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Differentiating *Iberoformica* and *Formica* (*Serviformica*) with Description of the Sexual Castes of *Formica* (*Serviformica*) *gerardi* Bondroit, 1917 stat. rev.

K Gómez[1], P Lorite[2], F García[3], A Tinaut[4], X. Espadaler[5], T Palomeque[2], O Sanllorente[2], J Trager[6]

1 - Independent Researcher, Barcelona, Spain

2 - Departamento de Biología Experimental, Universidad de Jaén, Jaén, Spain

3 - Barcelona, Spain

4 - Departamento de Zoología. Facultad de Ciencias. Universidad de Granada Granada, Spain

5 - CREAF, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

6 - Shaw Nature Reserve, Gray Summit, Missouri, USA

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Corresponding author
Kiko Gómez
Avda 303 nº 117, Castelldefels,
Barcelona, Spain
E-Mail: netodejulilla@gmail.com

Abstract

A list of morphological characters to separate *Iberoformica* and *Formica* (*Serviformica)* (*F. fusca* species group) is provided. Sexual forms of *Formica gerardi* Bondroit are described based on Iberian material and reinstated into the subgenus *Serviformica* based on genetic data and morphological characters. The status of †*F. horrida* Wheeler, 1915 is assessed.

Introduction

Iberoformica subrufa (Roger, 1859) constitutes the monotypic genus *Iberoformica* (Tinaut, 1990) endemic to the Iberian Peninsula and the Mediterranean coast of southern France (Bernard, 1967). Roger (1859) included this species into the genus *Formica* together with *Formica cinerea* Mayr, 1853 and *Formica fusca* Linnaeus, 1758, thus, into the *Serviformica* subgenus/fusca species group.

Bernard (1967) synonymized *Formica gerardi* Bondroit, 1917 and *Formica pyrenaea* Bondroit, 1918 with *I. subrufa* (= *Formica subrufa* Roger, 1859) despite its pilosity and the fact of being the most xerophilous species in the *Formica* genus. He reasoned that types of these species were small, immature and seemed to be hybrids between *I. subrufa* and *Formica cunicularia* Latreille, 1798. Subsequent references consider *I. subrufa* as a distinct valid species of *Formica* (e. g. Collingwood & Yarrow, 1969).

According to Tinaut (1990), *I. subrufa* should be considered under a subgenus or species group different from those defined for *Formica* based on the finding of the smaller males and with other differential characters presented in this article. This new subgenus was called *Iberoformica*. The article also stated the defining characters for *Iberoformica* workers and gynes. Agosti (1994), synonymized *Iberoformica* and the rest of *Formica* subgenera within *Formica*.

Since 2002 studies endorsed the status of *Iberoformica* as a clade different from the rest of *Formica* species groups first (Lorite et al., 2002; Lorite et al., 2004; Lorite et al., 2012) and finally, as a genus closely related but separated from *Formica* (Muñoz-López et al., 2012).

Formica gerardi was described from Banyuls, France and was considered close to *F. cinerea* and *Formica glebaria* Nylander, 1846 (now a synonym of *F. fusca*) (Bondroit, 1917). Although considered a synonym of *I. subrufa* by Bernard (1967), it regained its status as species (Collingwood

& Yarrow, 1969; Collingwood, 1978). It was moved to the subgenus *Iberoformica* (Czechowski et al., 2012: 39) without explanation. Subsequent authors like Borowiec (2014: 435) treat the species as belonging to the subgenus *Serviformica* inside *Formica* but without giving it an official status. Bolton's online catalog (accessed 12/2017) treats the species as belonging in the genus *Iberoformica*.

We propose in this paper that, with the data available, *Iberoformica* is properly a monotypic genus with a single species, *I. subrufa*, and we consequently propose to exclude *F. gerardi* from *Iberoformica* and reinstate it into the genus *Formica*, subgenus *Serviformica*. We also describe the sexual forms of *F. gerardi*, which add even more evidence to our proposal, also supported by genetic data.

Materials and methods

Type material for *I. subrufa* and *F. gerardi* were seen at Bondroit collection (Brussels) and Forel collections (Geneva) respectively. *I. subrufa* samples analyzed cover the whole distribution area, from Southern Spain to South France. *F. gerardi* samples were collected throughout its distribution range (Cádiz, Barcelona, Burgos, Granada and Zaragoza). Sexuals were collected jointly with workers at the nest

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Genitalia were digested with NaOH diluted in distilled water for 24 hours. Resulting parts were mounted in Hoyer fluid.
Collection references:
ATPC: Alberto Tinaut Collection
FGPC: Federico García Collection
KGAC: Kiko Gómez Collection
XEGC: Xavier Espadaler Collection
Numbers and/or letters after collection codes design collection reference numbers that individually identify the specimen.
Measurements and indexes.
All measurements in mm.
HL: Head Length in frontal view measured from the basal clypeal to the apical occipital lines
HW: Head Width, maximum head width in frontal view
SL: Scape Length, excluding the basal constriction and the condylar bulb
EL: Eye Length, length in mm. of the eye's longest axis
WL: Weber Length, in lateral view from the pronotal declivity to the farmost line of the propodeal lobe
PW: Pronotum width in dorsal view, measured just before tegulae
PLD: In dorsal view, distance between propodeal declivity and mesoscutellum, excluding propodeum.
OI: Ocular index. EL/HW x 100
CI: Cepahlic Index. HW/HL x 100
SI: Scape Index. SL/HW x 100
MI: Mesosomal Index. PW/HW x 100
MDI: PW/PLD x 100

Molecular analysis

Several ant species were used for molecular studies (Table 1). Pools of 3 to 5 workers were used for DNA extraction. DNA purification was carried out using the NucleoSpin® Tissue kit from Macherey-Nagel. DNA was finally eluted in 100 µl.

Three nuclear gene fragments were used for phylogenetic analysis; *wingless* (*wnt*-1), *abdominal-A* (*abdA*) and *long-wavelength rhodopsin* (*lwRh*) as well as a fragment of the mitochondrial *COI* gene. Several sequences of these genes were directly retrieved from the Genbank (Table 1). The remaining sequences were obtained by PCR. The nuclear gene fragments were amplified using the primers and PCR conditions described in Palomeque & al. (2015). Primers and PCR conditions described in Sanllorente et al. (2012) were used for *COI* gene amplifications. PCR products were directly sequenced on both strands by the dideoxy sequencing method. The obtained sequences were deposited in the EMBL database (Table 1).

Table 1. Sequences used for molecular analyses. For each species it is indicated the location of the sample and the GenBank accession numbers for the used genes. Some of the sequences were obtained for the present study (ps) and the remaining sequences were retrieved from the GenBank.

Species	Location	*wnt-1*	*abdA*	*lwRh*	*COI*
Proformica longiseta	Sierra Nevada, Granada (Spain)	KX219899	LT883161 (ps)	KX219939	HM126584
Iberoformica subrufa	Canena, Jaén (Spain)	LT623167 (ps)	LT623178 (ps)	LT632330 (ps)	KJ499818
Polyergus rufescens	Tours (France)	KX219902	LT883159 (ps)	KX219942	KJ499816
Polyergus samurai	Natural History Museum and Institute, Chiba (Japan)	KX219903	LT883160 (ps)	KX219943	AB010930
Formica cunicularia	Campus Universidad Jaén (Spain)	LT623165 (ps)	LT623177 (ps)	LT632328 (ps)	AB010926
Formica frontalis	Sierra Nevada, Granada (Spain)	KX219882	LT883157 (ps)	KX219922	KX219955
Formica sanguinea	Tuscany (Italy)	KX219883	LT883158 (ps)	KX219923	KX219956
Formica gerardi	Sierra de Huetor, Granada (Spain)	MF276903 (ps)	LT883156 (ps)	MF276901 (ps)	MF276902 (ps)

Multiple-sequence alignments were performed using CLUSTALW. This dataset was used for phylogenetic analyses using the Maximum-Likelihood method (Saitou & Nei, 1987) implemented in the program MEGA version 6 (Tamura et al., 2013). The best-fit nucleotide substitution model with the lowest BIC (Bayesian Information Criterion) value was chosen for each molecular marker and for the concatenated nucleotide sequences of the four gene fragments (GTR+G+I). Node support was assessed with 1000 bootstrap replicates. Bayesian analyses were carried out for each locus separately and for concatenated nucleotide sequences using MrBayes version 3.2 (Ronquist et al., 2011). Two independent runs were performed with four MCMC chains and run for 1,000,000 generations. The reported value of the effective sample size (ESS) was above 1000 and the potential scale reduction factor (PSRF) was 1.0 for all parameters, so we considered the number of runs sufficient. Trees were sampled each 100th generations and a burn-in was set to 25% of samples. Finally, a 50% majority rule consensus tree was calculated from the obtained trees and the posterior probabilities were calculated using the command "sumt" in MrBayes.

Characterization of F. gerardi workers

The following combination of morphological characters has been used to isolate *F. gerardi* from other close species (*Formica lemani* Bondroit, 1917, *F. fusca*, *Formica decipiens* Bondroit, 1918, and European *Formica* of the rufibarbis group). Ecological requirements and habitat types used by those species are also indicative – *F. gerardi* is the most xerothermic species within European Formica– and are currently in use during field work.

- Colour light to dark brown, sometimes with reddish brown areas at the sides of pronotum and pro-mesonotum lateral juncture.
- Body surface appearing, at low magnification (<20X), as absolutely mat.
- Internal face of tibiae III with diluted pubescence. Pubescent setae could be described as flat, wide and very appressed over tibial surface. Instead, in *F. lemani*, *F. fusca*, *F. decipiens*, and European *F. rufibarbis* group, the internal face of tibia III pubescence density is much higher (see figure 2). *Formica picea* Nylander 1846, strangely enough, approaches *F. gerardi* condition in tibial pubescence density but has otherwise clear differences in surface shininess, pilosity and colouration.
- Pronotum and mesonotum with short erect setae
- Propodeum lower than in European *F. rufibarbis* group species.

Sexual castes description for *F. gerardi*

Queen

Revised Material:

SPAIN: Barcelona, El Muntanyá (Seva) 710m 18/07/2000, Espadaler, X. leg (1q) [XE00205-2]; Burgos, Alto de Solanillas (Castrovido) 990m 29/04/2016 (F. García) (3w, 1q) FGPC; Burgos, Alto de Solanillas (Castrovido) 29/04/2016 (F. García) (3w, 1q) FGPC; Cádiz, Montes de Propios (Jerez de la Frontera) 26/07/2008 (F. García) (3w, 1q) FGPC; Granada, Sierra Alfaguara (1w, 2q) B. Pascual leg (ATPC 6363); same data (2w, 1q) (ATPC 6364); same data, (1q each) (ATPC 6366, ATPC 6367) Huesca, Torre Ventosa (Sierra de Alcubierre) 05/2009 (F. García) (3w, 1q) FGPC; Palencia, Carrión de los Condes (2w, 1q) A. Tinaut leg (ATPC 6362); Zaragoza, Sierra de Alcubierre (1q) FGPC

HL=1.7 [1.36-1.91] , HW=1.71 [1.53-1.89] , SL=1.6 [1.3-1.81] , EL=0.63 [0.55-0.74] , WL=3.13 [2.86-3.57] , PW=1.67 [1.3-1.9] , PLD=2.61 [2.33-2.97] , OI (EL/HW)=37 [33-48] , CI (HW/HL)=100 [95-112] , SI (SL/HW)=93 [84-100] , MI (PW/HW)=98 [78-133] , MDI (PW/PLD)=64 [49-77] (n=9)

Head subquadrate, smaller basally. Mandibles striated, strong and with 6-7 acute teeth in the masticatory margin. Clypeus convex, with a medial carina. Frontal ridges short.

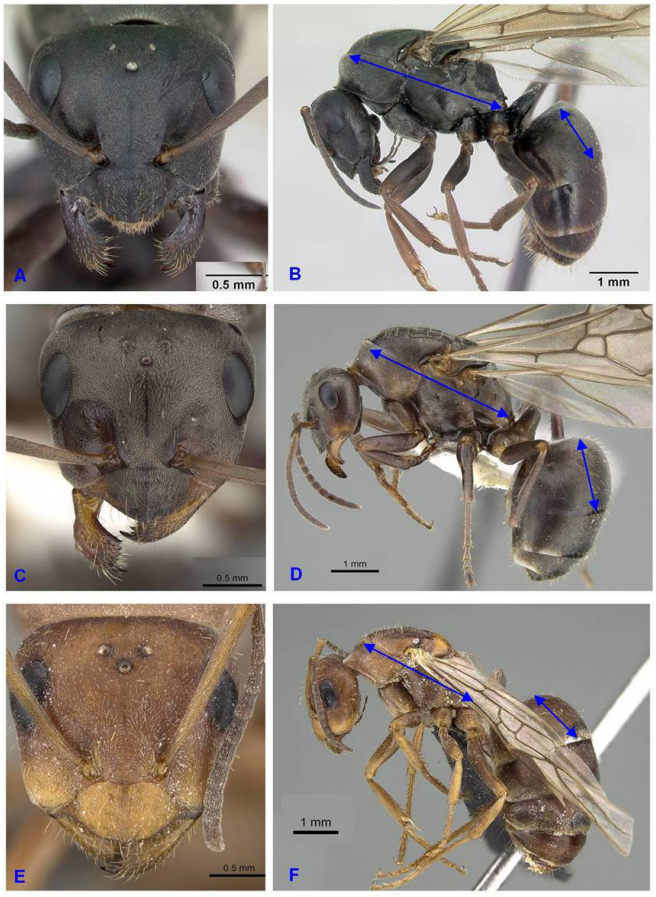

Fig 1. Queens of *Formica fusca* (A, B) [CASENT0173171], *Formica gerardi* (C, D) Q [XE00205-2] and *Iberoformica subrufa* (E, F) [KG030006-3]. Images from www.antweb.org

Scapes long, surpassing the occipital border, funiculus with four first segments elongated, the remainder subquadrate.

Pronotum dorsally visible and relatively low in lateral view in the smaller specimens. Scutum rounded in profile view, scutellum flat in profile view and subquadrate in dorsal view. Propodeum a straight line to the insertion with petiole. Scutoscutellum suture demarcated but not deep. Petiole squamiform, high, narrowly ovate in profile view. Subrectangular in frontal view, convex with a medial notch. Gaster as wide as mesosoma in dorsal view.

Whole body covered with a short, whitish pubescence. Long, erect to semierect white setae present following the frontal ridges to occipital margin of the head (5 to 10), abundant on clypeus (10-15), numerous (>10) and sudecumbent on pronotal dorsum, semierect on dorsum of mesosoma (>20) and abdomen. Rest of the head, propodeum and petiole with appressed pubescence only.

Body and head entirely shagreened and dull due to heavy sculpturation except frontal suture, central-anterior line of scutellum and two symmetrical lateral lines in its posterior half. Colour entirely dark brown to black, with the appendages lighter. A reddish band present in the borders of the pronotum and mesopleurae. Head below eyes and mandibles with a more or less developed reddish tinge.

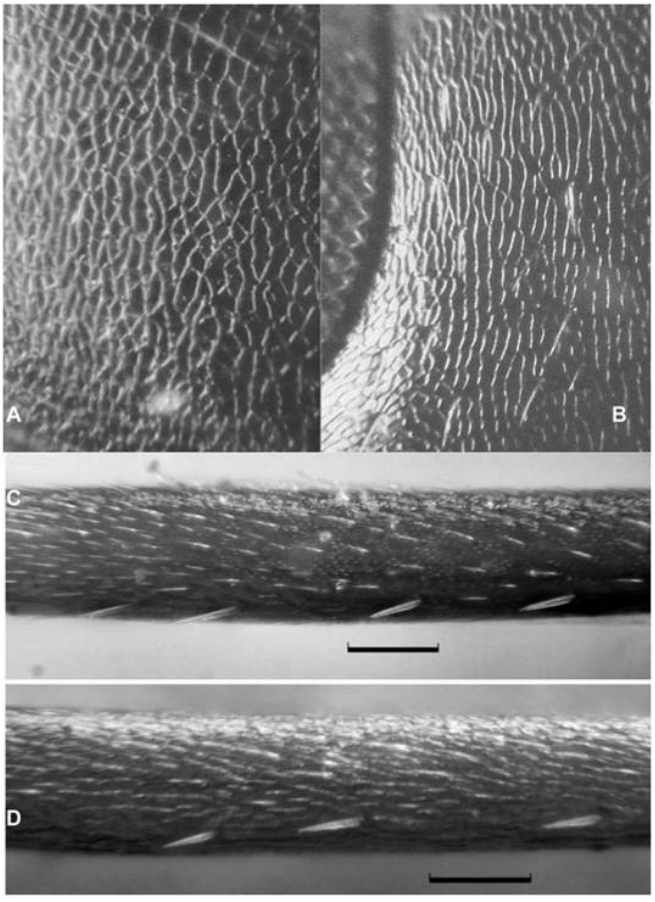

Fig 2. Detail of microsculpture in *F. gerardi* (A), coarse and deep creating a matt appearance, and *F. fusca* (B), superficial. Detail of pubescence in tibiae III, *F. gerardi* (C) and *F. lemani* (D); scale bar = 100 micrometers

Diagnosis:

The long scapes and dull frontal triangle places it in the *Serviformica* subgenus, and its dull cuticle (Figure 2) differentiates it from the rest of Iberian *Serviformica* queens in which scutellum is smooth and shining.

Male

Revised material:

SPAIN: Granada, Sierra Alfaguara, B. Pascual leg (1m each) [ATPC 6365, ATPC 6368]; Barcelona, El Muntanyá (Seva) 710m 18/07/2000, Espadaler, X. leg (2m) [XE00205-3, XE00206] XEGC; Cádiz, Montes de Propios (Jerez de la Frontera) 25/07/2008. (F. García) (1w, 1m) [FGPC0724] FGPCHL=1.30 [1.27-1.36] , HW=1.53 [1.48-1.58] , SL=1.27 [1.23-1.33] , EL=0.73 [0.71-0.76] , WL=2.73 [1.18-3.28] , PW=1.92 [1.66-2.14] , PLD=2.70 [2.47-2.89] , OI (EL/HW)=47 [46-49] , CI (HW/HL)=117 [113-123] , SI (SL/HW)=83 [81-84] , MI (PW/HW)=146 [130-162] , MDI (PW/PLD)=71 [67-80] (n=5).

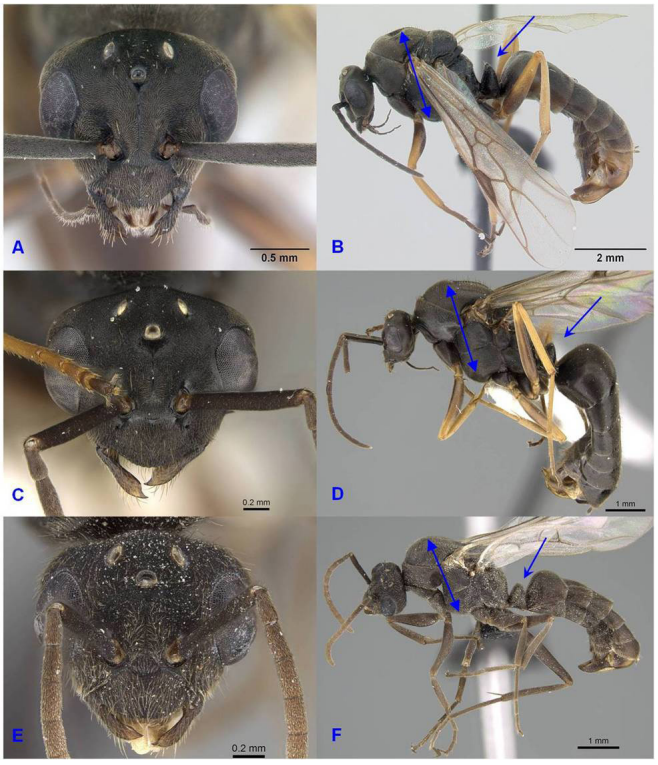

Fig 3. Males of *Formica fusca* (A, B) [CASENT0178770], *Formica gerardi* (C, D) [XE00205-3] and *Iberoformica subrufa* (E, F) [KG030006-4]. Images from www.antweb.org

Head triangular, widest at apex, wider than long (CI~117), vertex convex, lateral a straight line; clypeus convex, medial carina weak but present; mandibles sublinear, slightly rugulose; apical tooth present, followed by a edentate border with 0-1 denticles; eyes large (OI~47); three conspicuous ocelli present and elevated over the rest of the head, the center one oriented forward, the other two laterally; frontal ridges absent, vestigial laterally with exposed antennal sockets.

Scapes long (SI~83) surpassing the occipital border when laid back, the length between occipital border and apex clearly longer than distal to occipital border; funiculus filiform with all funicular segments longer than wide, similar in size.

Mesosoma clearly wider than head (MI~146). Pronotum almost not visible in dorsal view, slightly depressed in the medial line. Scutum rounded, notauli absent, parapsidal lines clearly demarcated. Scutelllum rounded dorsally and laterally, elevated over the scutum. Posteropropodeum clearly longer than dorsopropodeum, rounded in lateral view.

Petiole low; in profile view rounded, subovoid and almost symmetrical, with an acute apex; in frontal view trapezoidal, with straight dorsal line and vertical lateral sides connected by two 45 degree almost straight lines. Gaster long and cylindrical. Genitalia typical of genus *Formica* (Figures 4, 5). Sagitta with apex recurved and rounded, the border of its ventral half dentated. Digitus recurved.

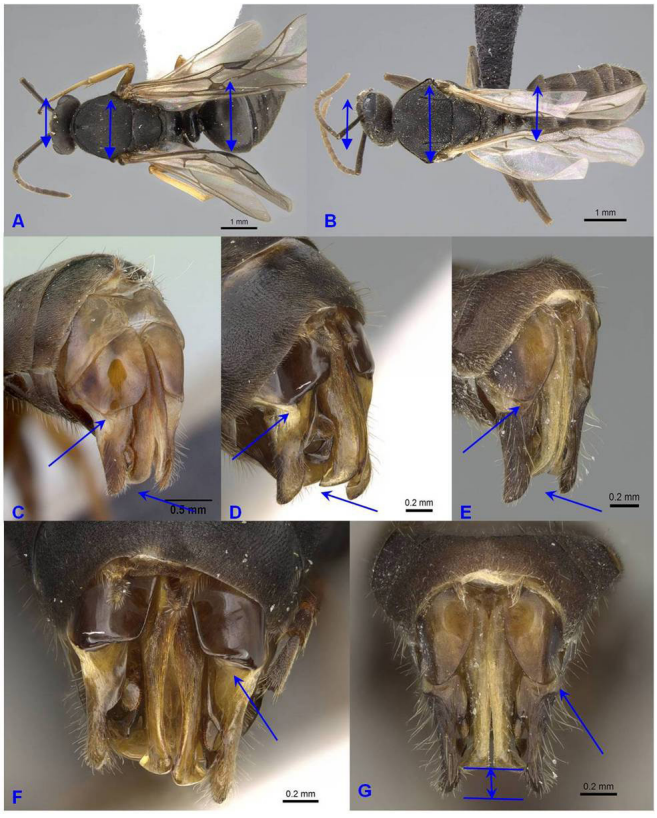

Fig 4. Dorsal view of *Formica gerardi* (A) [XE00205-3] and *Iberoformica subrufa* (B) [KG030006-4]. Detail of genitalia of *Formica fusca* (C) [CASENT0178770], *Formica gerardi* (D, F) [XE00205-3] and *Iberoformica subrufa* (E, G) [KG030006-4]. Images from www.antweb.org

Dark brown to black, with legs and funiculus light brown to brown. Head surface matt except for the frontal line from clypeus to central ocellus. Rest of body sculptured with the same pattern than worker, matt (Figure 3). 1-2 pairs of semierect to erect setae on clypeus medially on clypeus, one on vertex and one setae more below each lateral ocelli. Mesosoma dorsally with scattered yellow, short semierect to erect setae, slightly longer than pubescence, absent on

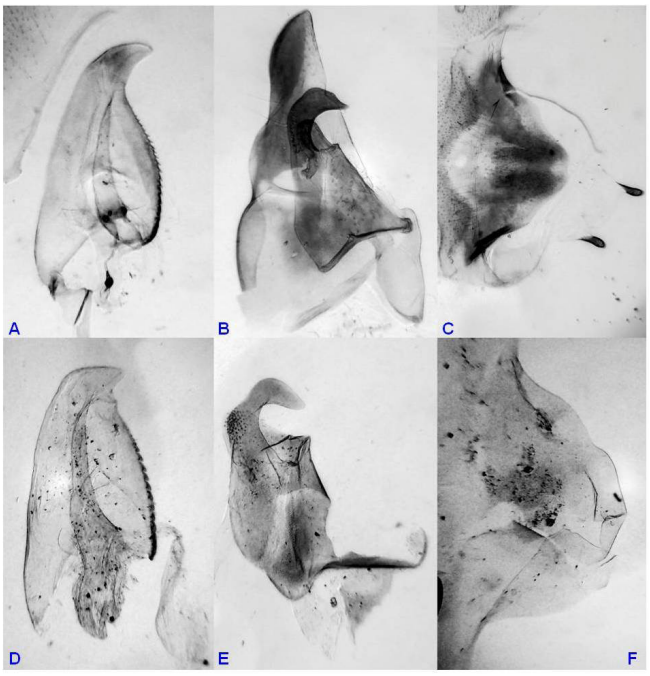

Fig 5. Dissected genitalia of *Iberoformica subrufa* (A, B, C) and *Formica gerardi* (D, E, F). Imaged by Federico García.

propodeum. Petiole with scattered erect short setae, as long as the pubescence. Whole body covered with yellowish, dense long pubescence, its length clearly longer than distance between pubescence lines, overlapping.

Diagnosis:

As in the worker and queen castes, the dull, matt appearance differentiates the *F. gerardi* male from all the other *Serviformica* males present in the Iberian Peninsula, which have shiny mesopleurae.

Discussion

Genetic evidence

Studies of chromosome numbers and molecular phylogenies provide support for our recognition of distinct generic placement of *I. subrufa* and *F. gerardi*

In an earlier study the karyotype of *F. gerardi* had been studied with a haploid chromosome number of n=27, (Lorite et al., 1998). Later, Lorite et al. (2002) showed that *I. subrufa* has a chromosome number of n=26. The authors already suggested in this work that cytogenetic data and morphologic differences (Tinaut, 1990) supported the separation of *I. subrufa* from the subgenus *Serviformica* and the maintenance of the subgenus *Iberoformica* for this species. Previously Agosti (1994) had synonymized the subgenus *Iberoformica* with *Formica*. The chromosome number in the genus *Formica* show low variation, with n=26 or n=27 (Lorite & Palomeque 2008). However, in spite of the low variation in chromosome numbers in the genus *Formica*, the chromosome numbers showed a heterogenous distribution among the different *Formica* subgenera. In the subgenus *Serviformica* n=27 was to be the usual chromosome number, as had already been reported for *F. gerardi*.

Lorite & al. (2004) characterized the satellite DNA in seven species of the genus *Formica*: *F. cunicularia*, *F. fusca*, *F. gerardi*, *F. rufibarbis*, and *Formica selysi* Bondroit, 1918 (*fusca* group), *Formica frontalis* Santschi, 1919 (*rufa* group), *Formica sanguinea* Latreille, 1798 (*sanguinea* group) and in *I. subrufa*. The study showed that satellite DNA sequences from *I. subrufa* were clearly different from those found in *Formica* species, resulting in a phylogenetic tree separated in two well supported clades. In the *Formica* clade the sequences of all species appeared intermixed, including the sequences of *F. gerardi*. These results support the differentiation of *I subrufa* in relation to the other *Formica* species as well as the similarity of the *F. gerardi* sequences with other species of the *fusca* group.

In a later study previous results were confirmed, and *Iberoformica* was raised to a genus status only composed by *I. subrufa*. In the present study a phylogenetic study was carried out on several species of the genus *Formica* and of its outgroup genera, *Polyergus* and *Proformica*, using sequences of nuclear satellite DNA and the mitochondrial 16S rRNA as molecular markers (Muñoz-López & al. 2012). Unfortunately *F. gerardi* was not included in this last study.

All recent molecular phylogenies have shown that the genera *Formica*, *Iberoformica* and *Polyergus* form a monophyletic clade (Blaimer & al. 2015, Sanllorente & al. 2017). In this paper we perform a new phylogenetic study including *F. gerardi*, and other species from the genera *Iberoformica*, *Polyergus* and *Proformica* and using four different genetic markers, three nuclear genes (*wnt-1*, *abdA*, *lwRh*) and a mitochondrial gene (*COI*). The phylogenetic approaches were carried out using one genetic marker alone or different combinations of them. The best bootstrap values are obtained when several molecular markers are considered together (Figure 6). All molecular markers, or combination of them, cluster together all *Formica* species in a well-supported clade and clearly separated from the *Iberoformica*, its sister genus.

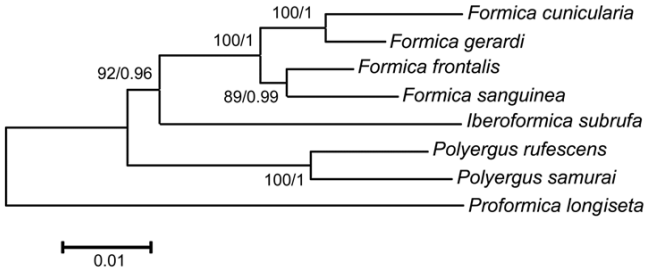

Fig 6. Phylogenetic tree using concatenated sequences of the abdominal A, wingless, long-wavelength rhodopsin nuclear genes and the mitochondrial cytochrome oxidase I gene. First number at nodes indicates the bootstrap values obtained in the maximum likelihood analysis (only when higher than 70%) and the second one the posterior probability values in the Bayesian inference analysis (only when higher than 0.7).

Morphological characters

We summarize in Table 2, the main characters which differentiate the genus *Iberoformica* and the *F. fusca* species group.

Table 2. Comparison of morphological characters between the genus *Iberoformica* and subgenus *Serviformica*.

	Iberoformica	*F. fusca* species group	*Figs.*
WORKER	Nodiform (not squamiform) petiole, becoming almost cylindrical	Petiole squamiform	7B, 7D, 7F
	Concave mesonotum that follows smoothly into the dorsal propodeal line, not meeting at an angle	Mesonotum concave, followed by a horizontal propodeum, both meeting at an angle	7B, 7D, 7F
	Whole body covered with short, thick, truncated white setae	Whole body bare, except for some scattered setae present in propodeum and mesonotum, these hairs thinner than those of *subrufa*	7
QUEEN	Meso and metathorax less developed: metanotal species (details in Tinaut & Ruano, 1992)	Meso and metathorax very developed, similar to the rest of Formica queens (macronotal species)	1B, 1D, 1F
	Gaster with first segment almost rectangular, longer than wide, giving the gaster an elongated appearance	Gaster with first segment wider than long, the gaster not elongated	1B, 1D, 1F
MALES	Small size, similar to workers	Size bigger than workers and only slightly smaller than queens	-
	Head almost as wide as mesosoma	Head clearly less wide than mesosoma	4A, 4B
	Frontal ridges present, short	Frontal ridges absent	3A, 3C, 3E
	Petiole high, squamiform and only slightly concave on the apex	Petiole low, triangular and clearly concave on the apex	3B, 3D, 3F
	Gaster long and narrow, narrower than mesosoma width	Gaster about the same width than mesosoma	4A, 4B
	Sagitta pointy	Sagitta blunt, subrectangular	4C-4G, 5
	Volsella very slender, finger shaped	Volsella semicircular	4C-4G, 5
	Stipes longer than volsella and lacinia	Stipes approximately same long than than volsella and lacinia	4C-4G, 5

Behavioral and ecological differences

Iberoformica subrufa and *F. gerardi* share the fact of being thermophilic ants, living in the Mediterranean forests clearings. Although both species can share the same habitat occasionally, *I. subrufa* may be present in the same localities as other highly thermophilic species like *Camponotus foreli* Emery, 1881 or *Cataglyphis velox* Santschi, 1929, while *F. gerardi* is more dependent on shaded areas.

Being less thermophilic, *F. gerardi* extends its distribution to the Northern Iberian meseta, where *I. subrufa* is present only in isolated areas, and the opposite in the South Iberian Peninsula, where *I. subrufa* is common and *F. gerardi* needs forest-shaded areas to live.

One main behavioral difference between both species is that *I. subrufa* has not known dulotic relation with *Polyergus* species, while various ants belonging in the *fusca* group are commonly enslaved by them.

In its revision of the genus *Polyergus*, Trager writes about *Polyergus rufescens* (Latreille, 1798): *"*I have series from the Pyrenees with *F. gerardi*, where this is the most abundant potential host*"* (Trager, 2013: 511). One of us (F. García) has also found these two species in dulotic relation in Ayora (Valencia province, 39°06'59"N 1°12'37"W 850m , 18/02/2017), in a *Pinus halepensis* pinewood where *F. gerardi* was one of the most frequent species. *I. subrufa* was also present and frequent but was never found in dulotic relation with *P. rufescens*.

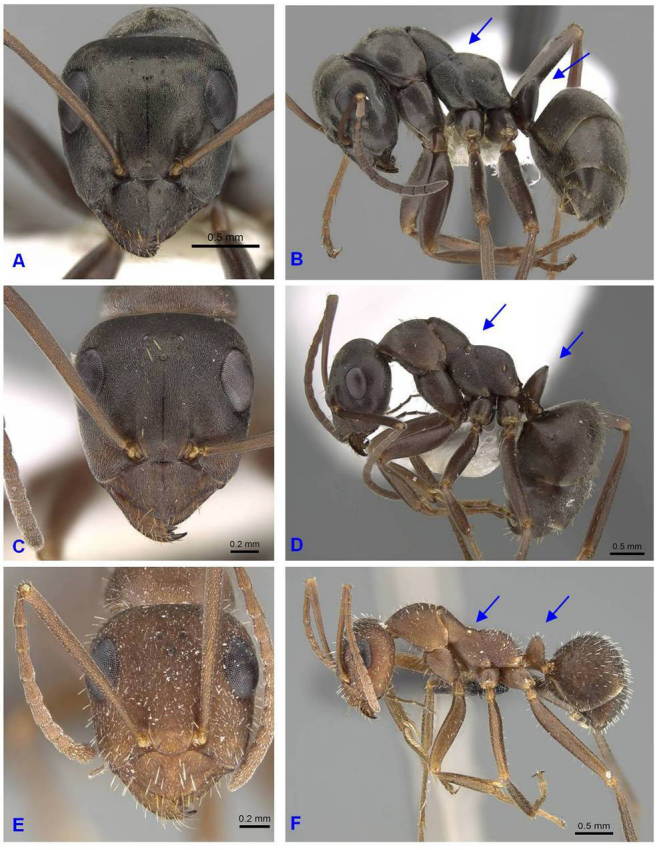

Fig 7. Workers of *Formica fusca* (A, B) [CASENT0280385], *Formica gerardi* (C, D) [XE00205-1] and *Iberoformica subrufa* (E, F) [KG030006-2]. Images from www.antweb.org

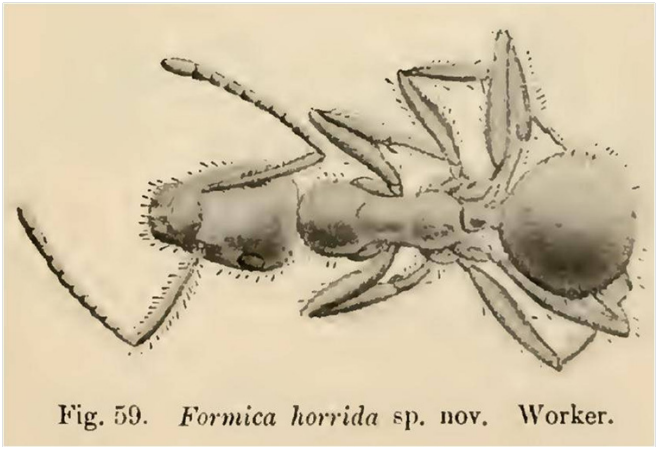

Fig 8. *Formica horrida* drawing. Reproduced from Wheeler 1915: 125.

The case of Formica horrida

The abundant pilosity formed by short and stout setae is the most visible character that defines *Iberoformica*. The only *Formica* species known to us that shares this character is the fossil *Formica horrida* Wheeler, 1915. This species was described from the Baltic amber and might be a good candidate to be included into the genus *Iberoformica*.

We must refrain to include this species into *Iberoformica* until more material is available. The material type seems to be lost and the only existing image does permit appreciation of the typical sinuous *Iberoformica* mesonotal profile.

Conclusion

We have presented evidence that *Formica gerardi* presents genetic, morphologic and behavioral characteristics that place it in the ant genus *Formica*, more concisely into the fusca-group, so we propose its reinstatement into the genus *Formica*.

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