Cataglyphis tartessica sp.n., a new ant species (Hymenoptera: Formicidae) in south-western Spain

Fernando AMOR & Patrocinio ORTEGA

Abstract

A new ant species, *Cataglyphis tartessica* sp.n., is described based on the morphological traits of its workers, queens, and males. The species is endemic to Spain and phylogenetically closely related to *Cataglyphis floricola* TINAUT, 1993, of which *C. tartessica* sp.n. was previously considered to be a bicoloured morph. The more relevant aspects of the new species' natural history are also described.

Key words: Ant, *Cataglyphis*, new species, endemism, Tartessos, Andalusia, Spain.

Fernando Amor (contact author) & Patrocinio Ortega, Estación Biológica de Doñana (CSIC), Av. Américo Vespucio, 41092, Sevilla, Spain. E-mail: fernandoamor01@gmail.com

Introduction

Species of the genus *Cataglyphis* (FÖRSTER, 1850) are among the most conspicuous and characteristic ants of arid and semiarid zones of the Palearctic, which span from Mauritania to the Gobi Desert. They are relatively easy to find because they preferentially occupy open habitats and their workers are large. Various species within the genus *Cataglyphis* have drawn the attention of researchers as a result of their diverse and original reproductive strategies (PEARCY & al. 2004, AMOR & al. 2011a, LENIAUD & al. 2012) and their extraordinary adaptations to hot environments, including landmark navigation and foraging activity regulation (WEHNER & al. 2006, COLLETT & COLLET 2009, WEHNER 2009, AMOR & al. 2011b, MANGAN & WEBB 2012; see LENOIR & al. 2009 for a review of the genus *Cataglyphis*).

Cataglyphis is a very homogeneous genus that is divided into monophyletic groups based on male genital morphology (AGOSTI 1990). *Cataglyphis floricola* was initially described as a complex of two morphs, one black and one bicoloured (red and black) (TINAUT 1993). However, a recent integrative taxonomic study of *C. floricola* that used distribution, molecular, chemical, and morphometric data revealed that there is no gene flow between the morphs in the contact zones of its parapatric populations; the study thus concluded that the morphs are, in fact, different species (AMOR 2011). Because the black morph was used as the holotype in the description of *C. floricola* (TINAUT 1993), we name the bicoloured morph *Cataglyphis tartessica* sp.n. The description of the new species is based on the morphological characteristics of its workers, males, and queens.

Material and methods

All *Cataglyphis tartessica* specimens, workers, males, and queens, were gathered between 2008 and 2010. A total of 181 workers belonging to 31 nests were collected from five different localities that represent the species' distribution area: Doñana Biological Reserve (DBR) 36° 59' 38" N, 6° 26' 47" W, Aznalcázar (AZN) 37° 16' 90" N, 6° 13' 58" W, Alcalá de Guadaíra (ALC) 37° 19' 18" N, 5° 50' 40" W, Utrera (UTR) 37° 11' 38" N, 5° 45' 23" W, and Bornos (BRN) 36° 48' 45" N, 5° 46' 37" W. In addition, 30 males were collected: 15 from DBR, without knowledge of its origin nests and 15 from two nests in ALC. Finally, 25 brachypterous females and 47 ergatoid females were collected in DBR.

All measurements were made in millimetres using a micrometric ruler, Nikon SMZ800 stereomicroscope and ImageJ software; precision was 10^{-2} mm. The following morphometric measurements were made:

FL   Hind femur length.

HL   Head length. Measured from anterior clypeal border to occipital margin at its median.

HW   Head width. Maximum width of head measured at eye level in full-face view.

ML   Mesosoma length. Measured from anterior border of pronotum to posterior border of propodeum.

SL   Scape length. Length excluding the condyle.

The following morphometric measurements were also made for sexuals:

Mesonotum width: Maximum mesonotum width in dorsal view.

Wing length: Maximum forewing length.

We calculated the following commonly used indices (BOUDINOT & FISHER 2013, LENHART & al. 2013):

CI   Cephalic Index. CI = HW × 100 / HL.

SI   Scape Index. SI = SL × 100 / HW.

We characterised male genitalia using:

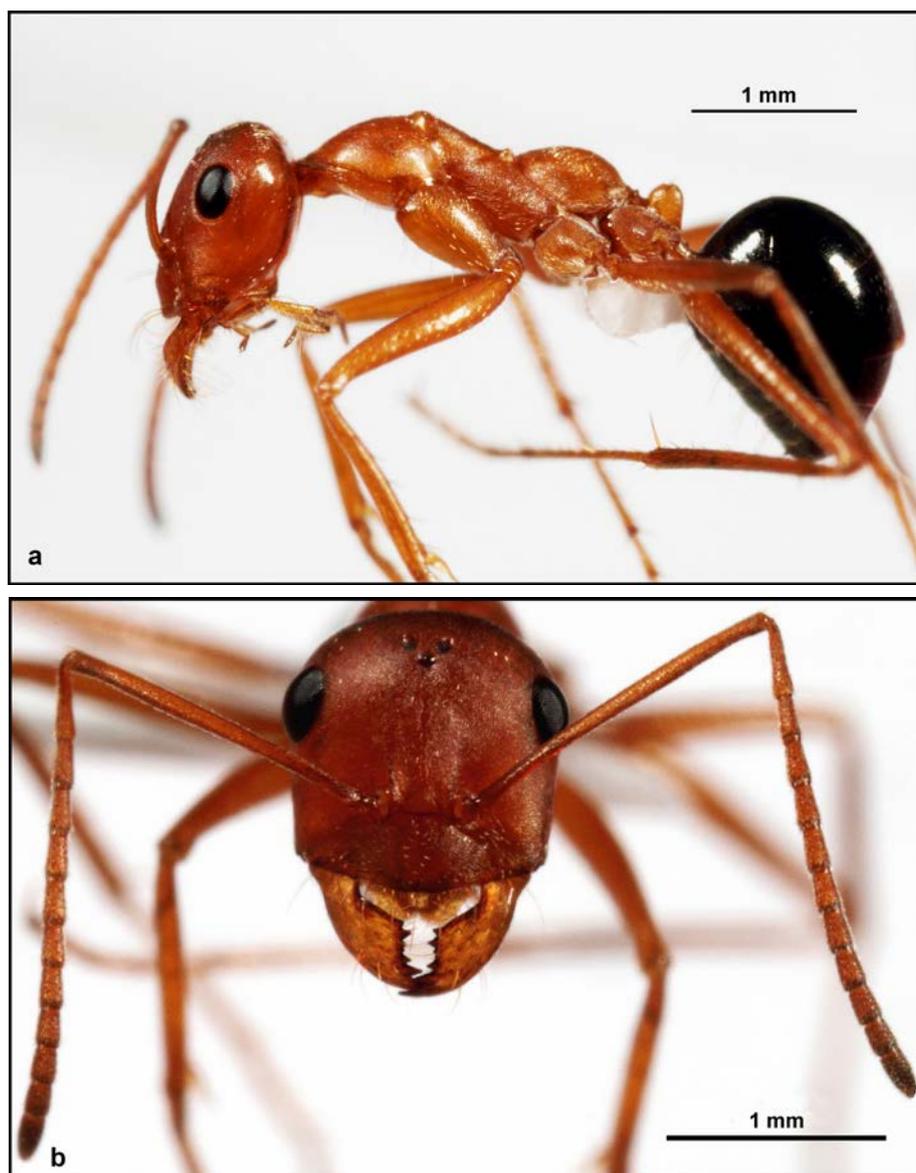Subgenital plate width: Distance between sclerotic apical ends of lobes.

Fig. 1: *Cataglyphis tartessica* sp. n., worker. (a) Body in profile. (b) Head in full-face view.

Paramere length: Distance between first basal process and paramere apex.

Penisvalva length and width: Maximum width and length of the penisvalva.

Volsella (digitus) length: Measured from the apex to the orthogonal bend, next to the origin of the cuspis.

All reported values are means ± standard deviation (SD).

Repositories

Collections to which types have been distributed (registration numbers in brackets):

Museo Nacional de Ciencias Naturales de Madrid (MNCN _Ent75407-11)

British Museum of Natural History, London (E 2013-56)

Alberto Tinaut Collection (13205 - 13206)

Cataglyphis tartessica sp.n.

Type material examined: H o l o t y p e (worker): Spain, Huelva, Doñana Biological Reserve 36° 59' 38.44" N, 6° 26' 47.74" W, 2009-07-03; coll. Museo Nacional de Ciencias Naturales de Madrid (MNCN_Ent75407). P a r a t y p e s :

72 queens (25 brachypterous and 47 ergatoids; DBR), 30 males (DBR and ALC), and 181 workers (DBR, AZN, ALC, UTR, BRN) collected between 2008 and 2010.

Description of holotype worker: HL: 1.17 mm, HW: 1.13 mm, SL: 1.42 mm, ML: 1.90 mm, FL: 1.85 mm, CI: 96.58, SI: 125.66. Bicoloured: shiny black gaster, black eyes and ocelli, rest of body amber. Integument densely microsculptured, matte, except on slightly shiny gaster. Abundant pubescence not obscuring integument texture. Head rectangular; vertex smooth and rounded, with two to three suberect hairs. Compound eyes large and ovoid located in upper half of face sides; ocelli normal. Mandibles triangular and slightly striated. Pilosity particularly present on outer face and on or near margins; long and posteriorly curved or J-shaped hairs in external margin particularly notable. Masticatory margin armed with 6 teeth; apical tooth largest and most pointed, preapical tooth of intermediate length, and remaining teeth small and irregular. Clypeus with ridge in centre and 7 stout setae along front edge; one pair of setae straddling posterior clypeus ridge. Posterior (basal) area of maxillae with six long and anteriorly curved

Fig. 2: *Cataglyphis tartessica* sp. n. (a) Brachypterous queen. (b) Ergatoid queen (minute wing insertion indicated with an arrow).

Tab. 1: Measurements in millimetres of *C. tartessica* sp.n. workers (n = 181).

Cataglyphis tartessica workers	
Variable	mean ± SD
Head length	1.23 ± 0.12
Head width	1.15 ± 0.12
Scape length	1.47 ± 0.12
Mesosoma length	1.94 ± 0.16
Femur length	2.03 ± 0.14
Cephalic index	93.60 ± 3.94
Scape index	128.10 ± 7.66

or J-shaped hairs. Sparse pubescence on genae and ventral cephalic capsule. Pubescence more abundant in occipital area between and behind the eyes.

Mesosoma typical for this genus; propodeum evenly convex, long legs. Propodeal spiracle a long, narrow ellipse. Metapleural gland just above hind coxa; orifice protected by tuft of guard hairs. Scale-like petiole thick, with rounded apex. Sparse pubescence on mesonotum; abundant silver pubescence on pronotum, pleura, propodeum, petiole, and coxae.

Gaster shiny due to a very lightly microsculptured integument and very sparse pubescence. Apex of gaster with circular acidopore (nozzle-shaped) and fringed with setae. Long setae on gastral sternites; only sparse setae present on dorsal side of most apical tergites.

Description of paratype workers (Tab. 1, Fig. 1): Workers from different sampling locations showed morphometric variation. The biggest difference in body size occurred between workers from BRN and AZN populations (ML: 2.13 ± 0.2 vs. 1.77 ± 0.11, n = 35, from nest 5, and n = 30, from nest 6, respectively). Workers also differed, generally, in their number of setae and mandibular teeth (5 - 7).

Tab. 2: Measurements in millimetres of *Cataglyphis tartessica* sp.n., brachypterous and ergatoid queens.

Cataglyphis tartessica queens	Brachypterous		Ergatoid	
Variable	mean ± SD	n	mean ± SD	n
Head length	1.26 ± 0.14	7	1.20 ± 0.11	15
Head width	1.33 ± 0.09	24	1.13 ± 0.05	46
Scape length	1.25 ± 0.07	10	1.30 ± 0.04	15
Mesosoma length	2.25 ± 0.16	25	1.90 ± 0.11	47
Mesonotum width	0.86 ± 0.08	25	0.52 ± 0.03	47
Femur length	1.64 ± 0.09	23	1.75 ± 0.10	46
Cephalic index	104.45 ± 13.4	7	94.89 ± 12.00	15
Scape index	96.23 ± 5.60	7	115.58 ± 4.70	15

Description of queens (Tab. 2, Fig. 2): A notable feature of *C. tartessica* is the presence of two morphs of queens, brachypterous (short-winged queen) and ergatoid (wingless queen), which are described separately.

Description of brachypterous queens: Same body colouration as worker. but with bigger head, mesosoma, and gaster; head squarer, scape shorter. Compound eyes and ocelli normal. Strong, slightly striated mandibles; apical tooth more pointed and developed than in worker, other teeth small and short. Mesosoma (scutum, scutellum, and metanotum) less developed than those seen in species with macropterous queens, but very different from those of ergatoids and workers (AMOR & al. 2011a). Short wings with weak venation; tegulae (scale-like sclerite covering forewing base) and wing stumps present and distinct. Legs shorter than those of ergatoids and workers (FL: 1.64, 1.75 and 2.03 respectively). Scale-like petiole large and thick, with rounded apex. Gaster similar but larger than that of worker. Pubescence very sparse.

Variability: Little differences in mesonotum size and degree of thoracic development.

Description of ergatoids: Looks like a worker; hard to distinguish between the two using the naked eye. Scape length intermediate to those of brachypterous queens and worker. Mesosoma only slightly developed, with very small scutum, scutellum, and metanotum, in profile view appearing slightly elevated; scutum-scutellum suture very slightly impressed or disappeared. Metanotum plate arcuate and wrinkled. Wing insertion points extremely reduced (Fig. 2). Leg length intermediate to those of brachypterous and worker.

Variability: At a glance, some ergatoids without wing insertion points; they can only be distinguished from workers by their physogastric abdomen and behaviour.

Description of males: External morphology (Tab. 3): Head, scape, mesosoma, petiole, and coxae dull black; funiculus, legs, and gaster dull amber. Large, light brown wings with strong venation.

Head ovoid and small. Prominent large ovoid compound eyes located in mid to upper half of face sides; prominent large ocelli also present. Cephalic capsule with a slight blister in the occipital margin behind the ocelli. Scoop-shaped mandibles, small, fragile, and without striations, that taper into a small apical tooth. Antennae with

Tab. 3: Measurements in millimetres of males of *Cataglyphis tartessica* (n = 30).

Cataglyphis tartessica males (n = 30)	
Variable	means ± SD
Head length	1.18 ± 0.07
Head width	1.29 ± 0.15
Scape length	1.43 ± 0.12
Mesosoma length	2.63 ± 0.17
Mesonotum width	1.39 ± 0.15
Femur length	2.04 ± 0.10
Wing length	4.77 ± 0.28
Cephalic index	109.23 ± 10.24
Scape index	111.39 ± 8.14
Copulatory pieces	
Subgenital plate width	0.59 ± 0.07
Penisvalva width	0.55 ± 0.04
Penisvalva length	0.96 ± 0.05
Paramere length	0.89 ± 0.04
Volsella (digitus) length	0.74 ± 0.05

13 segments; the two basalmost funicular segments somewhat longer than the others.

Mesosoma massive, with well-developed scutum and scutellum; metanotum small. Pleural sclerites slightly striated next to wing insertions. Petiole scale-like, large, and thick, with bilobed or heart-shaped apex due to a slight, longitudinal constriction. Scutum, scutellum, and metanotum with very sparse pubescence. Scattered setae on scutum. Abundant pubescence on pronotum, propodeum, pleura, coxae, and petiole.

Gaster cylindrical densely microsculptured and with medium pubescence. Sternites with long and numerous setae, and tergites lacking setae.
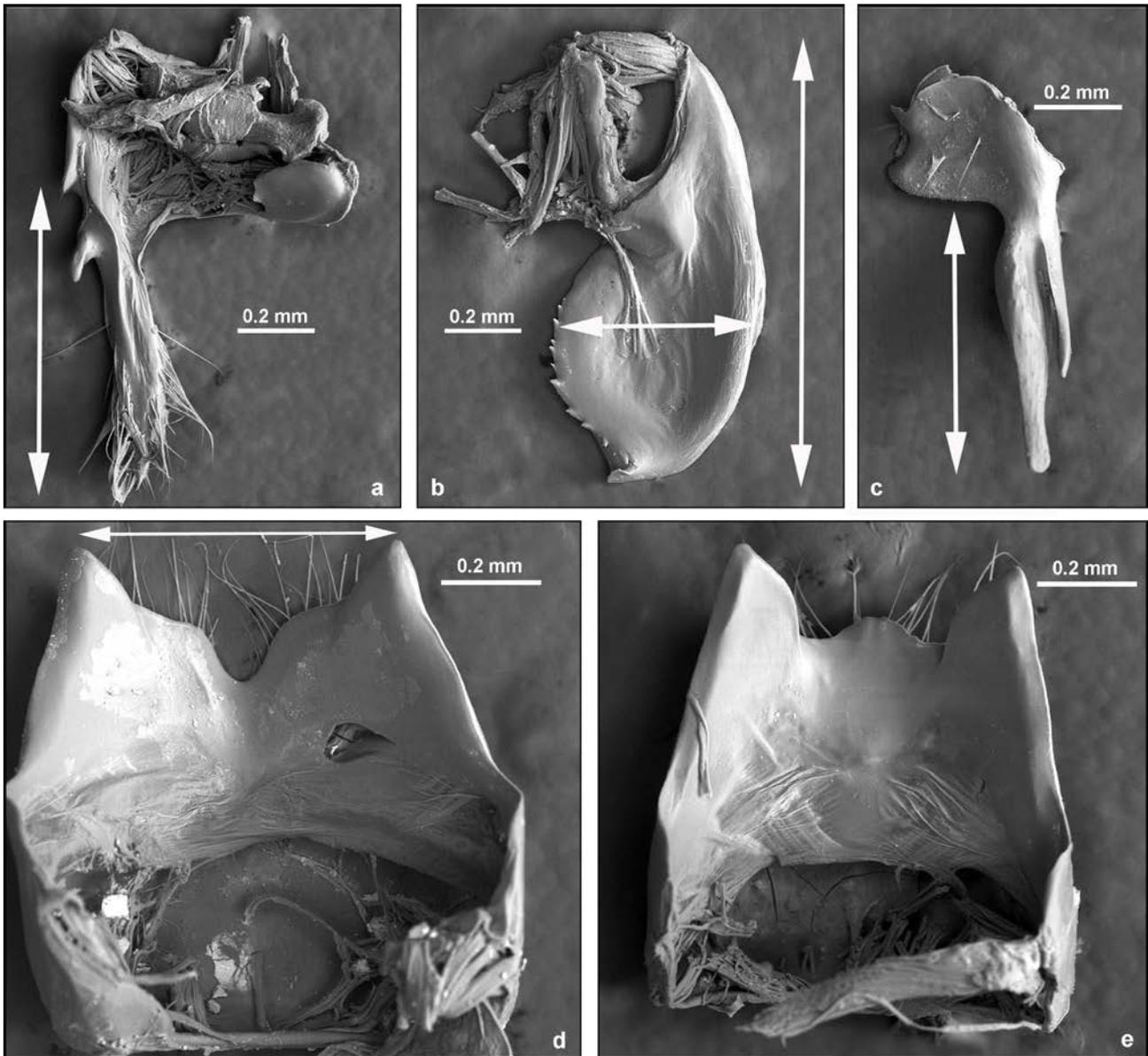
Fig. 3: Views in scanning electron microscopy of the copulatory appendages of (a - d) *C. tartessica* sp.n. and (e) *C. floricola*: (a) paramere; (b) penisvalva; (c) volsella, with digitus (the largest) and cuspis; (d) subgenital plate. Note the differences in size and shape between the subgenital plates. Measurements are indicated with double-headed arrows.

Genital morphology (Fig. 3): Paramere elongated and oval, with abundant long setae, and externally bearing a small finger-like process at its base next to cuspis. Volsella with digitus and cuspis straight and parallel, digitus larger than cuspis. Penisvalva twice as long as wide, with 7 (6 - 9) minute teeth in its internal arcuate margin, and a flat peak in its terminal end. Subgenital plate concave and bilobed posterolaterally, with rounded notch in centre of depression, at posterior margin; numerous setae present on its exterior face.

Variability: The extent of black colouration can vary among males; for example, the scape, which is usually black, can also be amber. The first funicular and gastral segments can be black in some males. The genitalia are very uniform; the number of penisvalva teeth can differ, and the posterior margin of the subgenital plate can be continuous (unbroken in the middle) or sometimes present a slight convexity.

Etymology: The name of this species comes from its current geographic distribution in southwestern Andalusia. It is distributed across the area thought to have been occupied by the ancient Tartessian civilisation, which existed three thousand years ago in the southwestern Iberian Peninsula (LÓPEZ-DAVALILLO 1999, GONZÁLEZ DE CANALES 2004).

Relationship to other *Cataglyphis* species: As previously noted, *Cataglyphis tartessica* sp.n. is phylogenetically closely related to *C. floricola* (see AMOR 2011), and belongs, as *C. floricola* (see TINAUT 1993), to the *Cataglyphis emmae* group (AGOSTI 1990). Apart from their different colouration, the two species are most notably distinguished by differences in the size of their brachypterous queens and males (brachypterous ML: 2.25 ± 0.16, n = 25 vs. 1.97 ± 0.08, n = 16, *C. tartessica* sp.n. – *C. floricola*, respectively; male ML: 2.63 ± 0.17, n = 29 vs. 2.20 ± 0.13, n = 23, *C. tartessica* – *C. floricola*, respec-
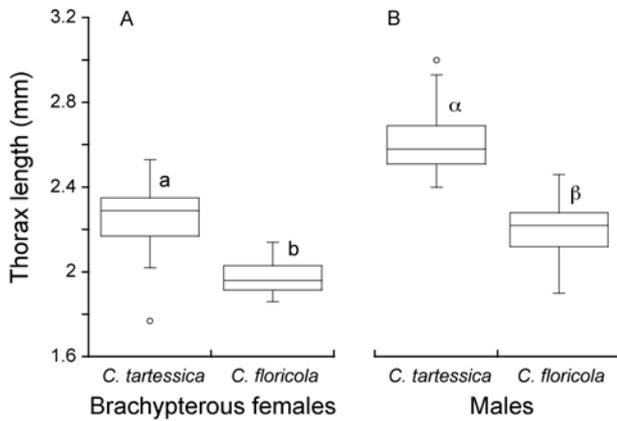
Fig. 4: Box (25% - 75% of data; with the median position) and Whisker (not outlier data range) graph showing the mesosoma length differences between *Cataglyphis tartessica* sp.n. and *C. floricola* sexuals (brachypterous females and males). Different letters denote significant differences.
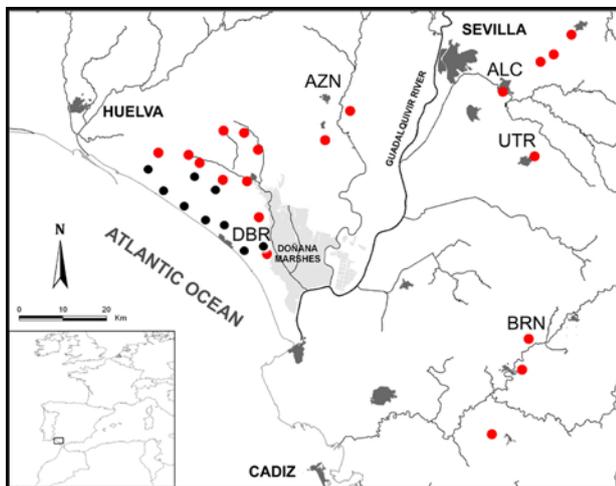

Fig. 5: Geographic distribution of *Cataglyphis tartessica* sp.n. (red dots) and *C. floricola* (black dots) in southwestern Spain. Note the parapatric relationship between the two distributions.

tively. Student's t-test: t = 6.33 and t = 9.71, respectively; $P < 10^{-6}$ in both cases; Fig. 4). Both species are ecologically very similar; they exhibit similar nesting and feeding preferences as well as comparable social structures and dispersal modes (F. Amor, unpubl.).

Natural history notes: *Cataglyphis tartessica* sp.n. is endemic to Spain. It occurs in habitats with sandy soils and has a small range. Its populations are located in southwestern Spain, in an arc of about 200 km around the lower stretch of the Guadalquivir River; its distribution is parapatric to that of *C. floricola* (Fig. 5). The Guadalquivir river estuary underwent very strong changes throughout the Quaternary (SALVANY & CUSTODIO 1995, RODRÍGUEZ-RAMÍREZ & al. 1996, ZAZO & al. 2005, SALVANY & al. 2010); these changes may have generated barriers that resulted in isolation and speciation. Thus, the current parapatric distribution of the two taxa could be interpreted as their first meeting since the Quaternary: now that the barriers have disappeared, their ranges have spread. The apparent stable boun-

dary between their populations – *C. floricola* occurs largely on the coast and *C. tartessica* sp.n. is found mostly inland – could be a consequence of each species being more fit under different ecological conditions.

Before the species' distributions were well characterised, *Cataglyphis floricola* (the black morph) was thought to occupy environments with more vegetative cover than *C. tartessica* sp.n. (previously identified as the *C. floricola* bicolour morph). Thus, the difference in their colouration was proposed to be related to different habitat preferences, which were linked to different environmental temperatures: Because *C. floricola* nested in areas characterised by lower temperatures, its colouration was black (CARPINTERO & al. 2002). However, current knowledge of their distribution patterns suggests that they do not prefer different levels of vegetative cover.

Cataglyphis tartessica sp.n. is a monomorphic, medium-sized ant (total body size: 4.51 ± 0.41 mm; n = 35), very similar in size and appearance to other *Cataglyphis* species of the southern Iberian Peninsula (Fig. 6). The species is monodomous (each colony occupies one single nest) and monogynous (each colony is headed by a single queen), with a mean number of workers per nest of 182.8 ± 130.6 (n = 106). Although the species range is rather small, local nest density is high, with about 6 nests per 10 m² that are in close proximity to each other (0.81 ± 0.35; n = 202).

Colonies of *C. tartessica* sp.n. reproduce by fission. This process is described in detail by AMOR (2011). Around the summer solstice, a third of the workers and cocoons of a reproducing colony are transported, one by one, by a small number of "transporter" ants; the distance from the mother nest to the new nest is 8 m on average. The gynes are transported while still in their cocoons, and the queen of the colony remains in the mother nest. The presence in the same population of two queen morphs, brachypterous and ergatoid, that differ in reproductive potential (that of the brachypterous being greater) could be a consequence of a conflict of interest within the colony. So, ergatoids may compete with the brachypterous for the colony leadership and escape policing activity through their morphological similarity to the workers. Supernumerary gynes are reduced by worker aggression (AMOR & al. 2011a).

The diet of *C. tartessica* sp.n. mainly consists of arthropod, which is typical of the *Cataglyphis* genus (CERDÁ & al. 1989). However, the species, which is mostly a scavenger, also opportunistically harvests other available food resources, a characteristic that is an adaptation to resource-poor environments. Thus, depending on location, we observe large differences in diet composition. Some diets contain a large quantity of plant material: in DBR in July, 80% of the diet consisted of *Halimium halimifolium* petals (CERDÁ & al. 1992, 1996). Others demonstrate a clear preponderance of arthropod corpses where *H. halimifolium* is absent: in ALC, also in July, 90% of diet consisted of arthropod corpses (AMOR 2011).

In *Cataglyphis tartessica* sp.n., foraging for food items is solitary, with individual ants searching for resources, as in all *Cataglyphis* species (WEHNER & al. 1983). However, although it is widely thought that the genus *Cataglyphis* has lost its ability to recruit as a result of selection imposed by high surface temperatures (RUANO & al. 2000), the foragers of *C. tartessica* are able to carry out rudimentary but very efficient recruitment, without indicating the food

Fig. 6: Comparative view among workers of four *Cataglyphis* species. Apart from the colour, note the similarity in size and design. (a) *C. tartessica* sp.n.; (b) *C. floricola*; (c) *C. rosenhaueri* SANTSCHI, 1925; (d) *C. iberica* EMERY, 1906.

location, when they find a large prey item near their nest. The result is cooperative prey-retrieval for large or heavy items that could not be exploited otherwise (AMOR & al. 2010). A similar, short-distance recruitment behaviour, used to exploit rich food patches, has already been observed in *C. bicolor* (FABRICIUS, 1793) in Tunisia (WEHNER 1987: 33).

Acknowledgments

References

AGOSTI, D. 1990: Review and reclassification of *Cataglyphis* (Hymenoptera, Formicidae). – Journal of Natural History 24: 1457-1506.

AMOR, F. 2011: Social structure, resource exploitation and distribution of the ant *Cataglyphis floricola* TINAUT 1993. − PhD thesis, Seville University, Spain, 136 pp.

AMOR, F., ORTEGA, P., CERDÁ, X. & BOULAY, R. 2010: Cooperative prey-retrieving in the ant *Cataglyphis floricola*: an unusual short-distance recruitment. − Insectes Sociaux 57: 91-94.

AMOR, F., ORTEGA, P., CERDÁ, X. & BOULAY, R. 2011b: Solar elevation triggers foraging activity in a thermophilic ant. − Ethology 117: 1031-1039.

AMOR, F., ORTEGA, P., JOWERS, M.J., CERDÁ, X., BILLEN, J., LENOIR, A. & BOULAY, R.R. 2011a: The evolution of worker-queen polymorphism in *Cataglyphis* ants: interplay between individual and colony-level selections. − Behavioral Ecology and Sociobiology 65: 1473-1482.

BOUDINOT, B.E. & FISHER, B.L. 2013: A taxonomic revision of the *Meranoplus* F. SMITH of Madagascar (Hymenoptera: Formicidae: Myrmicinae) with keys to species and diagnosis of the males. − Zootaxa 3635: 301-339.

CARPINTERO, S., REYES, J. & ARIAS DE REYNA, L. 2002: Segregación especial y coloración en la especie *Cataglyphis floricola* (Hymenoptera: Formicidae) en el Parque Nacional de Doñana (España). − Boletín de la Asociación Española de Entomología 26: 113-120.

CERDÁ, X., RETANA, J., BOSCH, J. & ALSINA, A. 1989: Daily foraging activity and food collection of the thermophilic ant *Cataglyphis cursor* (Hymenoptera: Formicidae). − Vie et Milieu 39: 207-212.

CERDÁ, X., RETANA, J., CARPINTERO, S. & CROS, S. 1992: Petals as the main resource collected by the ant, *Cataglyphis floricola* (Hymenoptera: Formicidae). − Sociobiology 20: 315-319.

CERDÁ, X., RETANA, J., CARPINTERO, S. & CROS, S. 1996: An unusual ant diet: *Cataglyphis floricola* feeding on petals. − Insectes Sociaux 43: 101-104.

COLLETT, M. & COLLET, T.S. 2009: Local and global navigational coordinate systems in desert ants. − The Journal of Experimental Biology 212: 901-905.

GONZÁLEZ DE CANALES, F. 2004: Del Occidente mítico griego a Tarsis-Tarteso. Fuentes escritas y documentación arqueológica. − Biblioteca Nueva, Madrid, 427 pp.

LENHART, P.A., DASH, S.T. & MACKAY, W.P. 2013: A revision of the giant Amazonian ants of the genus *Dinoponera* (Hymenoptera: Formicidae). − Journal of Hymenoptera Research 31: 119-164.

LENIAUD, L., DARRAS, H., BOULAY, R. & ARON, S. 2012: Social hybridogenesis in the clonal ant *Cataglyphis hispanica*. − Current Biology 22: 1188-1193.

LENOIR, A., ARON, S., CERDÁ, X. & HEFETZ, A. 2009: *Cataglyphis* desert ants: a good model for evolutionary biology in Darwin's anniversary year. A review. − Israel Journal of Entomology 39: 1-32.

LÓPEZ-DAVALILLO, J. 1999: Atlas histórico de España y Portugal. Desde el Paleolítico hasta el Siglo XX. − Editorial Síntesis S.A., Madrid, 223 pp.

MANGAN, M. & WEBB, B. 2012: Spontaneous formation of multiple routes in individual desert ants (*Cataglyphis velox*). − Behavioral Ecology 23: 944-954.

PEARCY, M., ARON, S., DOUMS, C. & KELLER, L. 2004: Conditional use of sex and parthenogenesis for worker and queen production in ants. − Science 306: 1780-1783.

RODRÍGUEZ-RAMÍREZ, A., RODRÍGUEZ-VIDAL, J., CÁCERES, L., CLEMENTE, L., BELLUOMINI, G., MANFRA, L., IMPROTA, S. & DE ANDRÉS, J.R. 1996: Recent coastal evolution of Doñana National Park (SW Spain). − Quaternary Science Reviews 15: 803-809.

RUANO, F., TINAUT, A. & SOLER, J.J. 2000: High surface temperatures select for individual foraging in ants. − Behavioral Ecolology 11: 396-404.

SALVANY, J.M. & CUSTODIO, E. 1995: Características litoestratigráficas de los depósitos plio-cuaternarios del Bajo Guadalquivir en el área de Doñana: implicaciones hidrogeológicas. − Revista de la Sociedad Geológica de España 8: 21-31.

SALVANY, J.M., MEDIAVILLA, C. & REBOLLO, A. 2010: The Pliocene and Quaternary formations of El Abalario, in the Huelva province littoral (Spain). − Estudios Geológicos 66: 209-225.

TINAUT, A. 1993: Cataglyphis floricola nov. sp. new species for the genus Cataglyphis FÖRSTER, 1850 (Hymenoptera: Formicidae) in the Iberian Peninsula. − Bulletin de La Societé Entomologique Suisse 66: 123-134.

WEHNER, R. 1987: Spatial organization of foraging behavior in individually searching desert ants, Cataglyphis (Sahara desert) and Ocymyrmex (Namibia desert). In: PASTEELS, J.M. & DE-NEUBOURG, J.L. (Eds.): From individual to collective behavior in social insects. − Birkhauser, Basel, pp. 15-42.

WEHNER, R. 2009: The architecture of the desert ant's navigational toolkit (Hymenoptera: Formicidae). − Myrmecological News 12: 85-96.

WEHNER, R., BOYER, M., LOERTSCHER, F., SOMMER, S. & MENZI, U. 2006: Desert ant navigation: one-way routes rather than maps. − Current Biology 16: 75-79.

WEHNER, R., HARKNESS, R.D. & SCHMID-HEMPEL, P. 1983: Foraging strategies in individually searching ants Cataglyphis bicolor (Hymenoptera: Formicidae). − Akademie der Wissenschaften und der Literatur, Mainz; Gustav Fischer Verlag, Stuttgart, 79 pp.

ZAZO, C., MERCIER, N., SILVA, P.G., DABRIO, C.J., GOY, J.L., ROQUERO, E., SOLER, V., BORJA, F., LARIO, J., POLO, D. & LUQUE, L. 2005: Landscape evolution and geodynamic controls in the Gulf of Cadiz (Huelva coast, SW Spain) during the Late Quaternary. − Geomorphology 68: 269-290.