



RESEARCH ARTICLE - ANTS

A New Ant Species, *Temnothorax ansei* sp.n. (Hymenoptera: Formicidae) from the Arid Environments of South-eastern Spain

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Abstract

We describe here a new ant species in the genus *Temnothorax*, species group *laurae*, based on morphological evidence supported by other biological information. It has been discovered at two locations in southeast Spain: Pulpí (Almería) and Lorca (Murcia). This species is a member of the *laurae* species group based on the following characters: large eyes, long and erect hairs on alitrunk, petiole and postpetiole, rectangular head and metanotal groove. Other characters unique to new species are: dark brown in color, decumbent pilosity, and smooth and shiny head and pronotum. In addition, this new species is distinctly nocturnal in its activity patterns. Based on the morphological measurements of the queens and the workers, as well as our observations in the laboratory, we predict that this species has a dependent colony founding. An identification key to the Iberian Peninsula species of the *laurae* group is also provided.

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Introduction

Temnothorax (Mayr, 1861), is a speciose genus of small and generally inconspicuous ant with a predominantly Holarctic distribution. The most recent catalogue lists 380 valid species and 47 valid subspecies (Bolton, 2015). Colonies are typically small, often with less than 100 workers (Prebus, 2015). *Temnothorax* is divided into nine species groups (Cagniant & Espadaler, 1997). One of those is *laurae* species group, whose members are characterized by large eyes relative to the length of the head capsule ($Ol > 30$), postpetiole more or less trapezoidal in dorsal view (Prebus, 2015), long and erect hairs on alitrunk, petiole and postpetiole, rectangular head, and the presence of metanotal groove (Tinaut, 1994; Cagniant & Espadaler, 1997). They are rarely collected, probably because of their small colony size and nocturnal activity patterns; caused by hot and arid environment they inhabit (Tinaut, 1994; Cagniant & Espadaler, 1997).

In the Iberian Peninsula, there are five known species belonging to the *laurae* group: *Temnothorax blascoi* (Espadaler, 1996), *T. caesari* (Espadaler, 1997b), *T. crepuscularis* (Tinaut, 1994), *T. universitatis* (Espadaler, 1997a) and *T. naeviventris* (Santschi, 1910). Two of these are present in the Segura river basin (south-east Spain): *T. blascoi* (Catarineu & Tinaut, 2012) and *T. universitatis* (see Table 2). Considering the difficulty of detecting individuals in this group, it is likely there are more undescribed species.

On July of 2014, in a pitfall transect, we collected two workers of a *Temnothorax* species, belonging to the *laurae* group, that we were unable to identify, at a location near Pulpí (Almería, Andalucía, Spain) 1.716W, 37.389N (decimal format). The same species was also collected in two pitfall transects in Lorca (Murcia, Spain) 1.774W, 37.670N and 1.774W, 37.685N (Fig 1).

Using nocturnal baits, with tuna, cookies, and Wilson media, we managed to locate and excavate five nests at the





Fig 1. Map of Spain with the location of the Segura river basin outlined and the two localities with *Temnothorax ansei* sp.n. indicated with black squares.

Pulpí site obtaining five living colonies. We were able to keep three of these colonies in the laboratory until males and queens were acquired.

Material and methods

Digital color images were obtained by AntWeb and are available online (Fisher, 2002; <http://www.antweb.org>). Measurements were taken of 27 workers, eight queens and five males with a stereo microscope Leica S6D at a micrometer magnification of up to x80. Morphometric characters and indices are based on Seifert *et al.* (2014), Prebus (2015), and Seifert & Csösz (2015):

BI. Buschinger Index: SPST/ SPL.

CS. Cephalic size: the arithmetic mean of HL and HW

EL. Eye Length: maximum diameter of compound eye, including all structural visible ommatidia irrespective of the pigmentation status, measured in oblique lateral view.

HL. Head Length: maximum distance from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin of head, measured in full-face view.

HW. Head Width: width of head directly behind the eyes, measured in full-face view.

OI. Ocular Index: $EL/HW \times 100$.

SPL. Minimum distance between the center of the propodeal spiracle and the margin of subspinal excavation, measured with both end points positioned in the same focal level.

SPST. Distance between the center of the propodeal stigma and the spine tip, the stigma center refers to the midpoint defined by the outer cuticular ring but not to the center of the real stigma opening that may be positioned eccentrically.

TL. Tibia Length: maximum length of the tibia.

WL. Weber's Length: diagonal length of mesosoma in lateral view from the posteroventral margin of propodeal lobe to the anterior-most point of pronotal slope, excluding the neck.

The varying degrees of inclination of pubescence and pilosity are often of high diagnostic value throughout a broad spectrum of ant genera. In this context, we use the terms “erect”, “suberect”, “subdecumbent”, “decumbent”, and “appressed” following Wilson (1955).

Description

Temnothorax ansei sp.n.

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Type material examined

Holotype: a worker from a location nearby Pulpí (Almería, Spain), 1.716W, 37.389N (decimal format), Elevation 243 m, 23 July 2014, collected by C. Catarineu and labelled with the specimen code W01-10S501.

Paratypes: 26 workers, 10 queens and nine males with the same data as holotype; six workers from Lorca (Murcia, Spain); three workers from 1.774W, 37.670N, Elevation 591 m; three workers from 1.774W, 37.685N, Elevation 464 m). All the paratypes were collected by C. Catarineu from July 2014 to June 2015.

Repositories

The National Museum of Natural Sciences (MNCN, Madrid, Spain) holotype, two workers, one queen and one male (registration number C.T. 2730). The California Academy of Sciences, USA, two workers, one intermorph, one queen and one male (CASENT0763773, CASENT0763775, CASENT 0919826, CASENT0919953 and CASENT 0919954). The Natural History Museum, London, U.K., two workers, one queen and one male. Museum d'Histoire Naturelle, Genève, Switzerland, two workers, one queen and one male (MHNG ENTO numbers 10129 to 10132). University of Granada, Spain, two workers, one queen and one male. Coll. Xavier Espadaler (Autonomous University of Barcelona, Spain) two workers, one queen and one male. Coll. Joaquin L. Reyes-López (University of Cordoba, Spain) eight workers, three queens, one intermorph and one male. Coll. Chema Catarineu (Murcia, Spain) 11 workers, five queen, one intermorph and three male.



Fig 2. *Temnothorax ansei* sp.n. worker in lateral view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0763775_P, published with permission.



Fig 3. *Temnothorax ansei* sp.n. worker in dorsal view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0763775_D, published with permission.



Fig 4. Head of *Temnothorax ansei* sp.n. worker in frontal view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0763775_H, published with permission.

Description of worker (Figs. 2-4)

Measurements (in mm): HL 0.66–0.76, HW 0.50–0.59, CS 0.58–0.68, EL 0.16–0.24, WL 0.80–0.98, SPST 0.18–0.26, SPL 0.10–0.14, BI 1.60–2.50, TL 0.48–0.60; OI 29.55–44.19 (n=27 workers).

Head, mesosoma and gaster dark brown, mandibles, legs and antennae brownish yellow. Hairs on alitrunk, petiole and postpetiole long and erect (mean mesonotum hair length=104µm). Mandibles, legs, funiculi and scapes with short decumbent pubescence. Head, pronotum and gaster with short and sparse decumbent pubescence. Head rectangular with parallel sides. Occiput straight. Eyes large (EL/CS=0.26-0.39). Antennae 12-segmented, antennal scape reaching occiput. Mandibles with five teeth: one apical longer, one subapical of intermediate length and the three smaller and irregular. Antennal club three-segmented, funiculus concolorous. Head smooth and shiny with some longitudinal costulae between the frontal carinae present, costulae never reaching occiput. Malar area costulate and reticulate. Clypeus smooth and

shiny, a median longitudinal carinae, and two lateral carinae present and conspicuous. Frontal triangle smooth and shiny. Alitrunk with metanotal groove. Pronotum smooth and shiny. Mesonotum and propodeum laterally weakly reticulate, smooth and shiny dorsally. Propodeal spines long (SPST/CS=0.29–0.41), integument between spines smooth and shiny. Petiole and postpetiole finely reticulate-rugulose laterally, smooth and shiny dorsally. Petiole triangular in profile, with rounded apex and with four long setae on postero-dorsal surface. Postpetiole rounded in profile, trapezoidal in dorsal view, wider than long, and wider than petiole, with six long setae. Gaster smooth and shiny.

Variability: propodeal spines can vary in size, apex of petiole varies from less to more rounded.

Description of queen (Figs. 5–7)

Measurements (in mm): HL 0.66–0.71, HW 0.51–0.58, CS 0.59–0.64, EL 0.19–0.24, WL 0.90–1.04, SPST



Fig 5. *Temnothorax ansei* sp.n. queen in lateral view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0919953_P, published with permission.



Fig 6. *Temnothorax ansei* sp.n. queen in dorsal view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0919953_D, published with permission.



Fig 7. Head of *Temnothorax ansei* sp.n. queen in frontal view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT 0919953_H, published with permission.

0.19–0.25, SPL 0.09–0.14, BI 1.45–2.29, TL 0.50–0.59, OI 34.88–41.86 (n=8 queens).

Size and color as in workers. Hairs on alitrunk, petiole and postpetiole long and erect (mean mesonotum hair length=78 μ m). Eyes large (EL/CS=0.31–0.37), ocelli well developed. Antennae 12-segmented. Antennal scape reaching occiput. Antennal club three-segmented, funiculus concolorous. Mesosoma only slightly bigger than in workers. Anterior edges of pronotum slightly visible from the dorsal view. Pronotum, scutum and scutellum smooth and shiny. Mesopleurae with a few lateral costulae. Propodeum with lateral costulae, smooth and shiny between the spines. Petiolar node triangular in profile, its apex more acute than in workers. Well developed spines but somewhat smaller than in workers (SPST/CS=0.32–0.39). Petiole, postpetiole and gaster as in workers. Transparent wings, with very reduced veins. Pterostigma transparent, light yellow.

Variability: propodeal spines can vary in size, apex of petiole varies from less to more rounded.



Fig 8. *Temnothorax ansei* sp.n. intermorphic individual in lateral view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0919826_P, published with permission.



Fig 9. *Temnothorax ansei* sp.n. intermorphic individual in dorsal view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT 0919826_D, published with permission.



Fig 10. Head of *Temnothorax ansei* sp.n. intermorphic individual in frontal view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0919826_H, published with permission.

We have found two worker-queen intermorphs, one in the wild (Figs. 8-10), and the other born in laboratory conditions.

Description of male (Figs. 11–13)

Measurements (in mm): HL 0.49–0.58, HW 0.40–0.50, CS 0.44–0.54, EL 0.19–0.23, WL 0.98–1.08, TL 0.60–0.76, OI 45.00–50.00 (n= 5 males).

Head, alitrunk, petiole, postpetiole and gaster light brown; antennae and legs lighter. Hairs on alitrunk, petiole and postpetiole long and erect (mean mesonotum hair length = 84 μ m). Oval-shaped head, smooth and shiny. Very large eyes (EL/CS=0.42–0.46), nearly half of head length, located in the lower half of face sides. Ocelli well developed. Antennae 13-segmented. Scape surpassing the occipital margin and as long as the first 8 segments of the funiculus. Antennal club four-segmented. Mandibles with one apical tooth, one subapical and 2–3 smaller. Mesopleurae and propodeum smooth, with less prominent costulae than in worker and queen. Pronotum, prescutum, scutum and scutellum smooth and shiny. Notauli marked. Scutum and scutellum separated by a depression. Metanotum present, narrow and separated from scutellum and propodeum. Propodeum reticulated, with some lateral costulae



Fig 11. *Temnothorax ansei* sp.n. male in lateral view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0919954_P_1, published with permission.



Fig 12. *Temnothorax ansei* sp.n. male in dorsal view. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0919954_D, published with permission.

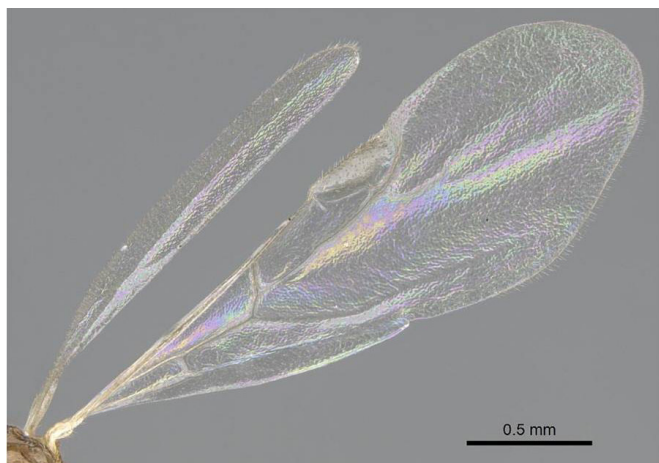


Fig 13. *Temnothorax ansei* sp.n. male wings. Photo credit: Michele Esposito, from www.AntWeb.org, CASENT0919954_P_2, published with permission.

and without spines, only with a very slight angle. Petiole low and with node rounded. Gaster smooth and shiny. Wings as queens. Variability: some males have the propodeum rounded.

Etymology

The species recognizes and honours the Asociación de Naturalistas del Sureste (ANSE), an organization rooted in the south-east of Spain since 1973 (ANSE 2015). This is a naturalist and environmentalist, non-governmental organization which, by its efforts on nature research, awareness, and conservation activism, has earned the respect and support of generations of scientists and citizens. Most significantly, for the last five decades, ANSE has been a force of scientific and environmental activism promoting the formal recognition of the previously poorly-valued semiarid ecosystems of the south-east of Spain, where *T. ansei*, our newly discovered species, finds its home.

Biology

Foraging workers of *T. ansei* sp. n. were attracted to the baits at night, or sometimes during twilight (in June and July, the workers begin to forage from approximately about 19:00 GMT). After feeding for a few minutes, they carried a small cookie crumb to their nearby nest, although never more than one meter away. Through careful monitoring in a territory of about 230 m², we were able to locate five nests, each with a single entrance hole in the soil of approximately 1 mm in diameter. These nests were very hard to detect as they lacked any external signs or evidence of ant activity.

We excavated the five nests and found that the main chamber was about 15-20 cm deep. Colonies ranged from two to 52 workers. Two of them had two wingless queens (Table 1). Three of these colonies were relocated to our laboratory and have been maintained there under controlled conditions to date. The other two, an incipient colony with only two workers and other with 13, did not survive in captivity. Ants were fed with honey-water and small crickets and have produced during two years new males and females. These sexuals were born from eggs laid by the queen in the laboratory. All 19 queens born in captivity lost their wings in the first 1-4 weeks, 13 of them in the first three days, and then continued living normally in the nest, cooperating with the others. This behaviour has also been observed in other species of the group, for instance *T. caesari* (Espadaler, 1997b). Eggs, larvae and pupae were placed by the workers in one group on the floor of one chamber altogether.

Table 1. Nest excavations data for the new species *Temnothorax ansei* sp.n., discovered in 2014 in the south-east of Spain.

Nest	Excavation date	queen wingless	workers	queen winged	male
1	01/11/2014	1	52		1
2	23/05/2015	2	20	1	
3	13/06/2015	3	21		2
4	13/06/2015	4	13		5
5	20/06/2015	5	2		

Table 2. Ant species sympatric with *Temnothorax ansei* sp.n.

Species/ Locality	Pulpí	Lorca S2	Lorca S3
<i>Aphaenogaster iberica</i> Emery	X		X
<i>Camponotus foreli</i> Emery	X	X	X
<i>Camponotus sylvaticus</i> Olivier	X	X	X
<i>Cardiocondyla batesi</i> Forel			X
<i>Cataglyphis iberica</i> Emery		X	X
<i>Crematogaster auberti</i> Emery	X	X	X
<i>Goniomma hispanicum</i> André	X		
<i>Goniomma kugleri</i> Espadaler	X		X
<i>Iberoformica subrufa</i> Roger			X
<i>Leptanilla sp</i>	X		
<i>Messor barbarous</i> Linnaeus	X	X	
<i>Messor bouvieri</i> Bondroit	X	X	X
<i>Oxyopomyrmex saulcyi</i> Emery			X
<i>Pheidole pallidula</i> Nylander	X		X
<i>Plagiolepis schmitzii</i> Forel		X	X
<i>Solenopsis sp</i>			X
<i>Temnothorax cristinae</i> Espadaler	X		
<i>Temnothorax formosus</i> Santschi			X
<i>Temnothorax universitatis</i> Espadaler			X
<i>Temnothorax luteus</i> Forel			X
<i>Temnothorax niger</i> Forel	X		
<i>Temnothorax racovitzai</i> Bondroit		X	
<i>Temnothorax specularis</i> Emery	X	X	X
<i>Tetramorium semilaeve</i> André	X	X	X

Ecology

Both collecting localities are semiarid habitats with sparse vegetation cover, dominated by *Stipa tenacissima* L. grassland at the Pulpí site and chamaephytes and little shrubs at the Lorca site. Altitudes are 243 m at Pulpí and 464–591 m at Lorca. The average annual rainfall is 272 and 313 mm at Pulpí and Lorca sites, respectively.

We found 25 ant species at the same habitat (Table 2), including *T. universitatis*, a species we consider, based on the morphology, to be the closest relative of *T. ansei* sp.n.

Discussion

Taxonomic position and diagnosis

This new species, *T. ansei* sp.n. clearly belongs to the *laurae* group, by showing characteristic features of this group such as large eyes in relation to the length of the head capsule (OI > 30). Additional traits consistent with the *laurae* group are head capsule elongated (CI < 85), postpetiole more or less trapezoidal in dorsal view and widest anterior to the midlength of the segment (Prebus, 2015). As many species within this group, *T. ansei* sp.n. is also found in arid environments.

Based on the morphology, the closest relative of *T. ansei*

sp.n. in the *laurae* group is species *T. universitatis*. We can differentiate between those two species because *T. universitatis* worker is light brown or dirty yellow, with head less shiny, alitrunk dorsally opaque and pronotum laterally rugulose.

From the other Iberian species in the *laurae* group, the main differences are:

Temnothorax blascoi is smaller, light yellow, with dense pilosity all over the body and with long and thin setae similar to *Temnothorax recedens* Espadaler.

Temnothorax caesari has mesosoma olivaceous brown, less shining and less quadrangular head. Dorsal striae in pronotum and mesonotum. Pilosity erect on head and gaster.

Temnothorax crepuscularis is yellow, with metanotal groove unmarked, abundant semi-erect setae on head and gaster, head and alitrunk rough, petiole and postpetiole dorsally rough.

Temnothorax naeviventris is light yellow, with head and alitrunk coarse and opaque, and with pilosity erect in head.

Based on our original findings and the prior contributions by other authors (Santschi, 1910; Tinaut, 1994; Espadaler 1996, 1997a, 1997b), we propose the following dichotomous key to the Iberian *laurae* group species. This key is based on the external morphology of the workers:

Key to the worker caste of Iberian *Temnothorax*, *laurae* species group "Pulpí"

- 1 Metanotal groove absent..... *T. crepuscularis*
- Metanotal groove present 2
- 2 Dense pilosity all over the body.....3
- Sparse pilosity all over the body.....5
- 3 Head and gaster dark brown; mesosoma olivaceous brown; propodeal spines shorter and blunt..... *T. caesari*
- Light yellow; propodeal spines long, thin and acute.....4
- 4 Dorsal setae long, thin and curved*T. blascoi*
- Dorsal setae thick and blunt.....*T. naeviventris*
- 5 Light brown or dirty yellow; pronotum laterally dull.....*T. universitatis*
- Dark brown; pronotum laterally smooth and shiny....*T. ansei*

Biological observations

Ants show two contrasting strategies of colony founding. In the Independent Colony Foundation (ICF), a queen can raise the first generation of brood alone. The ICF strategy frequently involves claustral founding where queens are characterized by voluminous wing muscles which can histolize after dispersal. These queens must also have high metabolic reserves. In contrast, Dependent Colony Foundation (DCF), is a strategy in which the queen is helped by some workers to create a new colony-budding or fission (Hölldobler & Wilson, 1990; Heinze & Tsuji, 1995; Peeters & Ito, 2001; Keller *et al.*, 2014).

In a majority of species, mating and dispersals take place during a nuptial flight. There is always a trade off

between the costs and benefits of flight. Wing reduction or simplified thoracic structures could be some of the steps associated with the shift in mating and dispersal strategies from nuptial flight and ICF to DCF (Tinaut & Heinze, 1992).

In the past, DCF has been linked with a range of ecological factors, for example habitat patchiness, nest site limitation, food limitation, competition, predation, climate, or nest site instability (Heinze & Tsuji, 1995; Cronin *et al.*, 2013). Several studies suggested also a correlation between the loss of flight capability in sexually active females and the ecological conditions in arid and semi-arid environments (Tinaut & Heinze, 1992; Tinaut, 1994; Heinze & Tsuji, 1995). Unsurprisingly, at least 5 to 8 % of all ant species from Spain or Algeria produce queens incapable of dispersal and mating flights (Tinaut & Heinze, 1992).

In the polymorphic queen of *T. longispinosus* (Roger), dependent-founding queens are smaller than independent-founding queens and exhibited significantly lower flight activity. This reduced flight activity may facilitate returning to the natal nest after mating (Howard & Kennedy, 2007). Our data show that in *T. ansei* sp.n., queens are small and similar to the size of workers. The queen/worker volume has been related to nest founding strategies, independent or dependent (Stille, 1996). For *T. ansei*, this ratio is 1.91 (five workers and five queens from the same locality) and this fits with the dependent foundation (ratio 1.9–2.7), being very far from independent foundation range (ratio 5.1–9.1).

In *T. ansei* sp.n., we found that queens lost their wings within the nest. Espadaler (1997b), studying *T. caesari*, found that seven out of seven queens born in the laboratory lost their wings within two days, and without being fertilized. It is known that the queens that disperse by mating flights do not lose their wings inside the colony (Hölldobler & Wilson, 1990; Heinze & Tsuji, 1995), and the rapid loss of wings in females seems to indicate intranidal mating (Heinze & Tsuji, 1995). Furthermore, *T. ansei* sp.n. seems to be partially polygynous, both in the wild and in the laboratory. Two out of five nests excavated have had two wingless queens, and in the laboratory the three colonies nowadays have seven, six and two wingless queens respectively but this could be caused by laboratory conditions. Finally, we have found three worker-queen intermorphs (with our current data, the ratio intermorphs/workers is 3/32).

Our data shows that the *T. ansei* sp.n. colony founding strategy is likely to be Dependent Colony Foundation. Further research is needed to examine the mating behaviour and to confirm the colony founding strategy of this new species.

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References

- ANSE (2015). Asociación de Naturalistas del Sureste. Available from <http://www.asociacionanse.org/> (accessed date: 31 October, 2016).
- Bolton, B. (2015). AntWeb: Bolton World Catalog Ants. Available from <https://www.antweb.org/world.jsp> (accessed date: 31 October, 2016).
- Catarineu, C., & Tinaut, A. (2012). Introducción al conocimiento de los formícidos de la Región de Murcia (Hymenoptera, Formicidae). Boletín de la Asociación Española de Entomología, 36: 145-162.
- Cagniant, H. & Espadaler, X. (1997). *Leptothorax*, *Epimyrma* and *Chalepoxenus* of Morocco (Hymenoptera, Formicidae) Annales de la Société Entomologique de France, 33: 259-284.
- Cronin, A.L., Molet, M., Doums, C., Monnin, T. & Peeters, C. (2013). Recurrent evolution of dependent colony foundation across eusocial insects. Annual Review of Entomology, 58: 37–55. doi: 10.1146/annurev-ento-120811-153643.
- Espadaler, X. (1996). Diagnósis preliminar de siete especies nuevas de hormigas de la península ibérica (Hymenoptera: Formicidae). Zapateri. Revista Aragonesa de Entomología, 6: 151-153.
- Espadaler, X. (1997a). Catàleg de les formigues (Hymenoptera: Formicidae) dels països catalans. Sessió Conjunta d'Entomologia, 23-42.
- Espadaler, X. (1997b). *Leptothorax caesari* sp.n. (Insecta: Hymenoptera: Formicidae), a granivore with apterous males. Annalen des Naturhistorischen Museums in Wien. Serie B für Botanik und Zoologie, 145-150.
- Fisher, B.L. (2002). Antweb. The California Academy of Sciences, San Francisco, USA Available from <http://www.antweb.org> (accessed date: 31 October, 2016).
- Heinze, J. & Tsuji, K. (1995). Ant reproductive strategies. Researches on Population Ecology, 37: 135-149.
- Hölldobler, B. & Wilson, E.O. (1990). The ants. Cambridge: Harvard University Press. 732 pp. doi: 10.1007/978-3-662-10306-7.
- Howard, K.J. & Kennedy, D. (2007). Alternative mating behaviors of the queen polymorphic ant *Temnothorax longispinosus*. Naturwissenschaften, 94: 945-950. doi: 10.1007/s00114-007-0281-8.
- Keller, R. A., Peeters, C., & Beldade, P. (2014). Evolution of thorax architecture in ant castes highlights trade-off between

- flight and ground behaviors. *eLife*, 3: e01539. doi: 10.7554/eLife.01539.
- Mayr, G. (1861). Die europäischen Formiciden. Nach der analytischen methode bearbeitet. Wien: C. Gerolds Sohn, 80 pp. doi:10.5962/bhl.title.14089.
- Peeters, C. & Ito, F. (2001). Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annual Review of Entomology*, 46: 601-630. doi: 10.1146/annurev.ento.46.1.601.
- Prebus, M. (2015). Palearctic elements in the old world tropics: a taxonomic revision of the ant genus *Temnothorax* Mayr (Hymenoptera, Formicidae) for the Afrotropical biogeographical region. *Zoo Keys*, 483: 23–57. doi:10.3897/zookeys.483.9111.
- Santschi, F. (1910). Nouvelles fourmis de Tunisie (suite). *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord*, 1: 61-64.
- Seifert, B., Csósz, S. & Schulz, A. (2014). NC-Clustering demonstrates heterospecificity of the cryptic ant species *Temnothorax luteus* (Forel, 1874) and *T. racovitzai* (Bondroit, 1918) (Hymenoptera: Formicidae). *Contribution to Entomology*, 64: 47-57.
- Seifert, B. & Csósz, S. (2015). *Temnothorax crasecundus* sp.n., a cryptic Eurocaucasian ant species (Hymenoptera, Formicidae) discovered by Nest Centroid Clustering. *Zookeys*, 479: 37-64. doi:10.3897/zookeys.479.8510.
- Stille, M. (1996). Queen/worker thorax volume ratios and nest-founding strategies in ants. *Oecologia*, 105: 87-93. doi: 10.1007/bf00328795.
- Tinaut, A. & Heinze, J. (1992). Wing reduction in ant queens from arid habitats. *Naturwissenschaften*, 79: 84-85. doi: 10.1007/bf01131809.
- Tinaut, A. (1994). Nueva especie de *Leptothorax* (Mayr, 1855) del grupo *laurae* Emery, 1884 *Leptothorax crepuscularis* n.sp. (Hymenoptera, Formicidae). *Zoologia Baetica*, 5: 89-98.
- Wilson, E.O. (1955). A monographic revision of the ant genus *Lasius* (Vol. 113, No. 1). *The Museum*. doi: 10.1086/401086.

