Biology, Distribution and Taxonomic Status of the Parasitic Ants of the Iberian Peninsula (Hymenoptera: Formicidae, Myrmicinae)

by

Alberto Tinaut[1], Francisca Ruano[2], & Dolores Martínez[3]

ABSTRACT

In this study, we include a total of 15 species of Myrmicinae parasitic ants from the Iberian Peninsula. For each species, we review the data available on their biology, especially in relation to parasitism, and update their distribution and taxonomic status. Among the most noteworthy results, we confirm the presence of *Strongylognathus afer* in the Iberian Peninsula and we considerably broaden the distribution range for such species as: *Myrmoxenus ravouxi, Chalepoxenus kutteri* and *Anergates atratulus*. This study underscores the lack of biological data for most of Iberian species within the genera *Strongylognathus*.

Keywords: parasitic ant, Myrmicinae, Iberian peninsula.

INTRODUCTION

Social parasitism in insects is a relationship in which one species of social insect, the parasite, lives at the expense of the other species, the host, in such a way that the parasitic species inhabits the nest of the host but usually does not participate either in gathering food or in caring for the young. This behavior appears exclusively among social Hymenopterans, although cases approaching parasitism have been described for Isoptera (see Wilson 1971).

A summary of the principal currents in the evolutionary origin of social parasitism as well as the biological, ecological and evolutionary aspects of social parasitism can be found in Buschinger (1986), Hölldobler & Wilson (1990) and Tinaut & Ruano (1999).

In Hymenoptera, social parasitism appears in apids, vespids and formicids. In formicid parasitism, slightly more than 200 species (see Hölldobler & Wilson 1990) are known, and these show the greatest complexity in terms of the types of parasitism, from commensalism to

[1]Departamento de Biología Animal y Ecología, Facultad de Ciencias. Universidad de Granada. 18071 Granada. SPAIN email:hormiga@goliat.ugr.es (Author for correspondence)
[2]Departamento de Agrobiología y Protección Vegetal. Estación Experimental del Zaidín. CSIC. Profesor Albareda, 1. 18008 Granada. SPAIN email:fruano@eez.csic.es
[3]Departamento de Biología Animal. Facultad de Biología. Universidad Complutense. 28040 Madrid. SPAIN email:lolahorm@eucmax.sim.ucm.es

strict parasitism. In the case of strict parasitism, three types can be distinguished (see Hölldobler & Wilson 1990): 1) temporary parasitism, in which the parasitic species needs the host only for the initial periods of the formation of new societies; 2) permanent parasitism or inquilinism, in which the parasite remains its entire life in the host nest; and 3) dulosis, in which host workers are taken as slaves to the parasitic nest by periodic raids on the nest of the host species by the parasite workers. Within dulosis, we can also consider three forms: facultative intraspecific, facultative interspecific and obligatory interspecific (Mori & Le Moli 1988; Topoff 1990; for a review, see Le Moli & Mori 1987).

The ethological, morphological and evolutionary implications of the different types of parasitism have attracted intense interest ever since the beginning of myrmecological studies in which classical authors such as Forel and Wheeler published observations on the topic (for example, Forel 1898, 1906; Santschi 1906; Wheeler 1901, 1910), and this subject continues to receive ongoing attention, as reflected in the bibliography (see: Lenoir *et al.* 2001; Sanetra & Buschinger 2000; Zamora-Muñoz *et al.* 2002; Fischer & Foitzik 2004).

In addition to the specific studies on the biology of other aspects of parasitism, in recent years different faunistic works have been conducted to detail the distribution of the different species, as in the works on parasitic species of Lebanon and Syria (Tohmé & Tohmé 1979), Corsica (Buschinger 1985), Italy (Mei 1992; Sanetra *et al.* 1999), Greece (Buschinger & Douwes 1993), Turkey (Heinze & Kauffmann 1993) and Morocco (Sanetra & Güsten 2001).

For the Iberian Peninsula, works on parasitic ants are focused on Spain, with few references to Portugal (Salgueiro 2002, 2003), and are limited in general to faunistic lists indicating only the distribution of certain species (for example, Ceballos 1956; Emery 1909; Santschi 1919, and more recently Collingwood & Yarrow 1969). Other specific works on parasitism list some Iberian localities and species (Buschinger *et al.* 1986, 1988b; Sanetra & Buschinger 2000). All the information available on this subject for the Iberian Peninsula is contained in certain fundamentally taxonomic works dealing with exclusively Iberian species (Espadaler 1982; Tinaut 1981, 1990; Tinaut *et al.* 1992; 1994), the review by Espadaler and Restrepo (1983) on the genera *Epymyrma* and *Chalepoxenus* in the Iberian Peninsula, and the work of Buschinger (1995) on the biology of an endemic species *Epymyrma bernardi*. Recently, the authors of this article (see bibliography) studied the biology of another endemic species of the Iberian Peninsula, *Rossomyrmex minuchae* belonging to the subfamily Formicinae, not included in this work.

Clearly, the information on this formicid group in the Iberian Peninsula is meager and scattered. The aim of the present study is to compile and update all the taxonomic, faunistic and biological data available, both for each genus with species in the Iberian Peninsula and for each species inhabiting this peninsula.

SPECIES

In total, 15 parasitic species are known for the Iberian Peninsula, belonging to the Myrmicinae subfamily.

Genus *Myrmica* Latreille 1804

This genus, having a Holarctic distribution, includes more than 100 free-living species and 16 parasitic ones (Bolton 1988; Mei 1987; Radchenko & Elmes 2003) 13 Palearctic and 3 Nearctic, concretely the parasitic species are: *M. arnoldi* Dlussky 1963; *M. bibikoffi* Kutter 1963; *M. ereptix* Bolton 1988; *M. hirsuta* Elmes 1978; *M. kabylica* (Cagniant 1970), *M. karavajevi* (Arnoldi 1930), *M. laurae* (Emery 1907); *M. lemasnei* Bernard 1968; *M. luteola* Kupyanskaya 1990; *M. microrubra* Seifert 1993; *M. myrmicoxena* Forel 1894; *M. symbiotica* (Menozzi 1925), and *M. vandeli* Bondroit 1919, as the Palearctic species and *M. colax* (Cole 1957), *M. lampra* Francoeur 1968 and *M. quebecensis* Francoeur 1981 as the Nearctic ones.

This group of parasitic species has undergone numerous taxonomic revisions. Seifert (1988a) in a review of the genus *Myrmica* in Europe, Asia Minor and the Caucasus, cited only three of these species (*M. bibikoffi, M. hirsuta* and *M. myrmicoxena*) without mentioning *M. laurae, M. fariniensis, M. karavajevi, M. lemasnei* or *M. symbiotica*. We adopt the criteria of Bolton (1988), which make *Myrmica* synonymous with all the previous taxa to which these species have been assigned, such as *Sifolinia* Emery 1907 or *Symbiomyrma* Arnoldi 1930. Finally, Radchenko & Elmes (2003) include all the species also in the genus *Myrmica*, as did Bolton (1988), and undertook a detailed taxonomic work synonymizing some species, establishing the number of parasitic species (mentioned above).These parasitic species are distributed throughout the Holarctic and India, and each has a particular host which is a species of the genus *Myrmica* (Bolton 1988; Radchenko & Elmes 2003).

The biology has been studied fundamentally in *M. hirsuta* by Elmes (1983), while Cagniant (1970) has provided data on the biology of *M. kabylica*. Without workers, the 16 species are suspected of being inquilinist and therefore cohabitating with the host queen, except both in the case of *M. bibikoffi*, which has workers and is also the only species which is not strictly parasitic (Bolton 1988), as well as in the case of *M.*

arnoldii, which is suspected to be temporary social parasite (Radchenko & Elmes 2003). Many features of the behavior of these species are still unknown. Only two species of this group live in the Iberian Peninsula.

Myrmica lemasnei Bernard 1968

This is a very scarce species described from the eastern Pyrenees (Col de l'Ouillet) (Bernard 1968), but as Radchenko & Elmes (2003) explain, the holotype and only specimen described by Bernard is now lost. Other material coming from the same place and described by Kutter (1973) as cotypes differs in some details from the description of Bernard, making it unclear whether or not *M. lemasnei sensu* Kutter is the same species that Bernard described. As Radchenko & Elmes (2003) wrote: " … we suggest that the pragmatic solution to this problem is to accept Kutter's treatment of *M. lemasnei*" (Radchenko & Elmes 2003, p. 236). Known only from the Pyrenees, it has been cited in Spain from the area near Jaca (province of Huesca) by Espadaler (1981) in a nest of *Myrmica sabuleti* Meinert 1861, which is the only host currently known for this species (Bernard 1968). Probably the Pyrenees population of *M. sabuleti* is the "west-mediterranean form" described by Seiffert (1988a). It is a workerless social parasite and the only data concerning its biology refer to feeding habits of the queens and their relationships with the hosts (Espadaler 1980). Thus, the queen is known to obtain food either by placing itself between two workers performing trophalaxis or by causing larvae to regurgitate—that is, the parasite queen receives no direct attention from the host.

In this species, the female measures some 3 mm in length, as opposed to the workers of *M. sabuleti* (the host species), which are 3.9 to 4.5 mm in length while the host queen reaches 5 to 6 mm. In addition, *M. lemasnei* can be distinguished by the petiole, which can be as wide as the postpetiole. Both segments present spiniform processes in the ventral region (Fig. 1) (Espadaler 1981; Radchenko & Elmes 2003). The epinotal spines are short and obtuse at the apex, and the scape inserts on the head at almost a right angle. Other characters are the postpetiolar dorsum with distinct reticulation, surface of the head, alitrunk, and waist smooth or at most superficially punctured and appearing shiny.

Myrmica kavarajevi (Arnoldi 1930)

Widely distributed throughout Europe, including Russia to Ukraine (Radchenko & Elmes 2003). Recently found in northern Spain, in the Sierra de Entzia (Álava) by Espadaler *et al.* (2004) in a nest of *Myrmica scabrinodis* (Nylander 1846).

The principal morphological characters are summarized by Radchenko & Elmes (2003) and focused on the postpetiolar dorsum without reticulation, surface of the head, alitrunk, and waist smooth or at most superficially punctured, appearing shiny. The difference with regard to *M. lemasnei* is principally the pilosity of the gaster and the reticulation of the petiole, harder in *M. lemasnei* (Figs. 1 & 2)(Radchenko & Elmes 2003).

This is a workerless parasite, widely distributed, up to northern Spain, but nowhere common. Its host can belong to different species of the *scabrinodis* group (Radchenko & Elmes 2003), for instance: *sabuleti* Meinert 1861; *rugulosa* Nylander 1849 and others besides *scabrinodis* Nylander 1846. Their biology and behavior is very poorly known.
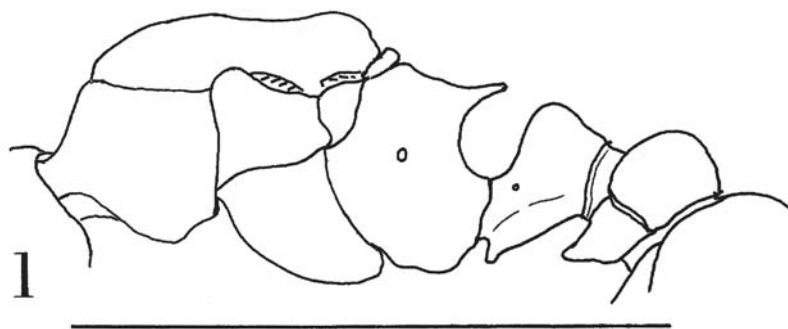

Fig. 1. Alitrunk, petiole and postpetiole in profile of *Myrmica lemasnei* queen (after Radchenko & Elmes 2003) (Scale = 1 mm).
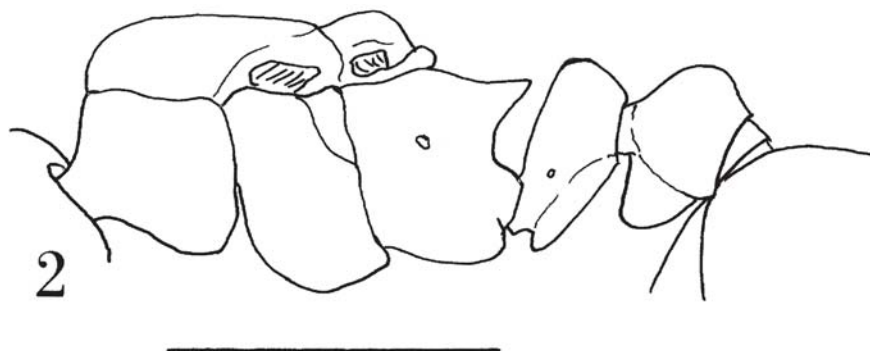

Fig. 2. Alitrunk, petiole and postpetiole in profile of *Myrmica karavajevi* queen (after Radchenko & Elmes 2003) (Scale = 1 mm).

Genus *Myrmoxenus* Ruzsky 1902

First, it should be highlighted that we are following the criteria of Schulz & Sanetra (2002) concerning the priority of the name *Myrmoxenus* and that *Epimyrma* Emery 1915 is a junior synonym, as was established by these authors. This genus, distributed throughout central and southern Europe, Turkey, and North Africa, is comprised of 11 species: *M. adlerzi* (Douwes, Jessen & Buschinger 1988); *M. africana* (Bernard 1948); *M. algeriana* (Cagniant 1968); *M. bernardi* (Espadaler 1982);. *M. birgitae (*Schulz 1994); *M. corsica* (Emery 1895); *M. kraussei* (Emery 1915); *M. ravouxi* (André 1896), *M. stumperi* Kutter 1950; *M. tamarae* Arnoldi 1968 and *M . zaleskyi (*Sadil 1953). The taxonomic position of the different species included here, as well as other invalidated ones are treated in different works, notably Buschinger (1982, 1989) and Buschinger *et al.* (1986). These species are social parasites of various *Leptothorax* (*Myrafant*) species, except *M. kraussei*, which parasitizes exclusively *L.* (*Temnothorax*) *recedens* (Nylander 1856).

The genus *Myrmoxenus* is characterized by having antennae with 11 articles, the petiole with a rounded peak and with a tooth, wide in profile, in the ventral region of the petiole and postpetiole (Fig. 3).

The biology and behavior of these species have been studied primarily by Buschinger and collaborators, so that the most relevant aspects of parasitism in this genus are well known for most of the species, the only species remaining poorly known being *M. africana, M. tamarae* and *M. zaleskyi* (Douwes *et al.* 1988 and Buschinger 1989). Buschinger (1989) provides a summary and review of the most pertinent aspects of this genus, including a detailed bibliography, and thus here we shall refer basically to this work. The genus *Myrmoxenus* exhibits an evolutionary transition from fully developed slave-making to a completely workerless parasitic condition. A gradation can be drawn from species such as *M. algeriana*, with more than 200 workers, or *M. ravouxi*, with more than 70 workers, to species with a low number (20 or less) of workers or none at all (depending on the locality), as in the case of *M. kraussei*, to completely workerless species, such as *M. corsica* and *M. adlerzi*. All these species are slave makers, and thus the parasite queen kills the host queen within a more or less brief period of time. This behavior occurs even in the case of the workerless species, in which the absence of workers precludes the ability to conduct raids, and thus the life span of these colonies is limited to the lifespan of the parasitic female, some 2 or 3 years for the workerless species and more than 10 years for species with workers, such as *M. ravouxi* (Buschinger & Winter 1982).
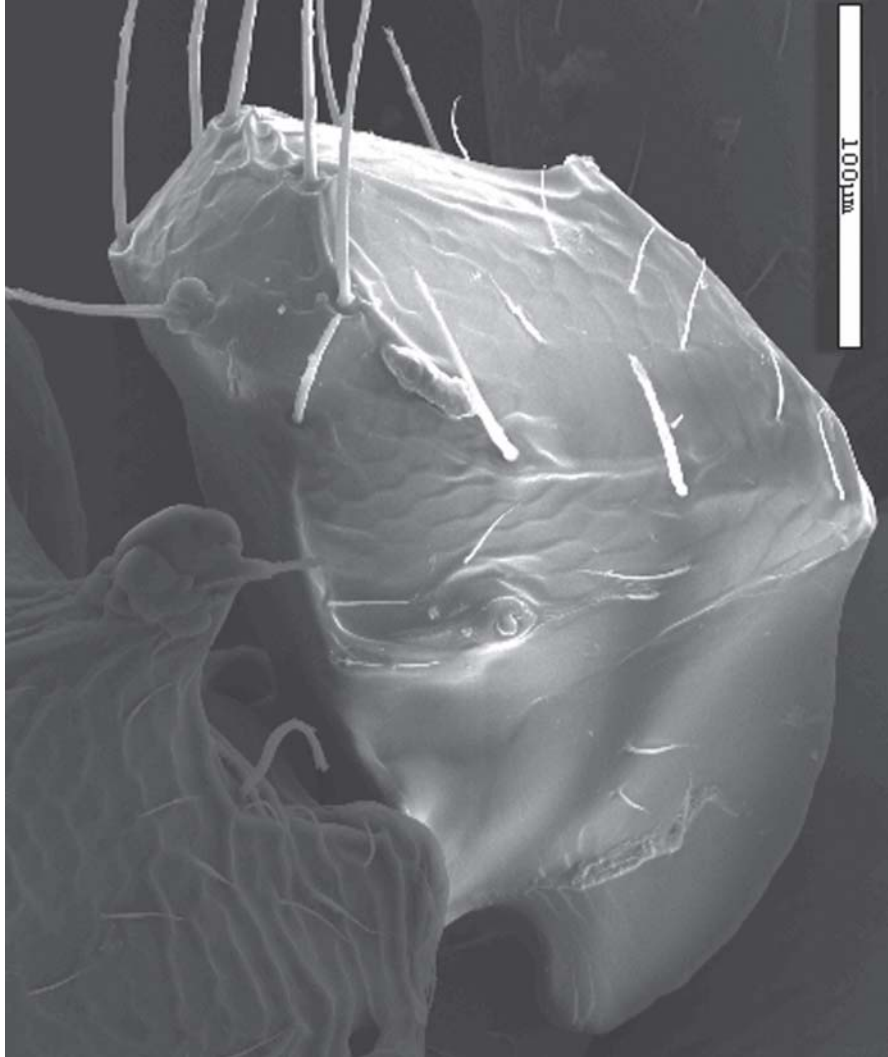
Fig. 3. Petiole of *Myrmoxenus kraussei* (Sª de Segura, Jaén, Spain).

With regard to mating behavior, there are two different groups, one with mating flights (*M. ravouxi*) and the another which mates inside the maternal nest (*M. algeriana*, *M. corsica*, *M. kraussei* and *M. adlerzi*). The latter females, after being fertilized, remain inside the nest until winter or spring (Buschinger *et al.* 1990; Buschinger & Winter 1982, 1983, 1985; Douwes *et al.* 1988). Colonies are founded at different times,

depending on the type of mating. For species with mating flights, the new nest is founded after mating and therefore during summer or autumn, while species that mate within the nest found a new nest in the next year. All species, except *M. algeriana*, are monogynous (Buschinger *et al.* 1990) and host nests contain only one queen each, except for *L. tuberum* (Fabricius 1775), which is facultatively polygynous.

Apart from the above-mentioned general review by Buschinger (1989), several faunistic works devoted almost exclusively to this genus deserve mention, especially Cagniant (1968a, b) for Algeria, Buschinger (1985) for Corsica, and Mei (1992) for Italy. From the Iberian Peninsula, Espadaler & Restrepo (1983) established three species, although the distribution is now better known and there are also still species that remain to be described (Espadaler 1997c).

Myrmoxenus ravouxi (André 1896)

This species is a slave maker with a reduced number of workers. For 56 ant nests, Buschinger and Winter (1983) reported an average of 23.1 workers, for a range of 1 to 77; meanwhile, the average number of host workers was 137.9, ranging from 4 to 514. The average lifespan of these nests exceeds 10 years. For most (75%) of the nests studied by these authors, *Leptothorax unifasciatus* (Latreille 1798) was the host species, while in the rest of the population the hosts were simultaneously *L. unifasciatus* and *L. nigriceps* (Mayr 1855), only one nest of 56 was composed only by *L. nigriceps* as the host. In the literature, *L. unifasciatus* appears as the most common host, but other host species have been cited, such as *L. affinis* (Mayr 1855) or *L. interruptus* (Schenck 1852) (Buschinger 1989).

M. ravouxi is a monogynous species (Buschinger & Winter 1983). The sexuals, which develop from hibernating larvae, make a mating and dispersal flight, and the young queens start to found their colonies in the autumn (Winter & Buschinger 1983).

The taxonomic status of *M. ravouxi* has been revised by Buschinger (1982), who made this species synonymous with *M. goesswaldi* Menozzi 1931. *M. ravouxi* was described in Drome, France (André 1896) and is currently known from central and eastern Europe (Buschinger 1989). This species appears to prefer cool and wet habitats, occupying southern Europe (Buschinger 1985a; Mei 1992 and our data), preferentially in mountainous regions. In the Iberian Peninsula this species has been cited exclusively in the province of Huesca by Espadaler (1997) and Espadaler & Restrepo (1983). We collected a solitary winged female in the Sierra de la Alfaguara (Granada) at some 1300 m in

altitude, with which we broaden its distribution range to the south of the peninsula (Fig. 4).

Morphologically, *M. ravouxi* is characterized by the profile of its subpetiole tooth, sharp at the apex, and also by the hairs, which are longer than in other species.

Myrmoxenus kraussei Emery 1915

Here again the main reference work will be Buschinger and Winter (1983) and Winter and Buschinger (1983), in which this species is compared with *M. ravouxi*. These two species provide a well-documented example of a transition between two types of social parasitism in ants. Thus, *M. kraussei* represents an evolutionary stage of degenerate dulosis with few or no workers, depending on the host-worker stock which the host colony presents when being invaded. In 82 colonies studied by Buschinger & Winter (1983), the average number of parasitic workers was 2.07 and 31.17 for the host. *M. kraussei* is monogynous and the host queen is killed by thrittling. Given the very low number of workers (Cagniant & Espadaler 1997), this species can conduct slave raids only under favorable conditions, but usually these new colonies decline when the host workers die, normally after two or three years (Buschinger & Winter 1983). The sexuals develop from the

Fig. 4. Distribution of *Myrmoxenus ravouxi* and *M. krausei* on the Iberian peninsula.

brood of the same year, mate inside the maternal colonies and the young queens hibernate there until they leave the nest to found a colony in the spring. The only known host is *L. recedens* and the colonies are normally found under rocks or moss in forested areas.

The taxonomic position of this species has been established by Buschinger *et al.* (1986) after a meticulous morphological, cytogenetic and cross-reference study, making *M. vandeli* Santschi 1927 and *M foreli* Menozzi 1921 synonymous with *M. kraussei.* Described from Sardinia (Emery 1915), this species is more thermophilous than the previous one and has been cited in many localities of the Mediterranean, from Morocco to Turkey (Cagniant 1968b; Cagniant & Espadaler 1997; Heinze & Kauffmann 1993), including Spain, France, Switzerland and former Yugoslavia (Buschinger *et al.* 1986; Mei 1992).

In the Iberian Peninsula, *M. kraussei* is distributed throughout the Mediterranean area from Algeciras to Lérida (Fig. 4) (Buschinger *et al.* 1986; Espadaler & Restrepo 1983; Espadaler 1997c; Tinaut 1989). It is characterized by the pilosity of the workers and the fine pointed setae on the queen. The coloration is generally yellow, the subpetiole strip rather triangular (Fig. 3).

Myrmoxenus bernardi Espadaler 1982

According to Buschinger (1989), and from the few nests studied since then, this species was considered a typical slave maker. Nevertheless, a subsequent study with a greater number of nests revealed that this species shows a special blend of life-history features (Buschinger 1995). Firstly, this species has a low number of workers, 0 to 24, with an average of 4 workers, suggesting a very low ability to conduct raids in nature, despite that it was found to do so in the laboratory (Buschinger 1995). This species is monogynous and its nests last 2 to 3 years, as is normal among workerless species. On the other hand, the workerless species in this genus have as a common characteristic rapid development of the larvae, which give rise to the sexuals without the need of hibernating. However, in *E. bernardi*, the sexuals hatch after hibernation. In addition, this species belongs to the group of those that mate inside the nest, forming the new colonies the following spring. Espadaler (1982) found females of the host species, raising the possibility that this species may cohabit with the host, this representing the only exception in the genus. Buschinger (1995) also found females of both species in some nests, but dissection of the host females demonstrated that they were not queens. Observation of the type of mating of the host species indicated that mating also took place in the nest, and that *M. bernardi* permitted the presence of recently fertilized young

queens in the nest. The only host known for this species is *Leptothorax gredosi* Espadaler & Collingwood 1982.

M. bernardi is known exclusively from the Sierra de Gredos (Avila) (Buschinger 1995; Espadaler & Collingwood 1982; Espadaler & Restrepo 1983) and its nests are situated under rocks. The host, however, presents a wider distribution in the Iberian Peninsula, extending from the Pyrenees to the Sierra Nevada, despite which no new locality has been found for the parasitic species.

This species is characterized both in females and workers by their nearly absent sculpture. Workers have a superficial promesonotal suture and in dorsal view a small scutellum but without definite sutures (Espadaler 1982).

Genus *Chalepoxenus* Menozzi 1922

The distribution area of this genus coincides largely with that of *Myrmoxenus*, being known from the Iberian Peninsula to Kazakhstan (Buschinger *et al.* 1988b; Mei 1992). Seven species have been described: *C. muellerianus* (Finzi 1921), *C. insubricus* Kutter 1950, *C. siciliensis* Kutter 1973; *C. tramieri* Cagniant 1983; *C. brunneus* Cagniant 1985; *C. gribodoi* Menozzi 1922; *C. spinosus* (Arnoldi 1968). Of these, *C. gribodoi*, *C. insubricus* and *C. siciliensis* are considered synonyms of *C. muellerianus* (Buschinger *et al.* 1988b; Kutter 1973). These parasitize different *Leptothorax* species of the subgenera *Myrafant* and *Temnothorax*, the most common being *L. unifasciatus* and *L. massiliensis* Bondroit 1918, but the number of species vulnerable to parasitism is close to 10 (Buschinger *et al.* 1988b). Besides this apparent absence of specificity, this genus reveals a most peculiar phenomenon—faithfulness to the host species in the maternal nest; that is, the new females preferentially search for nests of the same *Leptothorax* species as in the maternal nest. This behavior explains the rarity of mixed ant nests (Buschinger *et al.* 1988b).

The biology of this genus has been studied mainly in *C. muellerianus, C. kutteri* and *C. brunneus* by Buschinger *et al.* (1988a, b), and here we shall refer exclusively to these works. The genus *Chalepoxenus* is a typical slave maker, lacking workers in *C. brunneus* and probably also in *C. spinosus* (Buschinger *et al.* 1988a). Young females using their stingers invade the ant nest to parasitize, kill or expel all adults, including the queen. The parasitic females care for the existing pupae, from which the first slaves emerge. The sexuals, at least in *C. brunneus*, emerge from hibernating larvae. This species shows a parallel with the workerless species of the genus *Myrmoxenus*, given that in neither case does the parasite kill all the host workers, since, being unable to carry

out raids, it is advantageous for a workerless species to have the highest possible initial number of slaves. In addition, Buschinger *et al.* (1988a) found a possibility of coexistence between the host queen and the parasite queen, supporting the hypothesis that *C. brunneus* represents a workerless parasitic species which is derived from actively dulotic congenera and represents a degenerate slave maker following the life-style of a true inquilinist.

From the Iberian Peninsula, only *C. muellerianus* and *C. kutteri* have been cited.

Chalepoxenus muellerianus (Finzi 1921)

Studied by Menozzi (1922) as *C. gribodoi* and by Ehrhardt (1987), this was the first species of its genus in which slave making was described.

C. muellerianus has a broader distribution than the preceding species, being known from the western Mediterranean to Turkey (Mei 1992; Schulz & Sanetra 2002). In the Iberian Peninsula, it behaves as a less thermophilous species than the above species and thus is known in the northern half of the Iberian Peninsula, in forests at altitudes of more than 1000 m (Fig. 5). The Pyrenees in the province of Huesca (Espadaler & Restrepo 1983; Espadaler 1997b), the area of Madrid and the Sierra de Guadarrama (Martínez 1987; Buschinger *et al.* 1988 b), Sierra de Albarracín in the province of Teruel (Martínez & Tinaut 1996; Buschinger *et al.* 1988 b), and the Serra da Estrela in Portugal (Tinaut & Ruano 1994). In the Iberian Peninsula, this species has been found parasitizing *L. unifasciatus* and *L. tuberum.* Schumann (1992) also reported *L. recedens* as a host.

C. muellerianus is characterized by yellowish-brown coloration and abundant pilosity over the entire body, including the legs. Head sculptured. The postpetiolar process practically absent (Fig. 6).

Chalepoxenus kutteri Cagniant 1973 (profiles petiole)

The only data available on the biology of this species come from Le Masne (1970a, b). This author studied numerous colonies and de-scribed their composition, as well as certain aspects of the host-parasite relationship. This species conducts slave raids, although the number of workers in natural populations does not exceed 20, whereas the number of host workers can reach 250. It is known that *C. kutteri* exchanges food with the host and that the parasite workers participate in some of the common tasks inside the nest, such as moving the larvae. Other observations on the nature of aggressiveness among the para-sites themselves and between the parasites and hosts led Le Masne (1970 b) to consider this as a slave-making species.
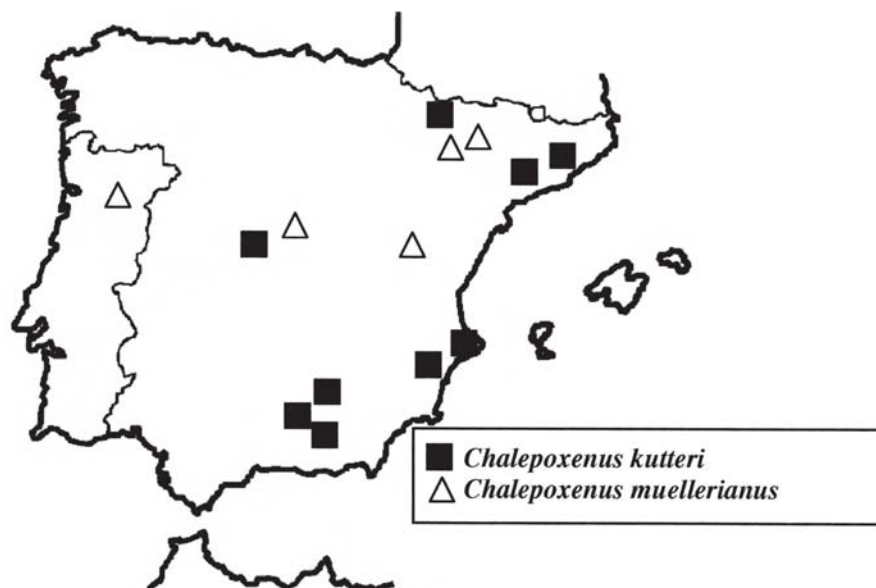
Fig. 5. Distribution of *Chalepoxenus kutteri* and *C. muellerianus* on the Iberian peninsula.

Different localities of the eastern, central and northern Iberian Peninsula (Fig. 5) have been cited for this species (Acosta *et al.* 1983; Espadaler 1997b; Espadaler 1997c; Espadaler & Restrepo 1983; Restrepo *et al.* 1985; Buschinger *et al.* 1988b; Lombarte *et al.* 1989; De Haro & Collingwood 1981). The nests of *C. kutteri* are found under rocks or moss, usually in cleared woodlands of *Quercus* sp. (Restrepo *et al.* 1985; Lombarte *et al.* 1989) or *Pinus halepensis* (De Haro & Collingwood 1981), in masses of vegetation near the coast but also in central Spain (Acosta *et al.* 1983). In the present work, we report this species in the southern half of the peninsula, in wet inland woods—the Sierra de la Alfaguara and in the foothills of the Sierra Nevada (both localities in the province of Granada), consistently under moss. As hosts in the Iberian Peninsula, various species have been reported from the genus *Leptothorax: L. recedens, L. rabaudi* Bondroit 1918, *L. specularis* Emery 1916, *L. unifasciatus* and *L. massiliensis*. Lombarte *et al.* (1989) pointed out a mixed nest formed by *L. rabaudi* and *L. lichtensteini* Bondroit 1918.

C. kutteri is characterized by its yellowish coloration and sparse setae distributed evenly over the entire body, although absent from tibia II and III. Head practically polished and shiny. Postpetiolar process present and very thin.
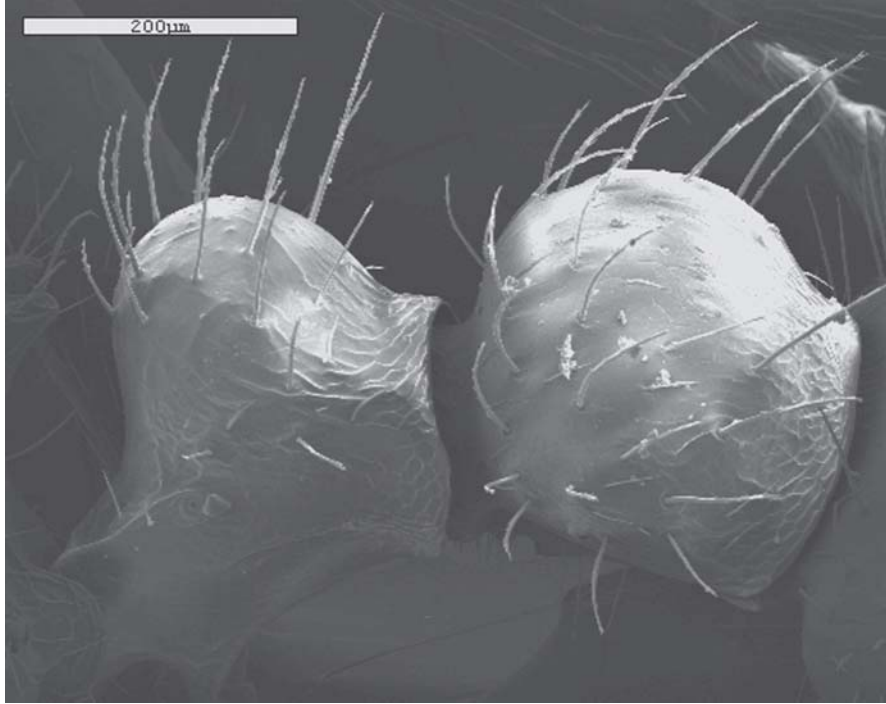
Fig. 6. Petiole and postpetiole of *Chalepoxenus muellerianus* (Sierra de la Estrella, Portugal).

Genus *Harpagoxenus* Forel 1893

To date, 4 species are known for this genus, two of which are distributed throughout central and southern Europe to central Russia, *H. sublaevis* (Nylander 1849) and *H. zaisanicus* Pisarski 1963, and two in North America, *H. americanus* (Emery 1895) and *H. canadensis* M.R. Smith 1939 (Buschinger 1981). The genus is morphologically characteristic for the frontal ridges carried to back of head, the typical thorax and the petiole and postpetiole with ventral processes (Figs. 7-9).

Most of the data on the biology of the genus pertain to *H. sublaevis*, *H. canadensis* and *H. americanus* (Alloway & Del Rio Pesado 1983; Buschinger 1983; Heinze *et al.* 1992; Del Rio Pesado & Alloway 1983; Schumann & Buschinger 1991; Wesson 1939). As a whole, this genus is a slave maker of different species in the subgenus *Mychothorax* (*L. acervorum* (Fabricius 1793), *L. muscorum* (Nylander 1846), *L. gredleri* Mayr 1855, *L.* sp. A and *L.* sp. B), the selection of the species to parasitize depending on density (Heinze *et al.* 1992; Schumann & Buschinger 1991) or prior existence in a maternal ant nest (Schumann
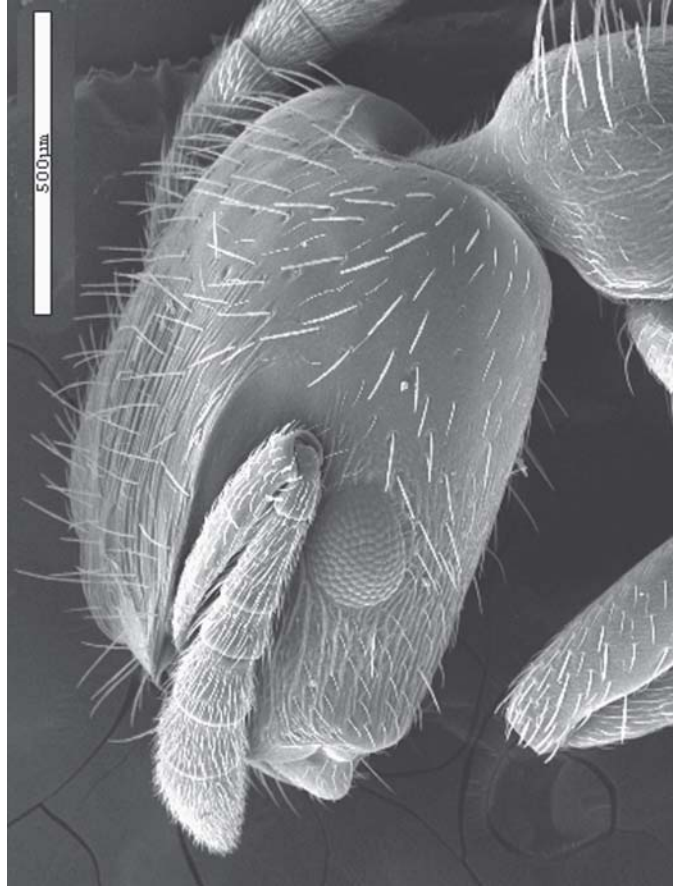
Fig. 7. Head of *Harpagoxenus sublaevis* (Germany).

& Buschinger 1991). In some cases, mixed colonies are found, depending on the degree of acceptance of the workers and of the order of the old parasitized nest (Schumann & Buschinger 1991). The colonies are monogynous and young females mate near the maternal nest (Buschinger 1983). The invasion mechanism of the females is the usual one for other slave-making species, in killing the host female (Schumann & Buschinger 1991). Finally, in *H. americanus*, abdominal trophalaxis has been described between the parasites (donors) and the slaves, an extremely rare behavior among formicids and one which implies some role in the maintenance of the social relationships (Stuart 1981).

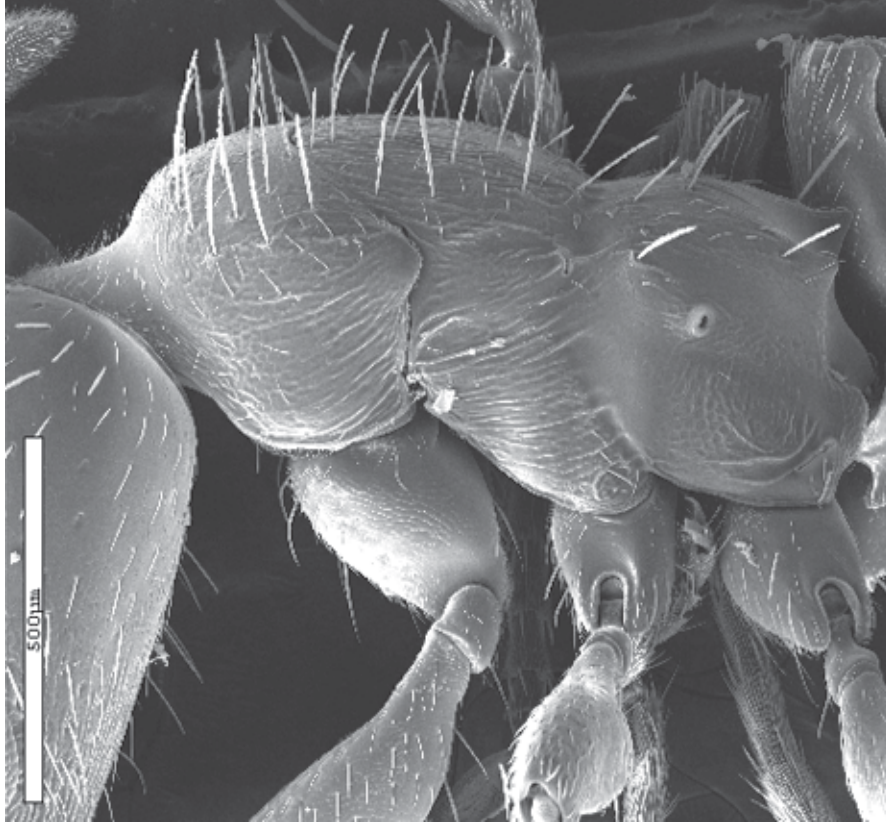Only *H. sublaevis* is known to inhabit the Iberian Peninsula.

Fig. 8. Thorax of *Harpagoxenus sublaevis* (Germany).

Harpagoxenus sublaevis (Nylander 1849)

This is one of the best-known species with respect to its biology, notably in the works of Buschinger & Alloway (1979) and Buschinger (1983) on the sexual behavior and the role of pheromones. The role of food in the behavior during a raid (Buschinger & Pfeifer 1988) or the differential selection of the slave-making workers towards the pupae of different species explains the frequency of *L. acervorum* or even mixed ant nests of *L. muscorum* and *L. acervorum* and, on the contrary, the rarity of *L. muscorum* as the only host species (Schumann & Buschinger 1991).

H. sublaevis is known in France, Scandinavia and northern Italy (Bernard 1968). Collingwood (1978) cited this species in the French Pyrenees, while Buschinger (1987) specified various localities in the
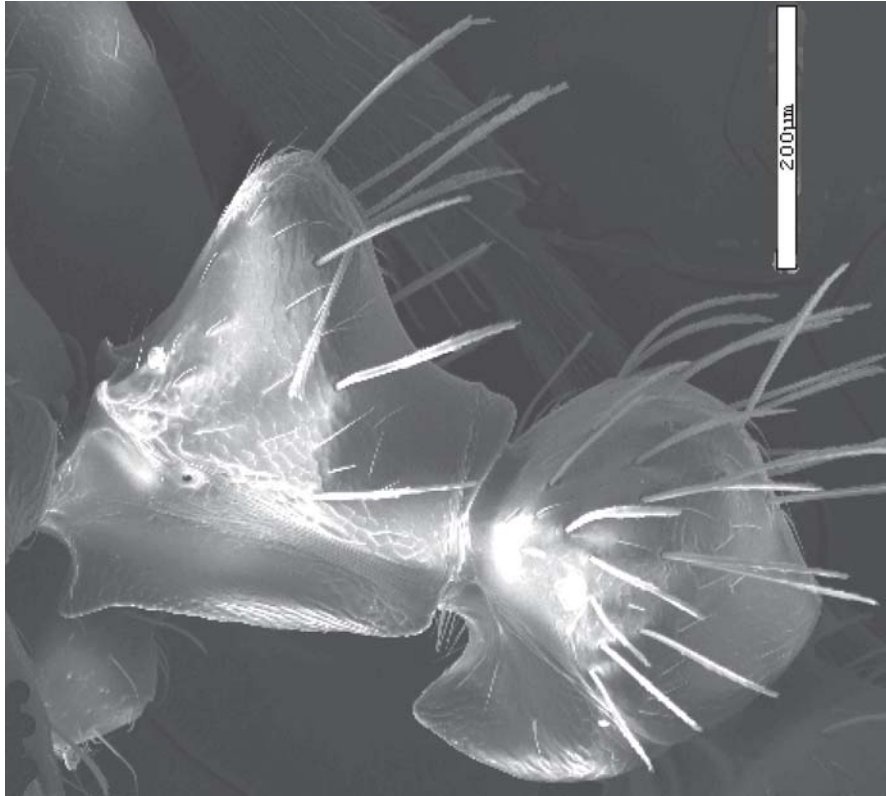
Fig. 9. Petiole and postpetiole of *Hapargoxenus sublaevis* (Germany).

French Pyrenees, including the Vallée d'Ossau. Therefore, it was not surprising to find this species in the Iberian Peninsula, as pointed out recently in Lleida (Espadaler 1997a), especially since its two host species (*L. acervorum* and *L. muscorum* Nylander 1864) are also found in the northern half of the Iberian Peninsula.

The workers of this species are characterized by a large and wide rectangular head (Fig. 7). The frontal ridges are prolonged far behind the eyes and the mandibles have no teeth.

Genus *Strongylognathus* Mayr 1853

This is one of the parasitic genera with probably the greatest number of species—22 valid species considering all recently established synonyms (Bolton 1995; Sanetra *et al.* 1999: Sanetra & Güsten 2001). The genus is typically Palearctic, being distributed mainly in central Europe and the Mediterranean region, although some species reach the eastern

region (Pisarski 1966). The Palearctic species have been reviewed by Pisarski (1966), Baroni Urbani (1969), Radchenko (1985), although in this case only for Russia, and by Sanetra & Güsten (2001) for North Africa. In this genus, two groups are clearly differentiated. One, characterized by a strongly indented head in the occipital region, is comprised of two species —only: *Strongylognathus testaceus* (Schenck 1852) from western Europe and central Asia, and S. *karawajewi* Pisarski 1966 of central Asia (Fig. 10). The other group, the so-called *huberi*-group, characterized by the absence of an occipital indentation is taxonomically more complex and diverse (Fig. 11). It includes 20 species distributed from Europe to Korea, which are difficult to identify without examining the sexuals.

All of the *Strongylognathus* species parasitize host colonies of the genus *Tetramorium* Mayr 1855. For the presence of sickle-shaped
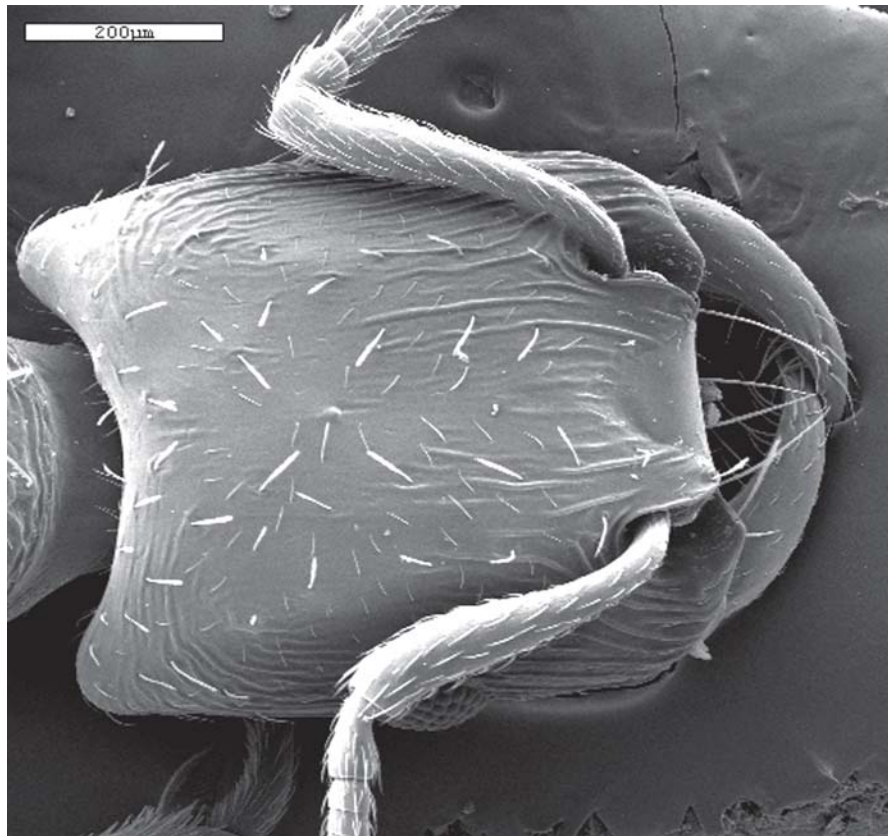

Fig. 10. Head of *Strongylognathus testaceus* (Sierra de Baza, Granada, Spain).
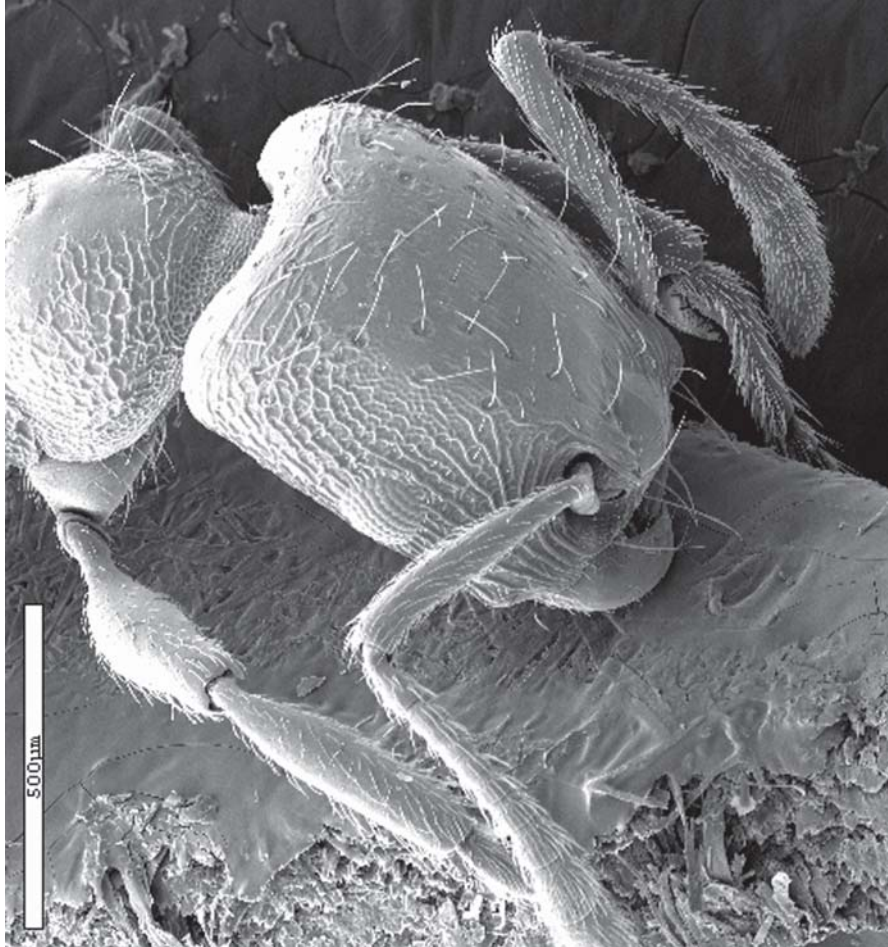
Fig. 11. Head of *S. huberi* (Sierra de la Estrella, Portugal).

mandibles similar to those of *Polyergus* Latreille 1804, it was assumed that *Strongylognathus* must be a slave maker, despite the scant and fragmentary information available on raids. The scarcity of observations of raids in this genus is due to the fact that raids are made primarily at night, as demonstrated in *S. alpinus* by Kutter (1923) and for some other species of the *huberi* group (Sanetra & Buschinger 1996; Sanetra & Güsten 2001). A typical outcome of laboratory slave raids was that, in addition to host larvae and pupae, even adult workers (and sometimes queens) were incorporated into the slave maker's colony (Sanetra & Buschinger 1996). In the case of *S. testaceus*, the *Tetramorium*

host queen has been found cohabitating with the parasite queen in several instances (Acosta & Martínez 1982; Sanetra *et al.* 1999). However, little is known about reproduction and the formation of new colonies. It can be assumed that the female must penetrate a host nest and, once within, does not kill the host female. Wheeler (1910) observed that the host queen produced nothing more than workers, while the parasite produced both workers and sexuals, although the number of workers was notably lower than in other species of the genus. These observations suggest that *S. testaceus* does not conduct raids, and thus this species might be considered as an intermediate stage between slave makers and inquilines.

On the Iberian Peninsula, 4 species of this genus have been cited: *S. testaceus* (Schenck 1852), *S. huberi* Forel 1874, *S. caeciliae* Forel 1897 and *S. afer* Emery 1884. The presence of *S. testaceus* has in no case been placed in doubt, but the problem has been raised for the species of the *huberi* group. Baroni Urbani (1969) considered all records from the Iberian Peninsula for *S. huberi* and *S. afer* to be synonymous with *S. caeciliae*, thereby reducing the number of species on the Iberian Peninsula to *S. testaceus* and *S. caeciliae*. According to our new findings, 3 species, *S. testaceus*, *S. huberi* and *S. caeciliae*, occur on the Iberian Peninsula with certainty. However, given the systematic complexity of this genus as well as the presence of some isolated populations, the occurrence of cryptic species cannot be ruled out. A more comprehensive populational study of samples of sexuals and workers is needed for a definitive resolution of this issue.

Strongylognathus testaceus (Schenck 1852)

This species, one of the parasites most commonly found in *Tetramorium* nests, is distributed from Great Britain to Siberia. As commented in the introduction of the genus, biological data for this species is scant.

On the Iberian Peninsula this species appears to be linked to mountainous habitats (Fig. 12). It is cited in the province of Huesca (Collingwood & Yarrow 1969), the province of Lérida (Espadaler 1979), the area of Madrid (Acosta & Martínez 1982), the Sierra de Guadarrama (Martínez 1987), the provinces of Castellón and Teruel (De Haro & Collingwood 1991), the Sierra de Albarracín (Martínez & Tinaut 1996; Sanetra & Buschinger 2000), the province of Segovia (Martínez & Serrano 1985), the province of Cuenca (Sanetra & Buschinger 2000) and the Sierra de Cazorla in the province of Jaén (Espadaler 1997c). In addition, we report this species for the first time in the province of Navarre as well as different localities of the Sierra Nevada, from 1400 m to 2300 m, and in the Sierra de Baza in the province of Granada as
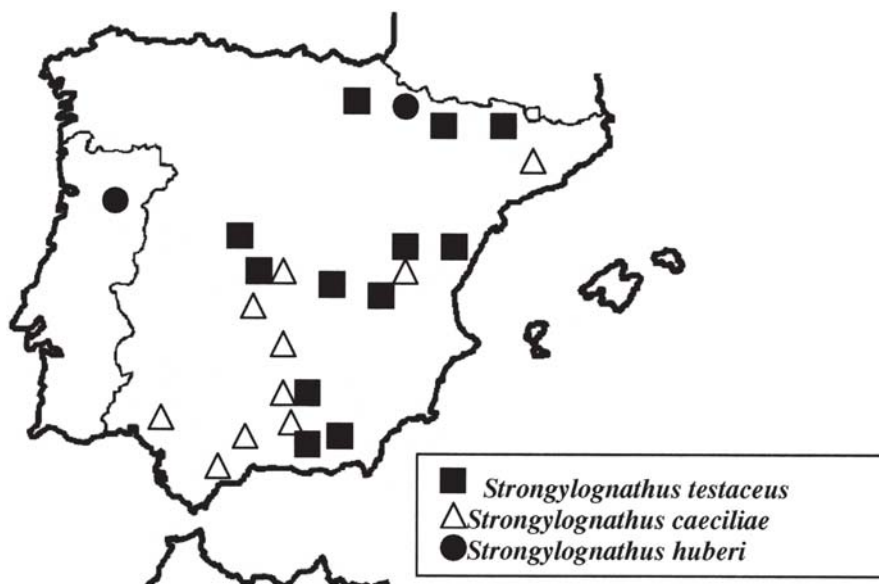
Fig 12. Distribution of Strongylognathus testaceus, S. caeciliae, and S. huberi on the Iberian peninsula.

well as the Sierra de los Filabres in the province of Almería. In all these cases *S. testaceus* parasitizes *Tetramorium caespitum* (Linneus 1758) and also *T. impurum* (Foerster 1850) at higher altitudes (Sanetra & Buschinger 2000). However, identified by mtDNA sequences, the latter form has recently been found to represent a cryptic species within the *caespitum/impurum* complex (Schlick-Steiner *et al.* unpublished results), though male genital morphology is clearly of the *impurum* type (Sanetra unpublished).

This is the only species of the genus present on the Iberian Peninsula that has a strongly indented occipital region of the head (Fig. 10), a character maintained even in the sexuals.

Strongylognathus caeciliae Forel 1897

This species is considered endemic to the Iberian Peninsula, first described from a female collected near Pozuelo de Calatrava (province of Cuidad Real). Forel (1900) ascribed to this species a male specimen collected in the province of Seville while the workers remained undescribed. In a partial revision of the *S. huberi* group, Baroni Urbani (1969) considered all records of *S. huberi* var. afer Emery 1884 and *S. huberi* Forel 1894 previously cited for the Iberian Peninsula as being

identical to *S. caeciliae*. In addition, the latter author (Baroni Urbani 1969) included some workers from Passo de Monrépos (Sierra del Aguila, province of Huesca), deposited in the City Museum of Natural History of Verona (Italy), into this species. Thus, we are confronted with the problem of accepting that this heterogeneous material including different castes and sexes truly belongs to the same species, a doubt already posed by Baroni Urbani (1969). Indeed, it was discovered 30 years later by Sanetra *et al.* (1999) that the worker series from Passo de Monrepos pertains to *S. huberi* , a species which is easily discernible from other species of the genus even in the worker caste.

The subsequent confirmation of the presence of more species of this genus in the Iberian Peninsula leaves the exact identity unresolved for workers and the male ascribed to *S. caeciliae*, as well as for a good part of the previous and subsequent citations for this species. This problem could be resolved by the capture of all the castes in the type locality; however, this has not yet proved possible, despite different collection efforts.

Therefore, we have identified the Iberian material based both on the traits given by Baroni Urbani (1969) and Sanetra *et al.* (1999) for *S. huberi* and by Sanetra & Güsten (2001) for *S. afer* (which is very similar to *S. caeciliae*) as well as on material which we have studied from different regions of Spain and from the collection of Medina. The most important characteristic is the polished head, thorax and petioles.

According to all of this evidence and to the literature available, *S. caeciliae* is found distributed in Tomares in province of Seville (Medina 1889, 1891a,b; Dusmet 1923; Martínez & Espadaler 1986), Sabiote (Jaén) (Acosta & Martínez 1982), Despeñaperros (Sierra Morena, Jaén) (De Haro & Collingwood 1977), Ciudad Real (Martínez & Espadaler 1986), in the province of Toledo, Madrid (Acosta & Martínez 1982; Acosta *et al.* 1983), Teruel (De Haro & Collingwood 1991), and in the province of Barcelona (Espadaler 1997a) (Fig. 12).

We have unpublished records from montane altitudes (800-1000 m) of the Sierra Nevada, Alpujarras and Sierra de Alfaguara in the province of Granada and also in Boquete Zafarraya (Malaga).

The citation from Tomares (province of Seville) by Medina (1889, 1891a,b) was attributed by this author to a female of *S. huberi* var. *afer*. In the Medina collection, we have not found this female, but rather 4 workers labelled in the collection as a variety of *Tetramorium caespitum* (Martínez & Espadaler 1986) and 5 unidentified females from Tomares, all belonging in our opinion to *S. caeciliae*. Therefore, we consider it quite probable that the female mentioned by Medina should also be *S. caeciliae*. In addition, workers collected from two colonies on the

Mediterranean coast (Torre de Maro and Boquete de Zafarraya, province of Malaga) were very similar to specimens of *S. afer* from Morocco in having a completely shiny head and pronotum without striations. *S. caeciliae* generally has the metapleural spines more pronounced than *S. afer*, but this is subject to large intraspecific variation. The petiole is slightly more triangular than in *S. afer*. These findings agree with the view that *S. afer* and *S. caeciliae* are probably synonyms (Sanetra & Güsten 2001).

S. afer was originally described from Algeria (Emery 1884), this species has been mentioned also in Tunisia and Morocco (Bolton 1976; Cagniant & Espadaler 1993; Sanetra & Güsten 2001). In the Iberian Peninsula (Medina 1891) was cited as a variety of *S. huberi*. This citation was reproduced by Dusmet (1923) on studying the collection of Medina and afterwards was again accepted by Ceballos (1956). This signifies that all the previous citations of *S. huberi* var. *afer* were made on the basis of a single specimen (a female) collected by Medina in the province of Seville in a nest of *T. caespitum*. We have collected some specimens in Torre de Maro and Boquete de Zafarraya (province of Malaga) on the Mediterranean coast. This material is quite similar to the specimens from Morocco, and thus could be assigned to *S. afer*. However, as commented above, Baroni Urbani (1969) considered the citations of *S. huberi* var. *afer* in the Iberian Peninsula to refer to *S. caeciliae*, and Sanetra & Güsten (2001) after a long review of *S. afer* in North Africa, expressed doubts about the possibility that *S. afer* and *S. caeciliae* are synonyms. Therefore, for the moment, we prefer not to consider *S. afer* a valid species in Spain.

As hosts, *T. semilaeve* André 1883 and *T. caespitum* have been cited (Acosta & Martínez 1982), although *T. semilaeve* should be the more common host, as is typical for other eumediterranean *Strongylognathus* species (Sanetra *et al.* 1999; Sanetra & Güsten 2001).

Strongylognathus huberi Forel 1874

This species is known from southern France, Switzerland and northern (Bolton 1976) as well as southern Italy (Sanetra *et al.* 1999). Acosta and Martínez (1982) report *S. huberi* from the Sierra of Albarracín in the province of Teruel, for the first time, and therefore for the Iberian Peninsula.

Another record from Passo de Monrepos in the province of Huesca, previously misidentified as *S. caeciliae* (Baroni Urbani 1969), was later added by Sanetra *et al.* (1999). This species was also found in Portugal (Serra da Estrela) by Tinaut and Ruano (1994).

An isolated population of *S. huberi* occurs in the high altitudes of the Sierra Nevada. In the literature, it was referred to as *S.* prope *caeciliae* (Tinaut 1990), *S. caeciliae* (Sanetra & Buschinger 1996), and *S.* prope *huberi* (Sanetra & Buschinger 2000). However, morphological differences seem to exist between these samples and typical *huberi* from others parts of Europe and the Iberian Peninsula. It has yet to be demonstrated whether these populations constitute a different species or only a high altitude form of *S. huberi.*

Rather little is known about the biology of this ant, with only a few observations made by Forel (1900) at the type locality. This author indicated the unexpected presence of a high number of parasite workers, noting that these contributed to the common tasks in the interior of a mixed nest. In addition, this author described some artificial experiments on the raid behavior of this species. Sanetra & Buschinger (1996) described slave raids from *S. caeciliae*, these being the *S. huberi* populations from Sierra Nevada (Sanetra pers. comm.). The host species cited are *Tetramorium caespitum*, *T. impurum* and *T. semilaeve* (Forel 1900; Acosta & Martínez 1982; Tinaut & Ruano 1994; Sanetra *et al.* 1999) but the latter is almost likely a misidentification.

S. huberi is differentiated from the workers identified as *S. caeciliae* in that the former is less shiny than *caeciliae* on the head and thorax and especially the petiolar nodes, which present a strong punctate-reticulate microsculpture (Figs. 11, 13-15). The occipital edge is more straight and the lateral edges of the head are more convex than in *caeciliae*. The metanotal spines and the petiole are more developed than in *S. caeciliae*. The metanotal spines are more developed and the petiole more triangular than in *S. caeciliae*. This agrees with the description given for *S. huberi* by Baroni Urbani (1969) and Sanetra *et al.* (1999) for the Italian fauna.

Genus *Anergates* Forel 1874

This monospecific genus is of great interest for the type of parasitism it exhibits as well as for its morphological and anatomical adaptations. The most notable traits of this group of parasites is the reduction in size, being even smaller than the host workers, as well as anatomical simplification (Figs. 16-17). That is, the mandibles are reduced to one or a few teeth, the tegument is unpigmented and very thin and microsculptered, the postpetiole is almost fused to the petiole and, finally, the males are of the pupoid type. In biological aspects, these parasites usually greatly modify their reproductive behavior, since fertilization frequently occurs within the same nest (see Hölldobler & Wilson 1990).
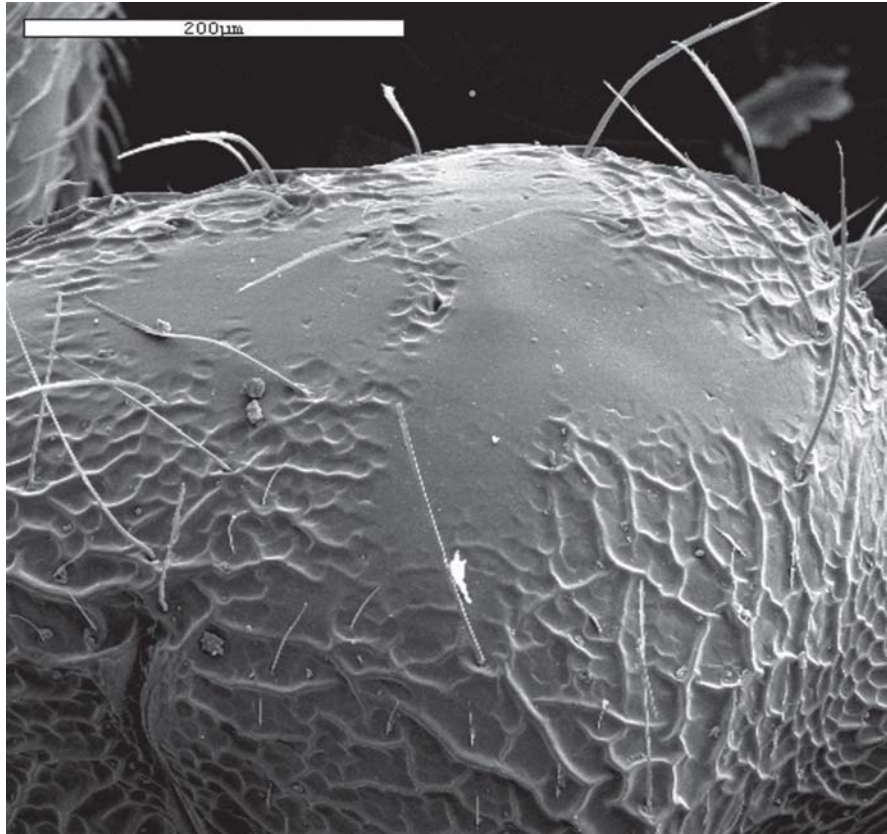
Fig. 13. Pronotum of *Strongylognathus huberi* (Sierra de la Estrella, Portugal).

Anergates atratulus (Schenk 1852)

This species is distributed throughout a large part of the Holarctic, being cited in North America as well as in central Siberia (Baroni Urbani 1967). On the Iberian Peninsula, it has been cited in the provinces of Gerona and Lérida (Espadaler 1979) and in the area of Madrid (Collingwood & Yarrow 1969). In the present work, we cite this species for the first time in the province of Cordoba, on the shore of the Guadalquivir. During this work, Sanetra & Buschinger (2000) have recorded this species from the high altitudes of the Sierra Nevada, province of Granada. These new records are at the southern distribution limit of this species, which has been reported only once in Sicily at a similar latitude (Sanetra *et al.* 1999). This implies that the species must be widely distributed throughout the Iberian Peninsula, but that
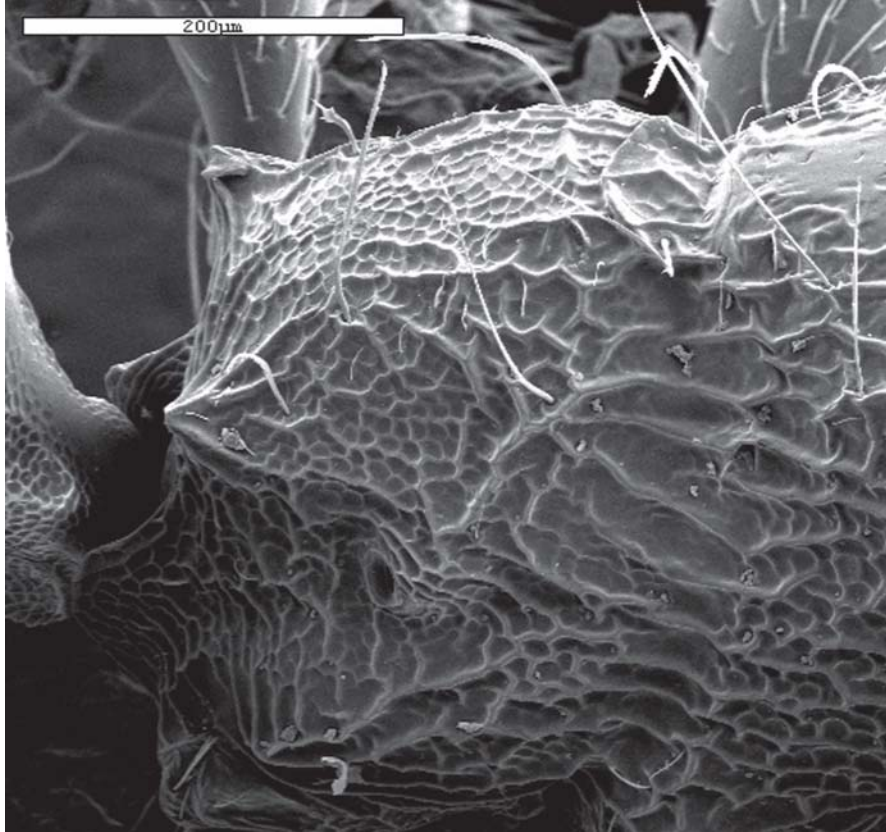
Fig. 14. Epinotum of *S. huberi* (Sierra de la Estrella, Portugal).

the absence of workers makes collection difficult or simply by chance, as suggested by Sanetra *et al.* (1999) to explain the distribution of this species in Italy.

Host species in Spain belong to the *T. caespitum/impurum* complex, as elsewhere in Europe. Sanetra *et al.* (1999) indicated *T. caespitum* and *T.* cf. *impurum* as hosts in Italy. In any case, the extremely complex taxonomy of the genus *Tetramorium* should be taken into account.

Genus *Teleutomyrmex* Kutter 1950

The genus *Teleutomyrmex* was discovered in 1949 by the myrmecologist Heinrich Kutter (1950) in Saas-Fee (Swiss Alps) and it constitutes, together with the genus *Anergates*, one of the most striking examples of adaptation to social parasitism, and one of the most extreme cases of that adaptation. Its biology was studied extensively by Stumper
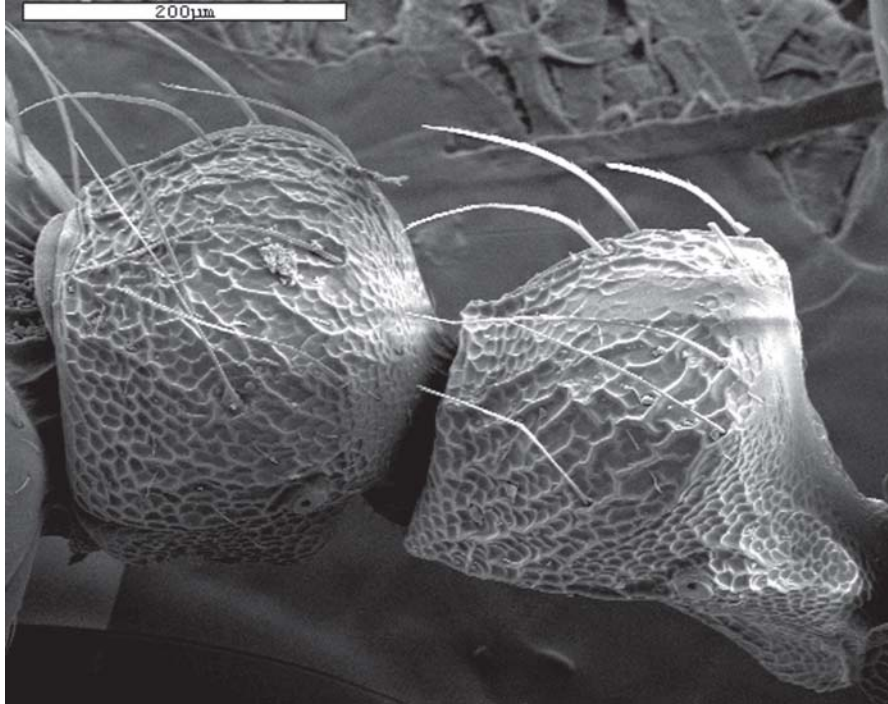
Fig. 15. Petiole and postpetiole of *S. huberi* (Sierra de la Estrella, Portugal).
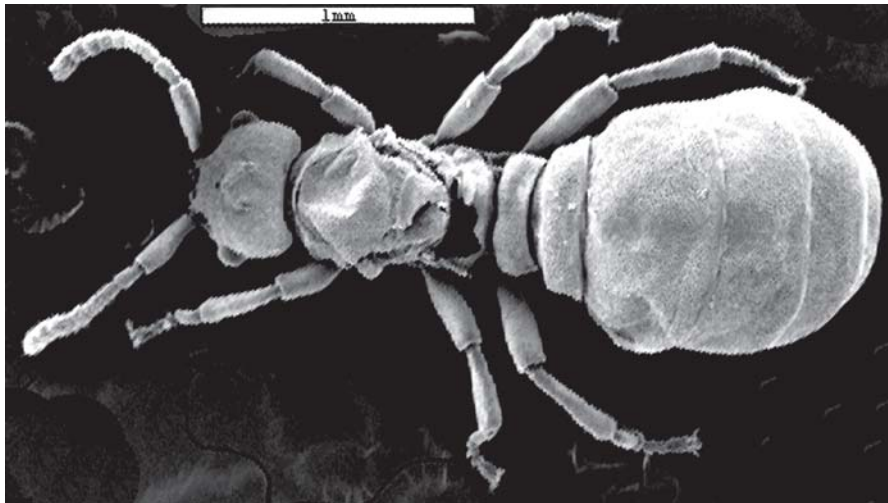

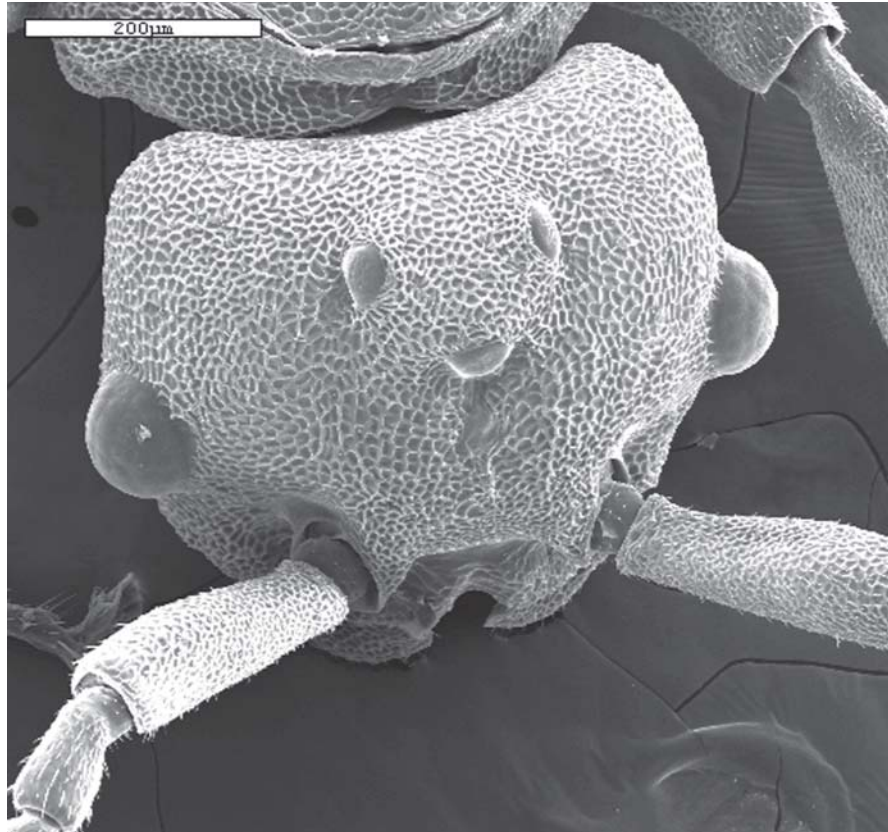Fig. 16. General view of *Anergates atratulus* (Córdoba, Spain).

Fig. 17. Detail of the miscrosculpture of the head and thorax in *A. atratulus* (Córdoba, Spain).

(1951), providing information on its behavior inside the host nest. Its host was considered to be *Tetramorium impurum* by Buschinger (1985, 1987), but the host species found by Tinaut (1990b) in the Sierra Nevada (Granada) was identified as *T. caespitum*. It turned out recently that the males from the Sierra Nevada show the genital morphology of *T. impurum*, as depicted by Kutter (1977). However, the high-altitude populations of the *caespitum/impurum* complex in central and southern Europe appear to be a previously unrecognized cryptic species (Schlick-Steiner *et al.* unpublished results).

With some similarities with *Anergates*, this genus is slightly thinner, not so pupoid as *Anergates*, with the head longer and shiny and the mandibles more developed (Figs. 18-19).

Since its original discovery in the Swiss Alps, this genus has been found on rare occasions again in the Swiss Alps (Stumper 1951;
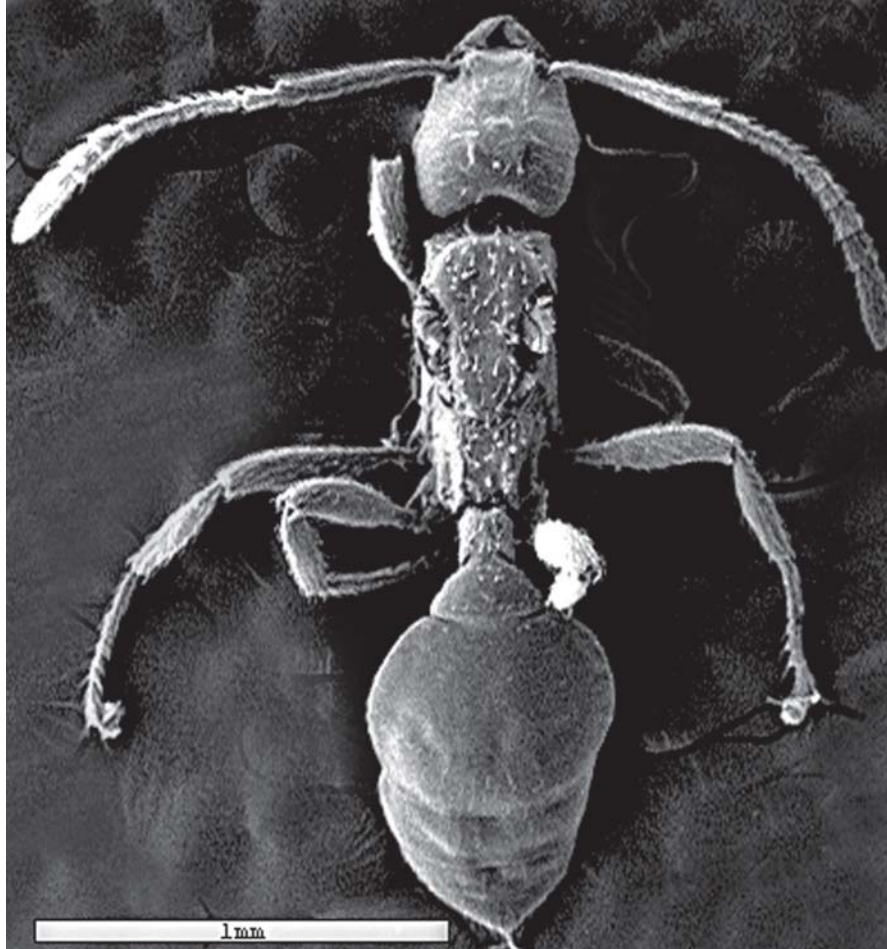
Fig. 18. General view of *Teleutomyrmex kutteri* (Sierra Nevada, Spain).

Buschinger 1999), the French Alps (Collingwood 1956; Buschinger 1985; Sanetra & Buschinger 2000), French Pyrenees (Buschinger 1987; Sanetra & Buschinger 2000) and the Sierra Nevada (Tinaut 1990b). Thus, the genus appears to be linked with high-mountain regions and meadow pastures. In this genus, only 2 species have been described up to now.

Teleutomyrmex schneideri Kutter 1950

In addition to its presence in the Swiss and French Alps, this species was cited by Buschinger (1987) in the French Pyrenees (Vallée d'Ossau).
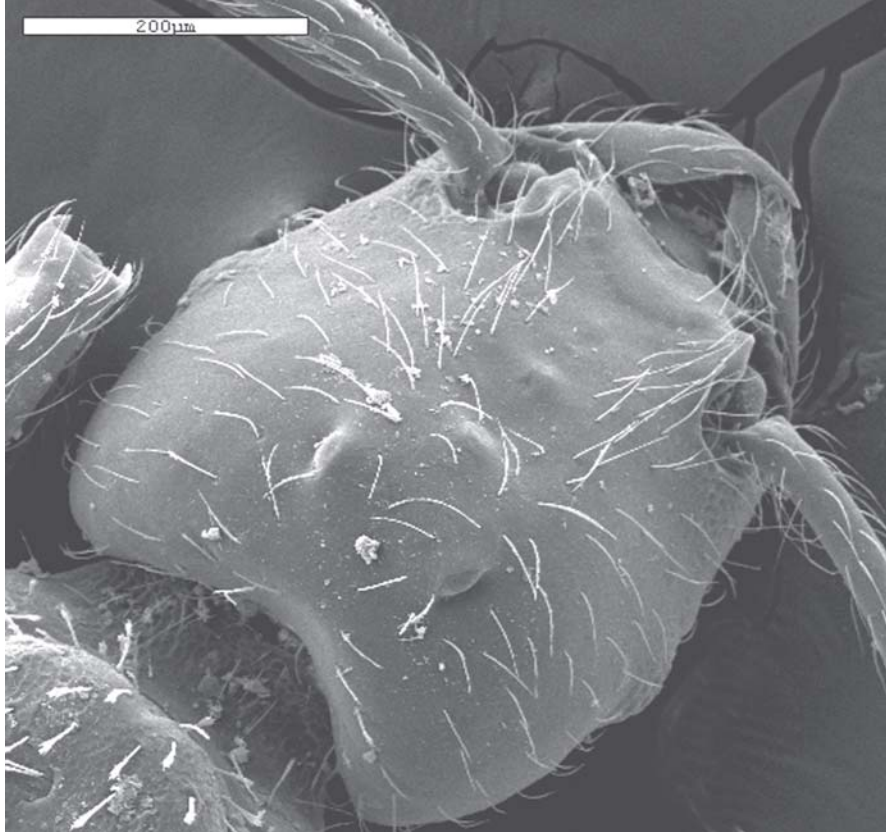
Fig. 19. Head of *T. kutteri* (Sierra Nevada, Spain).

Given its proximity to the valleys of the Huesca Pyrenees, it would not be surprising to record its presence on the Spanish side of the range, and thus we include this species in the present list.

The type species is the basis for all the and biological data known for this genus (Stumper & Kutter 1950). This species, and genus, is workerless. The female is highly modified and lives on the host female, receiving the same care from the host workers. The adaptation to live on a host female is reflected in the profile of the body, ventrally concave, and the elongation of the legs to grasp the host more firmly. In addition, the absence of a tibial spine appears to be related to the dependence on the grooming carried out by the host workers. The males are pupoid and mating occurs within the nest. The mechanism of invading a new nest is still unknown, but is assumed to be atypical, given the low mobility of the males and females.

Teleutomyrmex kutteri Tinaut 1990

Up to now, this species is known only in the Sierra Nevada (province of Granada) from a mountain meadow at an altitude of approximately 2250 m in the area know as Prados de Otero. It parasitizes a species of the *Tetramorium caespitum/impurum* complex. Since the discovery of this species in 1982, no new nest has been found, due undoubtedly not only to its rarity but also to the absence of workers (typical of the genus), making it more sporadic and difficult to find.

The morphological and anatomical similarity to *T. schneideri* suggests similarities in behavior and biology between the two species. The taxonomic differences are noted fundamentally by the type of setae situated on the petiole and postpetiole (Fig. 20) (Tinaut 1990).
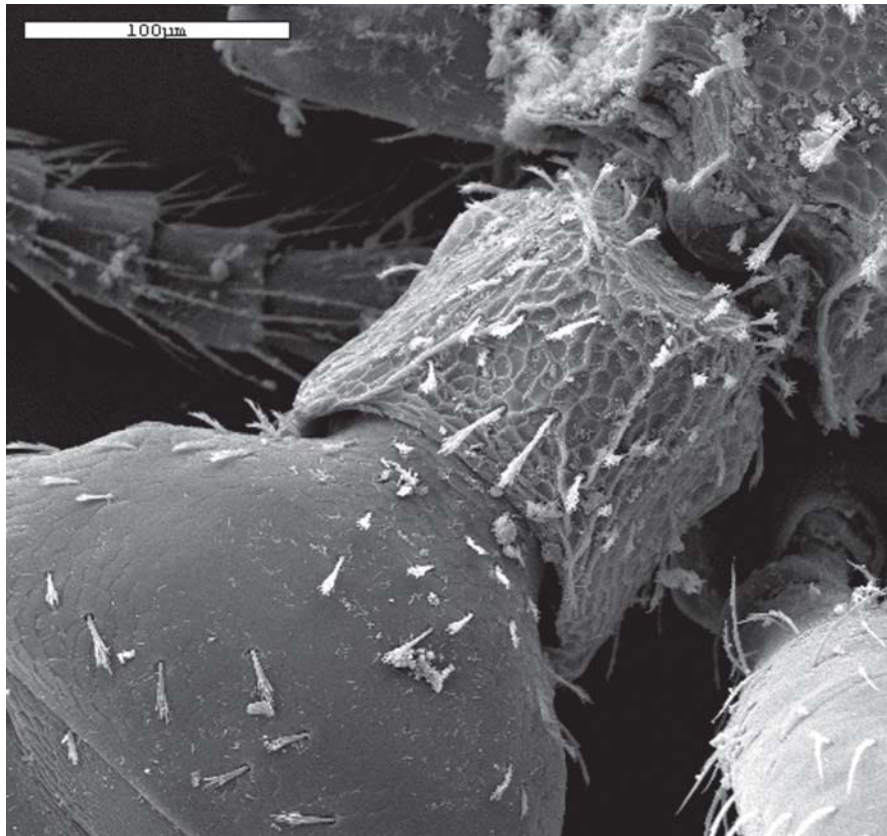

Fig. 20. Detail of the petiole and postpetiole in dorsal view of *T. kutteri* (Sierra Nevada, Spain).

It is noteworthy, finally, that this location in the Sierra Nevada harbors four Tetramorium parasites, the inquilines *Teleutomyrmex kutteri*, *Anergates atratulus*, *Strongylognathus testaceus*, and the slave-maker *S. huberi*, all using the same host species.

DISCUSSION

The total number of parasitic species of the Iberian Peninsula is very similar (Tinaut, Martínez & Ruano in prep.) to that known for other countries of Europe, such as France (Bernard 1968), Italy (Baroni Urbani 1969), Switzerland (Kutter 1978) or Greece (Buschinger & Douwes 1993), all of these ranging from 27 to 36 species. However, this number appears to be higher than for other Mediterranean countries such as Turkey, with 15 species (Heinze & Kauffmann 1993), Algeria, with 11 species (Cagniant 1973) or Morocco, with 8 species (Cagniant & Espadaler 1993). The case of Portugal may be special because only 6 parasites species are known, against a total of 100 species (Collingwood & Prince 1998), as this may simply reflect a lack of knowledge of the fauna as suggested by Collingwood & Prince (1998).

These differences may also be due to the level of knowledge of the total myrmecofauna in these different countries. However, without an attempt at an exhaustive analysis, if the number of formicid species known in a region can give an idea of the level of knowledge of that fauna, and if the proportion of parasitic species is related to the total number of species, then the proportions should be similar, regardless of the level of knowledge. Nevertheless, this is not the case, since, for example, in the Iberian Peninsula, the total number of species of formicids approaches 245, in Italy 225 and in France 195, implying a percentage of parasitic species of 13.5%, 16.1% and 16.0%, respectively, while in Algeria and Morocco, with 121 and 186 species, respectively, the percentages prove to be 9.1% and 4.3%, respectively—that is, far lower than for the Iberian Peninsula, Italy and France. This might have two possible explanations: either the finding of parasitic species does not follow the same pattern as free-living ones (that is, the probabilities are not proportional), or else there are environmental factors that explain the inequality in the distribution of parasitic species. In this sense Wilson (1971; see also Hölldobler & Wilson 1990) observed that social parasites are more abundant in the colder areas of Europe and North America. Wilson (1971) suggested that certain climates and environments predispose ant species towards parasitism. The coldest temperatures may facilitate the parasitism process by dulling the responses of the host colonies. This may explain not only the number of species found but also the distribution pattern in the Iberian

Peninsula, given that, in general, parasitic species appear with greater frequency in the northern half than in the southern half and, in this case, the distribution of these species is usually linked to high regions such as the Sierra Nevada or other mountains of the southern part of the peninsula.

In the subfamily Myrmicinae, the total number of parasitic species is also related with the total number of Formicidae fauna in each country: 16 species in France (Bernard 1968), 19 species in Italy (Baroni-Urbani 1969), 11 species in Switzerland (Kutter 1978), 14 in Greece (Buschinger & Douwes 1993), 6 in Turkey (Heinze & Kauffmann 1993), 5 to Algeria (Cagniant 1973), 4 to Morocco (Cagniant & Espadaler 1993) and 2 in Portugal (Tinaut & Ruano 1994; Collingwood & Prince 1998).

Nevertheless, the distribution pattern in the Iberian Peninsula of this group of parasitic species have a high frequency on the Mediterranean side (see Figs. 4-5, & 12), suggesting warmer requirements for the parasite species of this subfamily. In any case, the relation with the high mountain is frequent in the parasitic species of the genus *Tetramorium* (this paper and Sanetra *et al.* 1999). Exceptions to this rule would be the presence of some populations of *S. caeciliae* on the shores of the Mediterranean Sea, as found also by Sanetra *et al.* (1999) for *S. destefanii* Emery 1915. A similar situation may be true of *A. atratulus*, normally considered to have orophilous tendencies but nevertheless found in the province of Cordoba on the banks of the Guadalquivir. The distribution of this species may be determined by its host, which has a very wide distribution, probably reflecting incomplete taxonomic knowledge of the species of this genus. The rest of the species collected in the southern half of the Iberian Peninsula are usually found at altitudes of higher than 1000 m and up to 2500 m in the Sierra Nevada, as in the case of T. *kutteri*, as well as some species of *Strongylognathus* collected in mountain meadows (at 2100-2500 m).

In addition, the isolation of these mountain systems from others by depressions having hot climates, as well as the isolation of the Iberian Peninsula itself by the Pyrenees on the north and Mediterranean on the south has favored speciation, giving rise, at the moment, to 3 endemic species of this subfamily: *M. bernardi* of the Sierra de Gredos in the province of Avila; *T. kutteri* of the Sierra Nevada in the province of Granada and finally *S. caeciliae* from more or less from the north to the south of the peninsula in different mountain massifs. The endemic attribution of this last species could be changed depending of the taxonomic value of *S. afer*, present also in North Africa.

Most of the biological data provided in the present work are gener-alizations based on data published for these species, but from other

geographical areas. From the endemic species, only *M. bernardi* has been studied or is currently under study. Thus, there are many species for which even the basic processes of parasitism remain unknown, such as the mechanisms of invasion of host nests and formation of new nests, reproductive behavior, or other aspects of the life cycle, including activity inside the nest. This is not a problem only of the Iberian species, but a general problem, especially in the case of temporarily parasitic species (Buschinger & Seifert 1997). But such lack of information is not exclusive to this type of parasitism, given that in genera as diverse as *Strongylognathus* the information is fragmentary.

ACKNOWLEDGMENTS

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