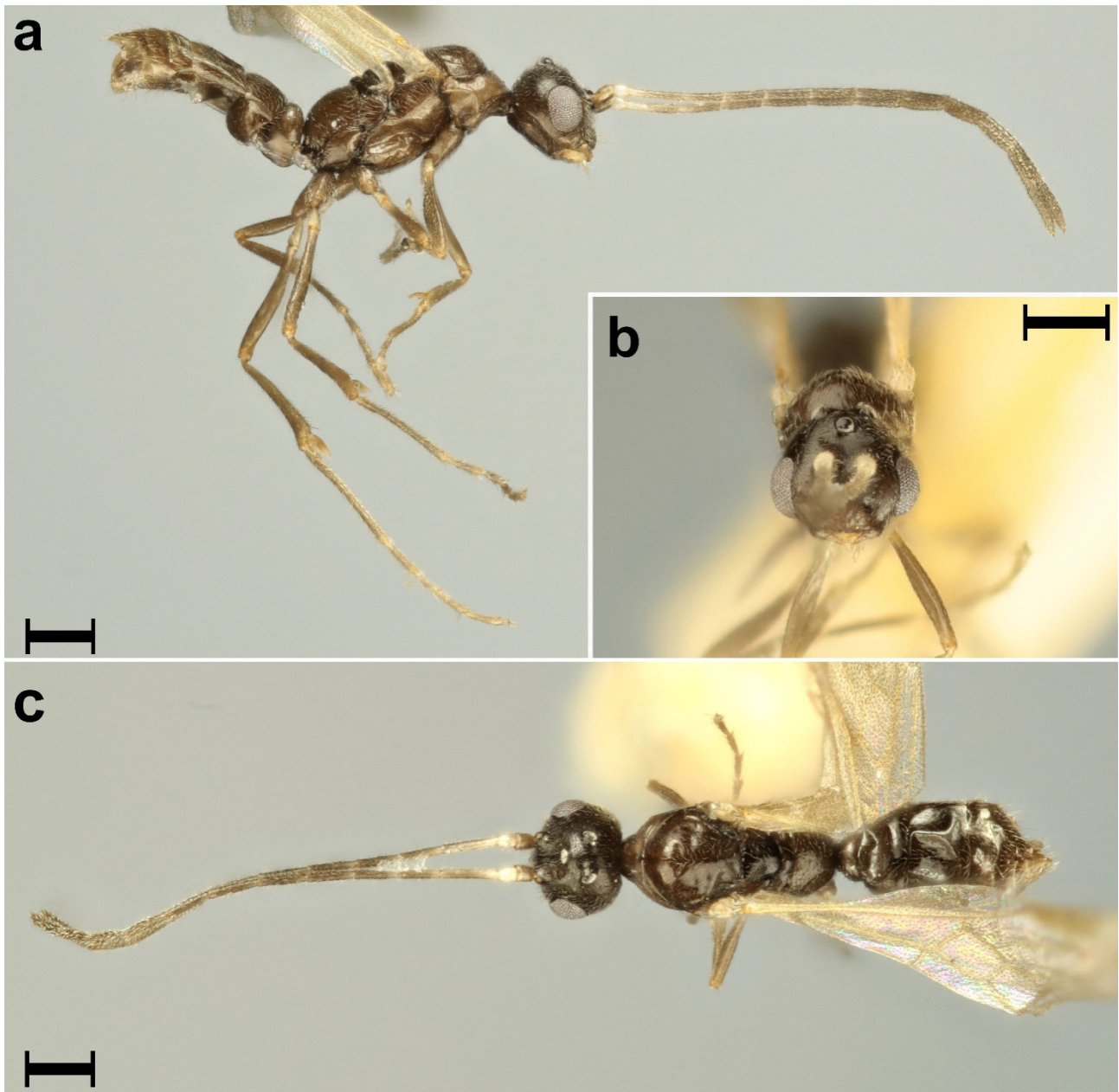
### *Hypoponera abeillei* (André)

*Ponera abeillei* André, 1881: 61 and xlviii. Syntype workers, France: Corsica, nr Ajaccio (Abeille de Perrin) (MNHN). [Male description: Santschi, 1921b: 167. Combination in *Ponera* (*Hypoponera*): Santschi, 1938: 79; in *Hypoponera*: Taylor, 1967: 12.]

**Male redescription.** The morphology of all examined *H. abeillei* males (Fig 4) was found to be coherent with the earlier description by Santschi (1921) and also fully congruent with the diagnostic characters of males from the genus *Hypoponera* defined by Bolton & Fisher (2011). Raw morphometric data are available in the supplementary material, while a synthesis is offered in Table 1. A formal description follows.

**Table 1.** Morphometric data on males of *Hypoponera abeillei*. All characters are reported in  $\mu\text{m}$  as mean  $\pm$  standard deviation (minimum, maximum); n = 9 for all characters except for PW (n = 8).

Morphometric characters		Indexes	
CL	384 $\pm$ 26 (343–416)	CS	373 $\pm$ 19 (341–400)
CW	358 $\pm$ 16 (336–384)	CW/CL	0.94 $\pm$ 0.05 (0.84–1.01)
PoOC	132 $\pm$ 6 (124–144)	PoOC/CS	0.36 $\pm$ 0.01 (0.34–0.37)
EL	183 $\pm$ 14 (169–208)	EL/CS	0.49 $\pm$ 0.02 (0.42–0.47)
EW	132 $\pm$ 11 (112–144)	EW/CS	0.36 $\pm$ 0.03 (0.28–0.39)
SL	91 $\pm$ 10 (80–106)	SL/CS	0.24 $\pm$ 0.03 (0.21–0.29)
MH	439 $\pm$ 40 (375–488)	MH/CS	1.18 $\pm$ 0.07 (1.04–1.27)
ML	862 $\pm$ 52 (796–944)	ML/CS	2.32 $\pm$ 0.07 (2.21–2.38)
MW	347 $\pm$ 38 (308–416)	MW/CS	0.93 $\pm$ 0.08 (0.83–1.05)
PeH	240 $\pm$ 13 (208–249)	PeH/CS	0.64 $\pm$ 0.05 (0.56–0.72)
PeL	165 $\pm$ 12 (143–179)	PeL/CS	0.44 $\pm$ 0.02 (0.42–0.47)
PeW	178 $\pm$ 11 (162–192)	PeW/CS	0.48 $\pm$ 0.02 (0.44–0.51)



**Fig 4.** *Hypoponera abeillei* male from Sicily (Italy). Scale bars: 0.5 mm (images a and c, lateral and dorsal view) and 0.25 mm (b, head view).

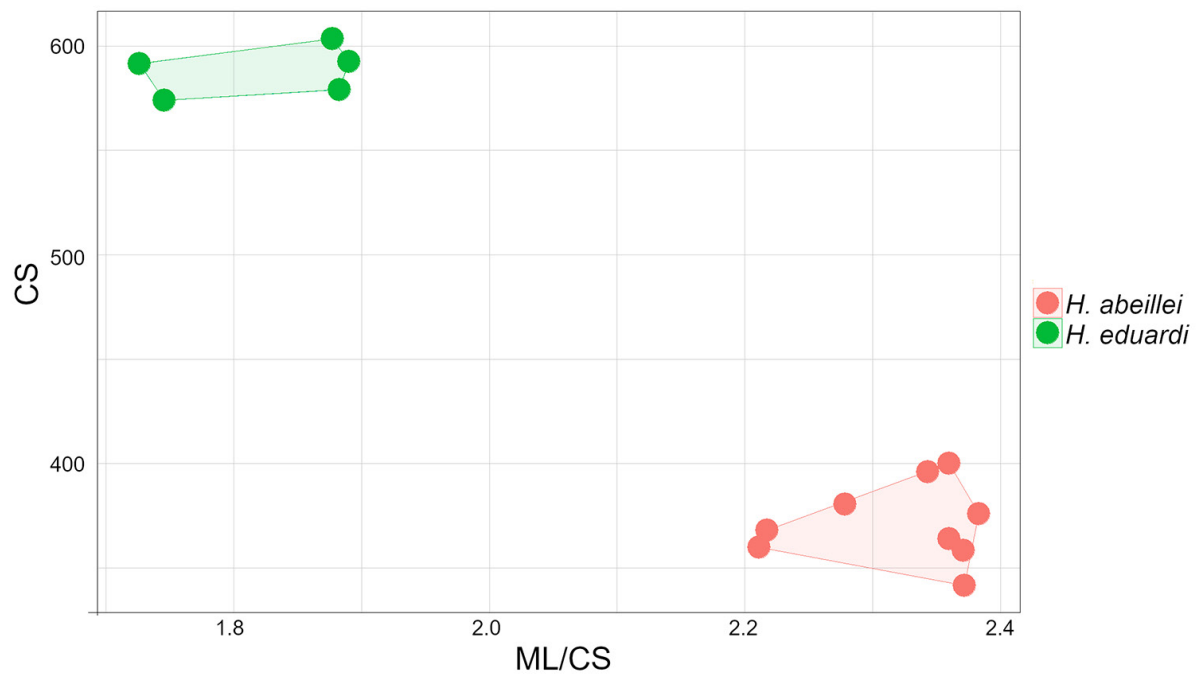
Head in dorsal view approximately as long as wide, with large ovoidal compound eyes and three well-developed ocelli. Minute setae project from between ommatidia. Mandibles only have apical teeth and do not meet at full closure. Lateral margins of head anterior to eyes strongly converging before reaching clypeus, and posterior to eyes strongly converging towards two lateral ocelli. Very long, filiform antennae of 13 segments, second funicular antennomere longer than either first and third and also longer than scape. Palp formula 1, 2. The posterior margin of the head (between lateral ocelli) was sub-horizontal. Mesosoma relatively long, its angles gently rounded, propodeum with conspicuous dorsal margin in profile view, mesonotum not overhanging pronotum, mesoscutellum convex. Notauli and epimeral sclerite absent.

Petiole dorsally rounded, ventrally unspecialized, subpetiolar process without dents or sharp angles. Helcium very low on anterior face of the first gastral segment, prora small, cinctus present, tergite of pygidium without median downcurved spine, pygostyles present. Mesotibia and metatibia each with single spur, metatibial spur pectinate, pretarsal claws simple. Jugal lobe absent from hindwing and wing venation as in queen. Whole body dark to light brown. Appendages grayish, but antennomere II, and generally part of antennomeres I and III whitish. Body sculpturing inconspicuous, overall appearance very shiny and dull, pilosity relatively sparse.

Comments. Diagnosis of *H. abeillei* males among the Mediterranean *Hypoponera* is possible by many easily observable characters. It appears safe to assume that the

non-ergatoid male of *H. ergatandria* must be very similar to that of *H. punctatissima* or at least to other species of the *punctatissima* group (REF). The cephalic size, as well as the ratio between the length of the mesosoma and the cephalic size, show huge differences between *H. abeillei* males and males of *H. eduardi* available for measurement, with no overlap (as mean  $\pm$  sd, CS:  $373 \pm 19$  in *H. abeillei* and  $588 \pm 12$  in *H. eduardi*; ML/CS:  $2.32 \pm 0.07$  in *H. abeillei*,  $1.82 \pm 0.08$  in *H. eduardi*, see Fig 5). These differences in size and body proportions are expected between the males of *H. punctatissima* and *H. ragusai* according to their descriptions. Additionally, the sculpturing of *H. abeillei* males is particularly inconspicuous, being smoother and shinier than

that of sympatric congenetics, while its pilosity is sparser. Antennomeres I & II are notably much thicker than the others (in particular, the pedicel has a globular shape), which are elongate. The males of other species have shorter antennal segments, with the scape and pedicel approximately as thick as the following antennomeres. The antennae are remarkably long in *H. abeillei* males compared to those of any other ant male of the region, which is approximately 2.2–2.3 times longer than the mesosoma. In a profile view, the propodeum of *H. abeillei* males presents a well-developed horizontal margin, which is more declivous in the other species. Concerning pigmentation, the whole body and appendages are blackish-brown, but the whitish appearance of some antennal segments is a unique trait.



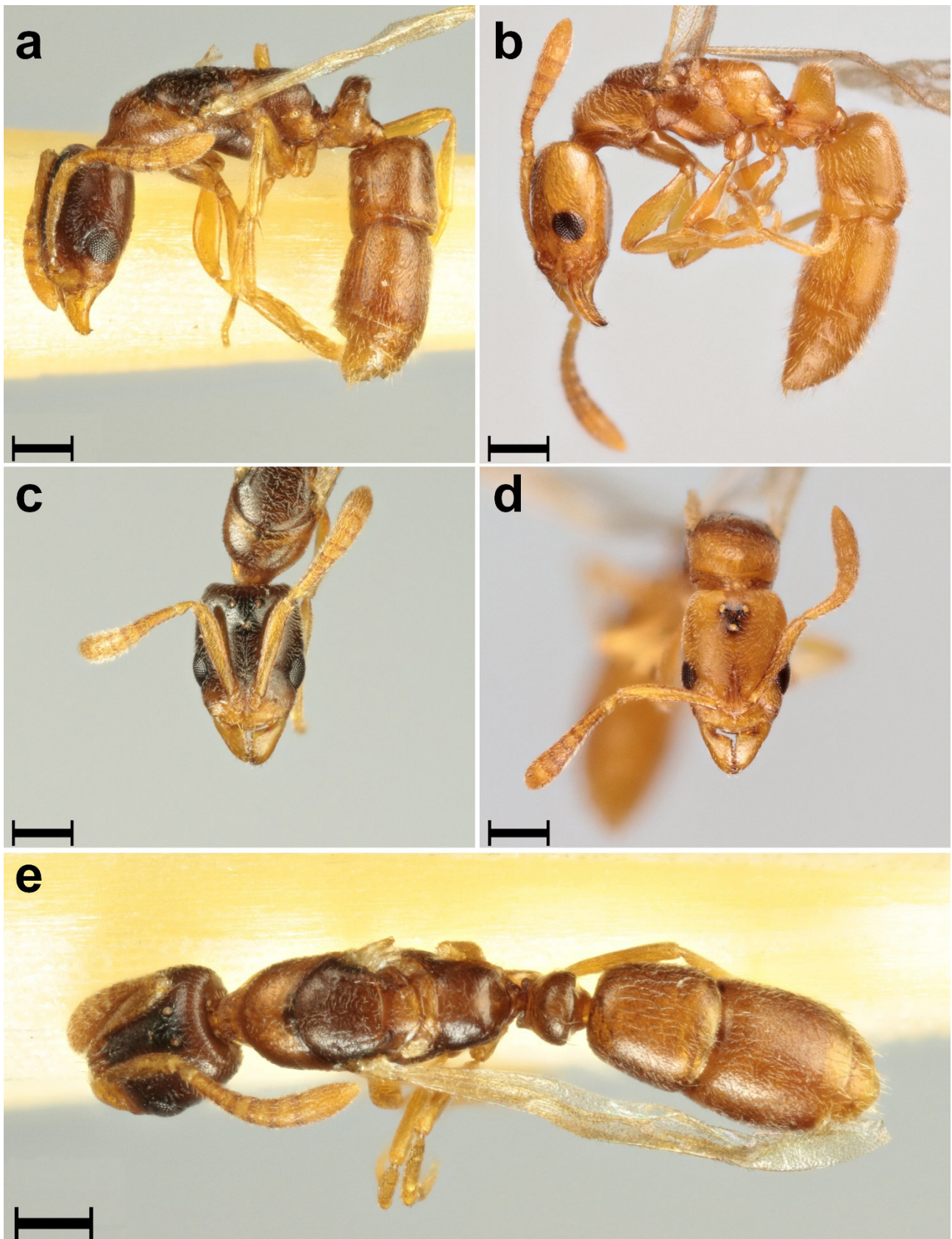
**Fig 5.** Morphometric differences between *Hypoponera abeillei* males and those of the sympatric *H. eduardi* (*punctatissima* group) according to cephalic size (CS) and the mesosoma length on cephalic size ratio (ML/CS).

Queen description. The morphology of all examined *H. abeillei* queens (Fig 6) was fully congruent with the diagnostic characters of queens from the genus *Hypoponera* as defined

by Bolton & Fisher (2011). Raw morphometric data are available in the supplementary material, while a synthesis is offered in Table 2. A formal description follows.

**Table 2.** Morphometric data on queens of *Hypoponera abeillei*. All characters are reported in  $\mu\text{m}$  as mean  $\pm$  standard deviation (minimum, maximum);  $n = 13$  for all characters except for PeL and PW ( $n = 5$ ).

Morphometric characters		Indexes	
CL	$580 \pm 23$ (550–625)	CS	$506 \pm 16$ (487–543)
CW	$432 \pm 13$ (416–462)	CW/CL	$0.74 \pm 0.02$ (0.71–0.77)
PoOC	$286 \pm 11$ (275–304)	PoOC/CS	$0.56 \pm 0.02$ (0.55–0.61)
EL	$154 \pm 8$ (143–176)	EL/CS	$0.30 \pm 0.02$ (0.28–0.35)
EW	$126 \pm 5$ (118–137)	EW/CS	$0.25 \pm 0.01$ (0.23–0.26)
SL	$409 \pm 23$ (375–462)	SL/CS	$0.81 \pm 0.02$ (0.77–0.85)
MH	$381 \pm 25$ (340–425)	MH/CS	$0.75 \pm 0.04$ (0.67–0.82)
ML	$834 \pm 43$ (784–900)	ML/CS	$1.65 \pm 0.05$ (1.57–1.73)
MW	$336 \pm 33$ (300–392)	MW/CS	$0.66 \pm 0.06$ (0.60–0.77)
PeH	$267 \pm 41$ (225–329)	PeH/CS	$0.53 \pm 0.08$ (0.45–0.65)
PeL	$229 \pm 14$ (208–244)	PeL/CS	$0.45 \pm 0.02$ (0.42–0.48)
PeW	$237 \pm 17$ (217–255)	PeW/CS	$0.47 \pm 0.03$ (0.43–0.50)

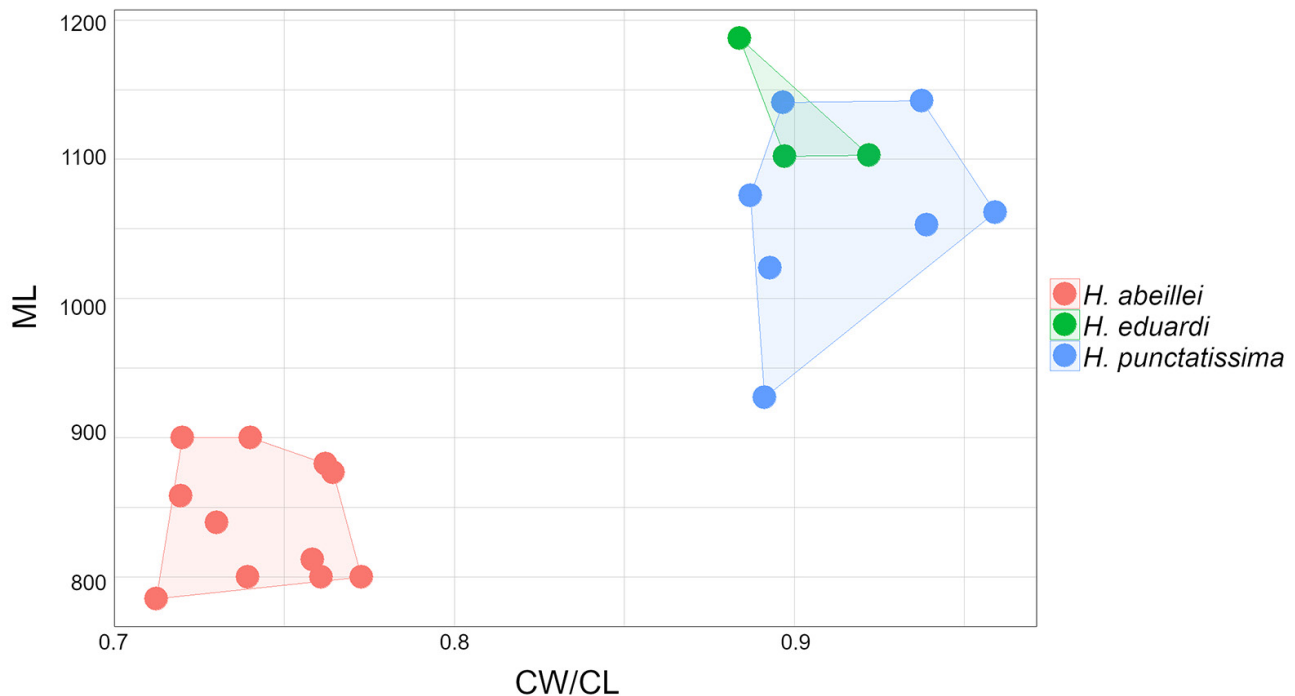


**Fig 6.** *Hypoponera abeillei* queens from Sicily (Italy). These two specimens, showing a dark (a, c, e) and a light-colored phenotype (b, d), were collected together. Scale bars: 0.5 mm. Note that slightly different orientation of the petiole in lateral-view pictures (above) may induce an incorrect perception of PeL differences between the two.

Head in dorsal view much longer than wide, compound eye large, ovoidal (obviously with > 50 ommatidia) located anterior to mid-length of the head, with small setae projecting between them. Three well-developed ocelli present. Lateral margins of head subparallel, weakly concave, posterior margin of the head straight, and anterior margin of clypeus gently concave. Mandible triangular and stout, with no basal groove or pit. Closed mandibles leave no space between masticatory margins (with around ten teeth or denticles) nor between basal margins and the clypeus. Clypeus simple, without extended lobes or teeth, median portion inserted as a small narrow triangle between anterior ends of frontal lobes. Frontal lobes small, almost confluent medially, separated only by median longitudinal impression; frontal lobe not raised nor specialized in any way, anterior margin well posterior to anterior clypeal margin. Frontal carinae and antennal scrobes absent. Antennae of 12 segments, apical five antennomeres gradually incrassate but not forming a sharply defined club. Mesosoma gently rounded anteriorly, anapleural sulcus well-developed, mesosoma with a full complement of flight sclerites; propodeum unarmed, forming an angle of about 135° in profile view between the dorsal and declivitous propodeal margins. Metapleural gland orifice small and simple, opening directed posteriorly. Propodeal spiracle small, circular to slightly

elliptical, located lateroventrally. Petiole thick but lesser than in workers, with a well-developed horizontal dorsal profile. Ventrally, the subpetiolar process is simple, without teeth or sharp angles. Mesotibiae, metatibiae, mesobasitarsi, and metabasitarsi all without spines and enlarged setae on their dorsal (outer) surfaces. Articulation of petiole to helcium simple; the latter arises low down on the anterior face of first gastral tergite, which forms a tall vertical surface above it. Mesotibia and metatibia each with one spur; metatibial spur always pectinate. Pretarsal claws are small and simple, without preapical teeth. Jugal lobe absent from hindwing, wing venation rather complete. Whole body and appendages light brown to ochraceous, head not infrequently darker than rest. Body sculpturing inconspicuous, overall appearance relatively shiny and dull, pilosity relatively sparse.

Comments. The morphology of *H. abeillei* queens is strongly different from those of the other Mediterranean species, thus facilitating their identification. First, the overall size of *H. abeillei* queens is much smaller than that of sympatric species (as mean  $\pm$  sd, in *H. abeillei* CS: 506  $\pm$  16, ML: 834  $\pm$  43; in *H. eduardi*, *H. punctatissima* CS: 654  $\pm$  47, ML: 1,081  $\pm$  72, see Fig 7). Their head shape is much more elongate (as mean  $\pm$  sd, in *H. abeillei* CW/CL: 0.74  $\pm$  0.02; in *H. eduardi*, *H. punctatissima*: CW/CL = 0.91  $\pm$  0.03, see Fig 7).

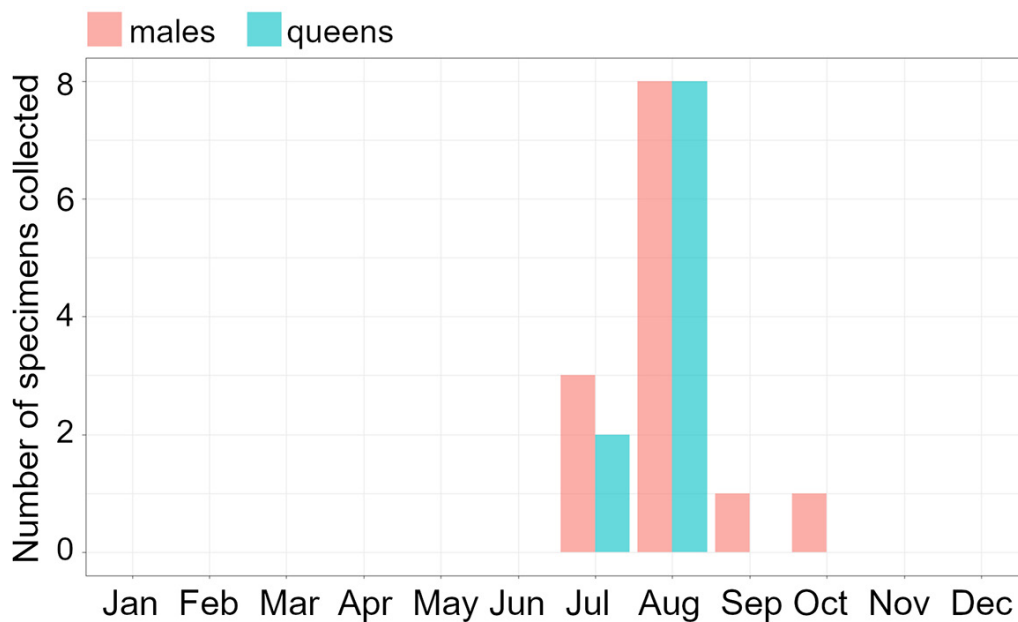


**Fig 7.** Morphometric differences between *Hypoponera abeillei* queens and those of the sympatric members of the *punctatissima* group (*H. eduardi* and *H. punctatissima*) according to the mesosoma length and the cephalic width on cephalic length ratio.

Besides these morphometric differences, the widest point of the head (CW) in *H. abeillei* is located near the eyes level. In contrast, the CW is usually distinctively placed at midlength between the eye and the posterior head margin in the other species, and the lateral margins are evidently more concave.

Nuptial flight phenology. Males and queens were collected from July to October, and most findings occurred in August (Fig 8). Queens were found as early as July 15 and as late as August 25, while males from found from July 27 to October 2. Most males (82%) and a significant number of queens (40%) were found drowning or dead on the water surface.





**Fig 8.** Seasonal distribution of findings of males and queens of *Hypoponera abeillei*, which were collected between 1987 and 2020, and found from July 15 to October 2.

## Discussion

*Hypoponera abeillei* appears to be relatively difficult to detect, yet widespread species in the W-Mediterranean basin. As almost all occurrence data for *H. abeillei* refers to winged sexuals whose dispersal range is unknown, it is difficult to define the species' ecological preferences. Still, most records are from coastal thermophilous sites. We found a large proportion of specimens drowning in the water. This situation often allows collecting sexuals of subterranean species otherwise difficult to detect (Espadaler & López-Soria, 1991; García et al., 2020). For instance, *Leptanilla SIC-1 sensu* Scupola & Ballarin (2009) was collected with drowning *H. abeillei* sexuals in Sicily. Our new distribution data extends the known range of *H. abeillei* to the islands of Malta, Mallorca, and Sardinia (in the latter case updating a very recent checklist, see Schifani et al., 2021) and define Italy's Apulia as the easternmost region inhabited by the 'western' *H. abeillei*. We provide the first information on the phenology of nuptial flights for this species: they concentrate during late summer to early autumn, which is quite similar to what is observed in other Mediterranean *Hypoponera*, all of which perform nuptial flights during summertime – although the rare exotic *H. ergatandria* can also fly during winter, see Seifert (2018).

The sexual castes of *H. abeillei* appear to be very easily identified within the Mediterranean region. Although sexuals of sympatric *Hypoponera* species are not described in all cases, differences from the *punctatissima* group appear as huge in sexuals as they are in workers, as evidenced in several morphometric characters. Verifying the potential existence of cryptic diversity within the current concept of *H. abeillei* was

not an aim of this study. It would require further investigations with the integration of other methods, yet the W-Mediterranean populations appeared rather homogeneous under our analyses. A slight variation in shape and a relatively significant color variation in queens did not suggest the existence of clearly discernible morphotypes. Rather, it appears to reflect a moderate degree of intraspecific polymorphism unassociated with geography. However, if the hypothesis of Bolton & Fisher (2011) that *H. abeillei* may also exist in the Afrotropics is correct, identification there would likely be more difficult due to the presence of more similar *Hypoponera* species. Unfortunately, since their sexual castes are still undescribed, we were unable to attempt a comparative study. Ergatoid males remain undocumented in *H. abeillei* and may not exist.

In the vast majority of ant species, at least one of the three main castes (male, queen, and worker) is hitherto undescribed, usually because sexuals are easily collectible only during brief periods of about a couple of months per year. Our descriptions make *H. abeillei* the eighth species whose male, queen, and worker castes are all described out of 153 valid *Hypoponera* taxa (corresponding to the 0.5%), while non-ergatoid males remain known only for ten taxa (0.6%; see Bolton, 2021). The *abeillei* group is considered to be by far the largest group in the West Palearctic and Afrotropics as it counts 45 out of the 57 species inhabiting these regions, yet *H. abeillei* becomes the only species with a described male. This condition is unfortunate in multiple ways: *i*) because the morphology of sexuals, and often males, in particular, may be highly informative on the relationships among species of the same genus (e.g., Alicata & Schifani, 2019); *ii*) because sexuals may be highly informative to distinguish otherwise morphologically cryptic species (e.g., Seifert, 2012; Wagner

et al., 2017); *iii*) because, in certain species, sexuals may be the most easily collectible caste, and their correct identification may play an important role in tracking their distribution – as it was for *H. abeillei*. It is also important to note that flight is the most common dispersal strategy in ants, which means that male and queen morphology likely plays a significant role in determining the dispersal capabilities of a species. Presently, dispersal capabilities and strategies are undocumented for almost all ant species.

Future investigation should aim to attain a better understanding of morphological variation across *Hypoponera* males and queens of other species across the world and the functional significance of blindness of workers of certain *Hypoponera* species.

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### Authors’ Contribution

Conceptualization: ES, AS

Methodology: ES

Validation: ES, AS, XE, MM

Formal analysis: ES

Investigation: ES, AS, MM, EB, XE

Resources: ES, AS, MM, EB, XE

Data Curation: ES, AS, MM, EB, XE

Writing – Original Draft: ES

Writing - Review & Editing: ES, AS, MM, EB, XE

Visualization: ES, MM

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Project Administration: ES

### References

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

Albert, G. & Arcos, J. (2015). Hormigas del Parque Natural de Serra Gelada y citas interesantes para la mirmecofauna alicantina (Hymenoptera, Formicidae). *Iberomyrmex*, 7: 3-6.

Baroni Urbani, C. (1962). Studi sulla Mirmecofauna d’Italia. *I. Redia*, 47: 129-138.

Boeiro, M., Espadaler, X., Azedo, A.R. & Serrano, A.R.M. (2002). Four new species to the ant fauna of Portugal (Hymenoptera, Formicidae). *Boletim da Sociedade Portuguesa de Entomologia*, 7: 253-259.

Boeiro, M., Espadaler, X., Azedo, A.R., Collingwood, C. & Serrano, A.R.M. (2009). One genus and three ant species new to Portugal (Hymenoptera, Formicidae). *Boletín de la SEA*, 45: 515-517.

André, E. (1881). Adresse les descriptions de trois nouvelles espèces de Fourmis. *Bulletin Bimensuel de la Société Entomologique de France*, 1: 60-62.

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

Bolton, B. (2021). An online catalog of the ants of the world. <https://antcat.org> (accessed November 25 2021).

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

Collingwood, C.A. (1985). Hymenoptera: Fam. Formicidae of Saudi Arabia. *Fauna of Saudi Arabia*, 7: 230-302.

Emery, C. (1895). Sopra alcune formiche della fauna mediterranea. *Memorie della Reale Accademia delle Scienze dell’Istituto di Bologna*, 5: 59-75.

Espadaler, X. & López-Soria, L. (1991). Rareness of certain Mediterranean ant species: fact or artifact?. *Insectes Sociaux*, 38: 365-377. doi: 10.1007/BF01241872

Espadaler, X. (1997). Catàleg de les formigues (Hymenoptera: Formicidae) dels països catalans. *Sessió Conjunta d’Entomologia*, 9: 23-42.

Espadaler, X. & Lopez-Colón, J.I. (2011). Hormigas (Hym., Formicidae) de una zona de yesos de la comunidad de Madrid (España). *Boletín de la SEA*, 49: 261-264.

Espadaler, X., Marí, M., Prats, I. & Calvo, J. (2013). Formigues (Hymenoptera, Formicidae) dels illots des Vedrà, es Vedranell i els illots de Ponent (Eivissa). *Bolletí de la Societat d’Història Natural de les Balears*, 56: 51-58.

García, F., Espadaler, X., Roig, X., Serrano, S. & Segura, A.D.C. (2020). Vuelos nupciales en hormigas: estudio de los sexuales ahogados en cuatro masas de agua ibéricas (Hymenoptera: Formicidae). In: 40 años sin Félix: homenaje al Dr. Rodríguez de la Fuente. *Monografías Tercer Milenio*, 10: 255-268. Sociedad Entomológica Aragonesa, SEA.

Mantero, G. (1908). *Res Ligusticae XL. Materiali per un catalogo degli Imenotteri Liguri. Parte V. Supplemento ai*

- Formicidi, Crisidi, Mutillidi, Braconidi e Cinipidi. *Annali del Museo Civico di Storia Naturale di Genova*, 4: 43-74.
- Mei, M. (1995). Arthropoda di Lampedusa, Linosa e Pantelleria (Canale di Sicilia, Mar Mediterraneo). Hymenoptera Formicidae (con diagnosi di due nuove specie). *Il Naturalista Siciliano*, 19: 753-772.
- Ortuño, V.M., Gilgado, J.D. & Tinaut, A. (2014). Subterranean ants: the case of *Aphaenogaster cardenai* (Hymenoptera: Formicidae). *Journal of Insect Science*, 14: 212. doi: 10.1093/jisesa/ieu074
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Roger, J. (1859). Beiträge zur Kenntniss der Ameisenfauna der Mittelmeerländer. I. *Berliner Entomologische Zeitschrift*, 3: 225-259.
- RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. <http://www.rstudio.com/>.
- Santschi, F. (1907). Fourmis de Tunisie capturées en 1906. *Revue Suisse de Zoologie*, 15: 305-334.
- Santschi, F. 1908. Nouvelles fourmis de l'Afrique du Nord (Égypte, Canaries, Tunisie). *Annales de la Société Entomologique de France*, 77: 517-534.
- Santschi, F. (1910). Nouvelles fourmis de Tunisie (suite). *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord*, 1: 70-72.
- Santschi, F. (1921). Nouvelles fourmis paléarctiques. 3ème note. *Boletín de la Real Sociedad Española de Historia Natural*, 21: 165-170.
- Schifani, E. (2019). Exotic ants (Hymenoptera, Formicidae) Invading Mediterranean Europe: a Brief Summary over about 200 Years of Documented Introductions. *Sociobiology*, 66: 198-208. doi: 10.13102/sociobiology.v66i2.4331
- Schifani, E., Nalini, E., Gentile, V., Alamanni, F., Ancona, C., Caria, M., Cillo, D. & Bazzato, E. (2021). Ants of Sardinia: an updated checklist based on new faunistic, morphological and biogeographical notes. *Redia*, 104: 21-35. doi: 10.19263/REDIA-104.21.03
- Schneider, C. A., Rasband, W.S. & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9: 671-675. doi: 10.1038/nmeth.2089
- Scupola, A. & Ballarin, R. (2009). The genus *Leptanilla* Emery, 1870 in Sicily (Hymenoptera: Formicidae). *Myrmecological News*, 12: 129-132.
- Sharaf M.R., Fisher, B.L., Al Dhafer, H.M., Polaszek, A. & Aldawood, A.S. (2018). Additions to the ant fauna (Hymenoptera: Formicidae) of Oman: an updated list, new records and a description of two new species. *Asian Myrmecology*, 10: e010004. doi: 10.20362/am.010004
- Seifert, B. (2012). Clarifying naming and identification of the outdoor species of the ant genus *Tapinoma* Förster, 1850 in Europe north of the Mediterranean region with description of a new species. *Myrmecological News*, 16: 139-147.
- Seifert, B. (2013). *Hypoponera ergatandria* (Forel, 1893) – a cosmopolitan tramp species different from *H. punctatissima* (Roger, 1859) (Hymenoptera: Formicidae). *Soil Organisms*, 85: 189-201.
- Seifert, B. (2018). *The Ants of Central and North Europe*. Lutra Verlags- und Vertriebsgesellschaft, Tauer, Germany.
- Taylor, R. (1967). A monographic revision of the ant genus *Ponera* Latreille (Hymenoptera: Formicidae). *Pacific Insects Monograph*, 13: 1-112.
- Vonshak, M. & Ionescu-Hirsch, A. (2009). A checklist of the ants of Israel (Hymenoptera: Formicidae). *Israel Journal of Entomology*, 39: 33-55.
- Wagner, H.C., Arthofer, W., Seifert, B., Muster, C., Steiner, F.M. & Schlick-Steiner, B.C. (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.
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, <https://ggplot2.tidyverse.org>.

