Chromosome Numbers in Spanish Formicidae III. Subfamily Myrmicinae (Hymenoptera)

by

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ABSTRACT

In this paper a review of chromosome numbers of analyzed Spanish Myrmicine ants is carried out. Several species in Iberian populations have been studied. The results are compared with those obtained in other populations. This work supplied cytogenetic information about 40 species of myrmicine ants presents in Spain.

Key words: Formicidae, Myrmicinae, karyotypes, chromosome numbers.

INTRODUCTION

The Hymenoptera form one of the most distinct and well-defined insect orders, and have long been perceived as a natural group. Haplodiploidy or male haploidy is the main characteristic of the order. The ants (Hymenoptera, Formicidae) are social insects. The nests of ants are formed by castes, which present morphological and genetic differences.

Several studies have been carried out on cytogenetics of ants. Much variation has been observed in the chromosome numbers (n=1 to n=42). This difference can be due to the evolution of this family that seems to have originated in the Mesozoic era (Wilson *et al.* 1967).

In the last few years our group has performed studies on Spanish Formicidae. We have analyzed the karyotypic evolution of ants (Palomeque *et al.* 1987, 1998, 1990b, 1990c, 1993a, 1993b, Lorite *et al.* 1996b) as well as several aspects about the chromosome structure of this group of insects (Lorite *et al.* 1996a, 1997, 1999c), and genome organization (Lorite *et al.* 1999a, 1999b, 1999c, 1999d). A revision of the chromosome numbers of Spanish formicine and dolichoderine ants has been also carried out (Lorite *et al.* 1998a, 1998b). In this paper we report a revision in the subfamily Myrmicinae, and wherever possible, a comparative analysis with other related species is carried out.

MATERIALS AND METHODS

Metaphase chromosomes have been obtained from testes of male

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prepupae using the technique described in Lorite *et al.* (1996b). In this paper the bibliography about ant cytogenetics has also been used.

RESULTS AND DISCUSSION

More than 350 species of ants of the subfamily Myrmicinae have been cytogenetically studied. The known distribution of haploid numbers in Myrmicinae ants is shown in Fig. 1. The chromosome numbers found are very variable, between n=4 in *Stenamma brevicorne* (Hauschteck 1962, Imai 1966), and n=34 in *Myrmecina* species (Imai *et al.* 1985). The modal number is n=10, and the median number is n=14.4, showing a bimodal distribution with an antimodal value of n=15.

In relation to the haploid chromosome numbers Imai *et al.* (1988) differentiated between two groups of species; species with n£12n and others with with n³12. These groups are based on two observations; (1) the distribution of known haploid numbers presented a bimodal distribution with an antimodal value of n=12-13, and (2) different chromosome polymorphims can be observed. The similarities between the histograms of Imai *et al.* (1977, 1984, and 1988) and those presented in this paper may be due to the fact that the majority of karyotyped ants are included in the subfamily Myrmicinae. However this distribution cannot be observed in other subfamilies of Formicidae, as happens with the subfamily Formicinae (Lorite *et al.* 1998a) and with Dolichoderinae (Lorite *et al.* 1998b).

With regard to myrmicine ants cited in Spain, 40 species have been studied found in 14 genera, *Aphaenogaster*, *Cardiocondyla*, *Epimyrma*, *Harpagoxenus*, *Leptothorax*, *Manica*, *Messor*, *Monomorium*, *Myrmecina*, *Myrmica*, *Pheidole*, *Stenamma*, *Strongylognathus* and *Tetramorium*, with haploid numbers between n=9 and n=28. No karyological data of the genera *Anergates*, *Chalepoxenus*, *Diplorhoptrum*, *Epitritus*, *Formicoxenus*, *Goniomma*, *Oxyopomyrmex*, *Phacota*, *Teleutomyrmex*, *Temnothorax* and *Tichoscapa*, another genus present in Spain (Martinez *et al.* 1985) has been found. In some cases the data available has been obtained from Spanish populations. Other data came from other countries.

Genus *Aphaenogaster*

The genus *Aphaenogaster* presents haploid numbers between n=11 in *A. subterranea* and *A. smythiesi* (Hauschteck-Jungen & Jungen 1983, Imai 1971), and n=23 in *A. beccarii* (Imai *et al.* 1984) with a modal value of n=17. The value n=17 is considered by Hauschteck-Jungen & Jungen (1983) as the ancestral number of European species of genus *Aphaenogaster*. However, for Japanese species, Imai (1971) considered

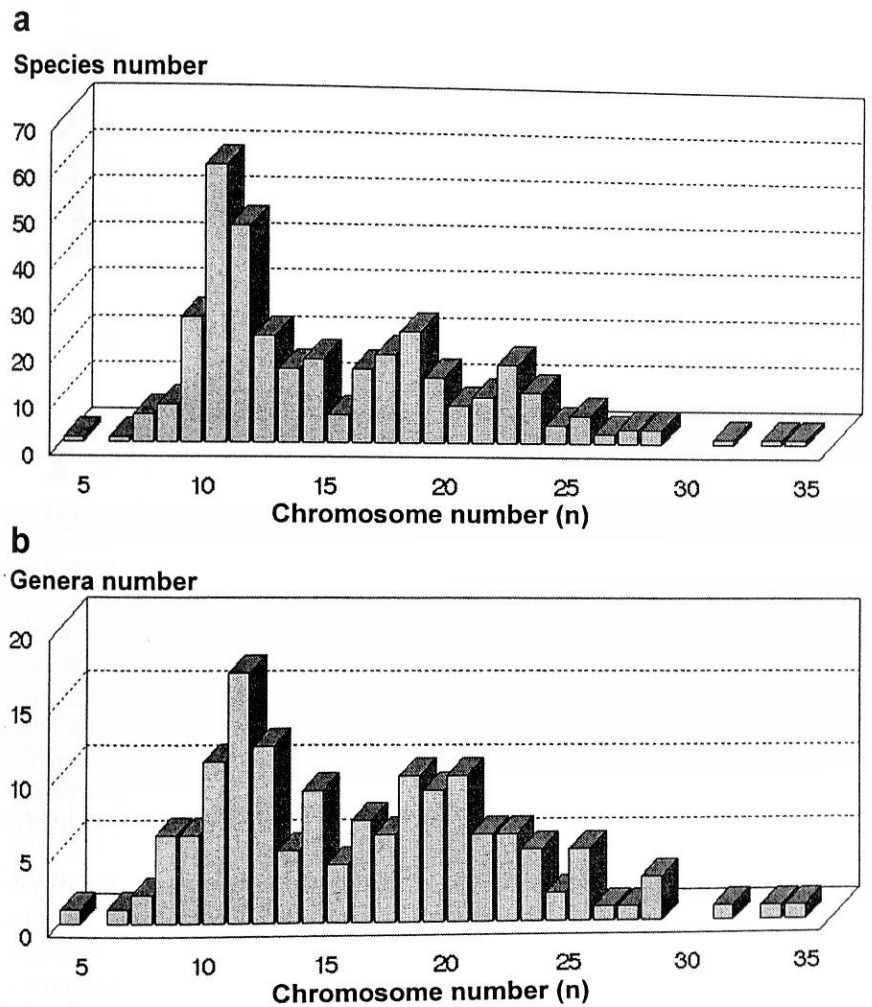

Fig.1. Distribution of haploid chromosome numbers in the analized species from the subfamily Myrmicinae (a). Distribution of haploid chromosome numbers in the analized genera from the subfamily Myrmicinae (b).

that the ancestral chromosome number is n=8, with chromosomes submetacentric to metacentric.

In Spain six species of this genus have been cited: *Aphaenogaster gibbosa*: In populations from Switzerland, Hauschteck-Jungen & Jungen (1983) observed n=11 with one acrocentric and ten metacentric chromosomes. However in populations from Jaén (Spain), we found a

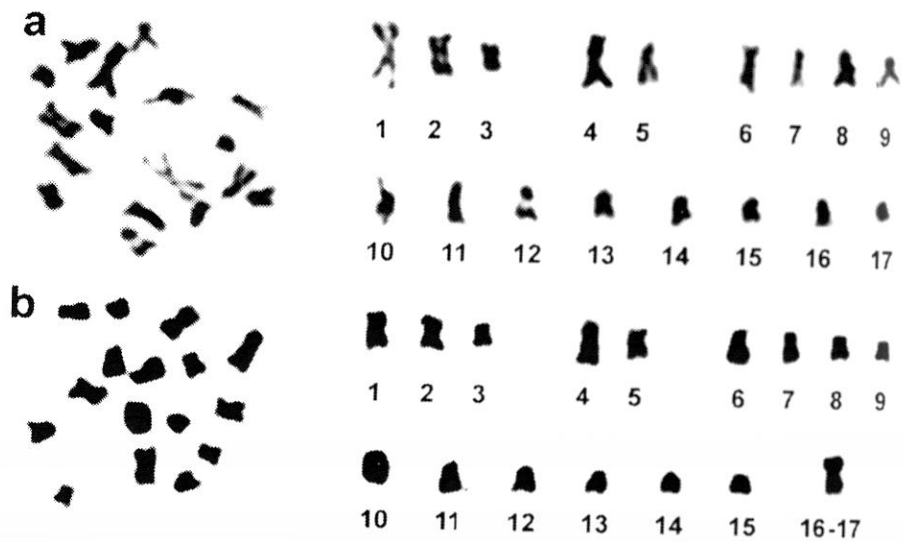

Fig.2. *Aphaenogaster gibbosa*, standard karyotype (a) and with fusion of chromosomes 16 and 17 (b).

chromosome number of n=17 (Palomeque *et al.* 1993a) with a karyotypic formula 3M+2SM+4ST+8T (Fig. 2a). The differences between both populations can be due to centric fission or fusion. Robertsonian polymorphisms are seen to be the more frequent evolutionary processes in ants (Imai *et al.* 1988, 1994). In addition to this, we found one population of this species with n=16, originated probably by a centric fusion between two telocentric chromosomes (Fig. 2b) (Palomeque *et al.* 1993a).

Aphaenogaster iberica: n=17, in populations from Jaén (Spain) we found n=17 (Palomeque *et al.* 1993a), with a karyotypic formula 3M+2SM+4ST+8T (Fig. 3a). In this species we can observe a polymorphism by the presence of a supernumerary chromosome segment on the largest submetacentric chromosome (Fig. 3b) (Palomeque *et al.* 1993b).

Aphaenogaster sardoa: n=17 in populations from Tunisia (Hauschteck-Jungen & Jungen 1983).

Aphaenogaster senilis: n=16, in populations from Jaén (Spain) with 3 metacentric, 3 submetacentric and 10 subtelocentric chromosomes (Fig. 4a). Like *A. iberica*, this species presents a polymorphism by the presence of a supernumerary chromosome segment in a submetacentric chromosome (Palomeque *et al.* 1993a, 1993b). The segment makes the morphology of the carrier chromosome change to subtelocentric (Fig. 4b).

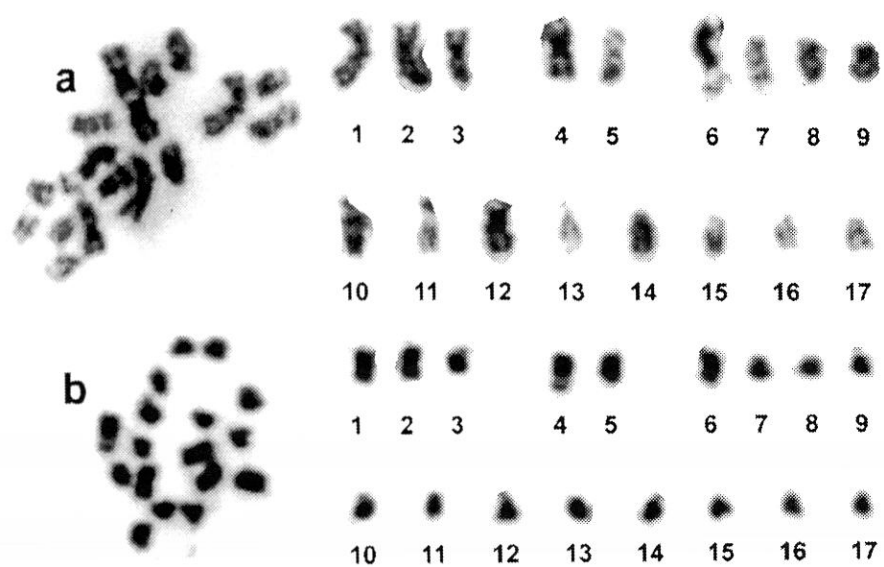

Fig.3. *Aphaenogaster iberica*, standard karyotype (a) and with a supernumerary chromosome segment on chromosome 4 (b).

Aphaenogaster subterranea: n=11, in Swiss and German populations (Hauschteck 1962, Hauschteck-Jungen & Jungen 1983), the karyotype formula is 10 SM+1A, coinciding with that observed by Imai (1966) in the Japanese population of this species.

Aphaenogaster testaceopilosa: n=17, in populations collected by Hauschteck-Jungen & Jungen (1983) in Málaga (Spain), Tunisia and Yugoslavia, this species presents 6 submetacentric to metacentric chromosomes and the rest are submetacentric to acrocentric.

Genus *Cardiocondyla*

Only two species of this genus have been karyologically studied *Cardiocondyla p*, with n=14 and *Cardiocondyla nuda*, with n=20 (Imai *et al.* 1984, Goñi *et al.* 1982). It is not possible to compare between the karyotypes of this species, since in the species studies by Goñi *et al.* (1982) only the chromosome number is reported. *Cardiocondyla nuda* are present in Spain.

Cardiocondyla nuda: n=14, in populations from India (Imai *et al.* 1984). The karyotype is formed by 6 metacentric chromosomes, three of them with a large size, and 8 acrocentric chromosomes.

Genus *Epimyrma*

All species of this genus cited in Spain have been studied.

Epimyrma bernardi: n=10, in populations from Sierra de Gredos

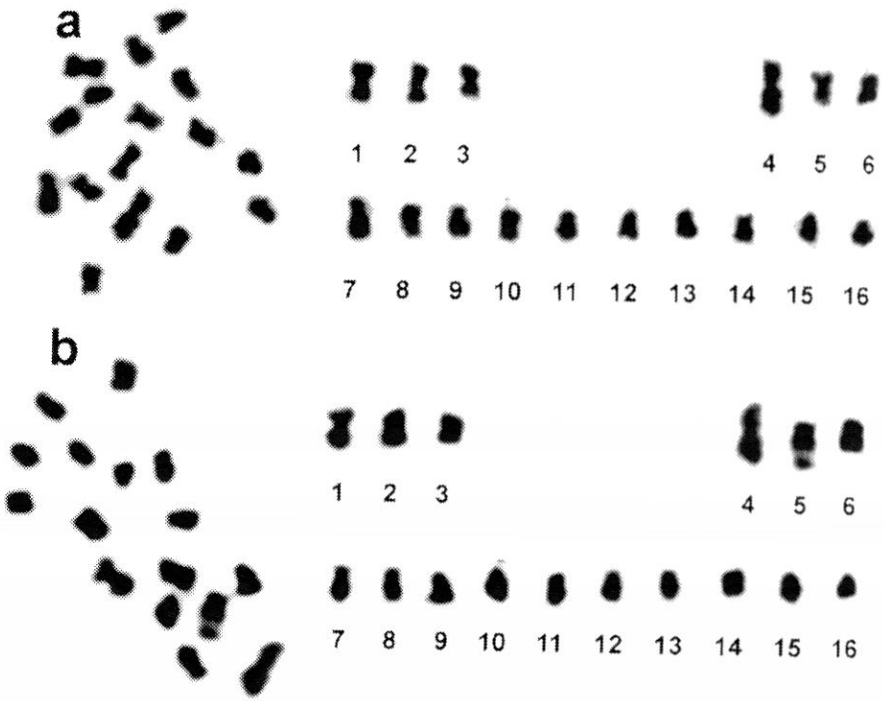

Fig.4. *Aphaenogaster senilis*, standard karyotype (a) and with a supernumerary chromosome segment on chromosome 5 (b).

(Spain)(Douwes *et al.* 1988).

Epimyrma kraussei: n=10, in several populations from Spain, France, and Italy (Buschinger *et al.* 1986).

Epimyrma ravouxi: n=10, in populations from Italy, Switzerland, and France (Douwes *et al.* 1988).

These species, as well as the other four studied species, present n=10 and very similar karyotypes. The karyotypes are formed by 6 small metacentric, 3 submetacentric and one large subtelocentric chromosomes (6M+3SM+1ST) (Buschinger *et al.* 1986, Douwes *et al.* 1988).

Genus *Harpagoxenus*

Only one species of this genus has been cited in Spain, *H. sublaevis*.

Harpagoxenus sublaevis: n=20 in populations from Switzerland (Hauschteck-Jungen & Jungen 1983), with 5 metacentric and 15 telocentric chromosomes.

Buschinger (1971) stated that *H. sublaevis*, together with the other parasitic species, are closer to *Leptothorax*. Kutter (1977) calls *Harpagonexus*, like some other social parasitic genera, a "satellite

genus" of *Leptothorax*, in the sense that these social parasites are all derived from *Leptothorax* species and are still parasiting on their ancestral forms or at least on a related species. Hauschteck-Jungen & Jungen (1983) think that *H. sublaevis* is rather distant from the genus *Leptothorax* based on the fact that the karyotype of *H. sublaevis* differs remarkably from that of parasitic *Leptothorax* species. The karyological differences between species are not a definitive feature to differentiate between the genera of ants. There are several genera with large uniform chromosome numbers like *Formica*, *Lasius*, and *Pheidole*, although other genera present very variable chromosome numbers, such as *Camponotus* (n=9 to 26), *Crematogaster* (n=12 to 25), *Monomorium* (n=8 to 35) and especially *Myrmecia* with n=1 to 42. (Hung 1969, Crozier 1970, 1975, Imai *et al.* 1977, 1984, Hauschteck-Jungen & Jungen 1976, 1983, Rosengren *et al.* 1980, Goñi *et al.* 1982, 1983, Crosland & Crozier 1986, Taber & Cokendolpher 1988, Imai & Taylor 1989, Lorite *et al.* 1998a, 1998b, this paper).

Genus *Leptothorax*

The haploid numbers found in the species of genus *Leptothorax* are very variable, between n=7 in *L. tuberum-interruptus* and n=17 to 23 in *L. muscorum* complex (Loiselle *et al.* 1990).

Leptothorax acervorum: n=13, in European populations from Switzerland, Sweden, France, and Germany as well as in North American populations (Hauschteck-Jungen & Jungen 1983, Loiselle *et al.* 1990). In all populations the same karyotype (8M+3SM+2A) is found.

Leptothorax corticalis: n=9 in the revision carried out by Crozier (1975).

Leptothorax gredleri: n=11, in populations from Switzerland, and Germany. Eight metacentric and three submetacentric chromosomes form the karyotype of this species (Loiselle *et al.* 1990).

Leptothorax interruptus: n=12, in populations from Switzerland, Germany, Yugoslavia, and Greece. Eight metacentric, three submetacentric and one small subtelocentric chromosomes (Hauschteck-Jungen & Jungen 1983) form the karyotype.

Leptothorax muscorum: The studies carried out by Loiselle *et al.* (1990) show that the taxon *L. muscorum* is really a complex of closely related species. These authors found a big variation between populations. In German populations the haploid number was n=17, but one colony had n=18. The populations from North America are more complex, because in these populations there are colonies with n=17, 18, 22, and 23. In addition, 4 or 5 (rarely 6 or 7) B-chromosomes added to the standard 17 or 18 chromosomes, were also found (Loiselle *et al.*

1990). The occurrence of B chromosomes has also been reported in several species of the genus *Leptothorax* (Imai 1974, Taber & Cokendolpher 1988) as well as in other species of ants (Crozier 1975, Imai *et al.* 1983, Palomeque *et al.* 1990c, Goñi *et al.* 1982, 1983).

Leptothorax nylanderi: n=11, in populations collected in several countries (Italy, Germany, France and Switzerland), the karyotype of this species is formed by metacentric to submetacentric chromosomes (Hauschteck-Jungen & Jungen 1983).

Leptothorax tuberum: n=9 in populations from France, Switzerland, and Sweden, the karyotype is formed by 8 metacentric and one submetacentric chromosomes (Hauschteck 1961, 1962, Hauschteck-Jungen & Jungen 1983). In Japanese populations of this species Imai (1966) found the same chromosome number.

Leptothorax unifasciatus: n=9 in populations from Germany and Switzerland (Hauschteck-Jungen & Jungen 1983).

Genus *Manica*

Only one species of this genus is present in Spain, *Manica rubida*. Other data of this genus are not available.

Manica rubida: n=22, in Swiss populations (Hauschteck-Jungen & Jungen 1983).

Genus *Messor*

Only three species of this genus have been karyologically studied, one of them cited in Spain, *Messor barbarus*. The other two species present haploid chromosome numbers of n=20 and n=22 (Imai 1966, 1969, Imai *et al.* 1984) with small subtelocentric and telocentric chromosomes.

Messor barbarus: n=22, observed by Hauschteck (in revision carried out by Crozier 1975).

Genus *Monomorium*

Large variations in the haploid chromosome numbers have been observed in this genus. Imai *et al.* (1984) found species with n=8 (*M. dichroum*) to n=35 (*M. latidone*) in several Indian species. For the species cited in Spain the following results have been obtained:

Monomorium minimum: n=11 in populations from North America (Crozier 1975). The karyotype formula is 9M+1SM+1A.

Monomorium pharaonis: n=11 in populations from North America (Peacock *et al.* 1954, Smith & Peacock 1957), before verification in Japanese populations by Imai & Yosida (1964) and Imai (1966, 1969). 7 metacentric, 3 submetacentric and one telocentric chromosomes form the karyotype. This species was the first to be karyologically studied. However, the results of Welden & Hasking (1953) about this species may be not considered since the data on this species seem to be no correct.

Monomorium subopacum: n=17, determined by Hauschteck-Jungen (in the revision carried out by Crozier 1975).

Genus *Myrmecina*

Four species of this genus have been karyologically studied, two with n=14, *Myrmecina americana* and *Myrmecina gramminicola* (Crozier 1975). The other two species *Myrmecina* sp. 1 and *Myrmecina* sp. 2 have the biggest chromosome numbers found in the subfamily Myrmicinae, n=33 and n=34 (Imai et *al.* 1985).

Myrmecina graminicola: n=14, determined by Hauschteck-Jungen (in the revision carried out by Crozier 1975).

Genus *Myrmica*

Seven species of this genus have been studied, all of them cited in Spain.

Myrmica laevinodis: n=24, in populations from Switzerland (Hauschteck-Jungen & Jungen 1983).

Myrmica lobicornis: n=24, (Hauschteck-Jungen & Jungen 1983).

Myrmica rubra: n=23, in Japanese populations (Imai 1969).

Myrmica ruginodis: n=24, in Swiss populations (Hauschteck-Jungen & Jungen 1983).

Myrmica sabuleti: n=23, in Swiss populations (Hauschteck-Jungen & Jungen 1983).

Myrmica schenki: n=23, in Swiss populations (Hauschteck-Jungen & Jungen 1983).

Myrmica sulcinodis: n=24, in Swiss populations (Hauschteck-Jungen & Jungen 1983). Hauschteck (1965) indicated that males present a chromosome number of n=28, and queens 2n=56. In addition, this author found that many cells in the tests have only 14 chromosomes. Crozier (1975) suggested that this could be due to a possible tetraploid origin of this species.

Genus *Pheidole*

The haploid numbers found in this genus are very stable, n=9 to 10 in 50 of the 88 studied species with submetacentric to metacentric chromosomes. Also, the species with n=9 are very frequent (13 species) (Imai *et al.* 1977, 1983, 1984, 1985, Goñi *et al.* 1983, Tjan *et al.* 1986, Taber & Cokendolpher 1988, among others). Only two species cited in Spain have been studied.

Pheidole megacephala: n=10, in populations collected in Malaysia (Imai et *al.* 1983).

Pheidole pallidula: n=10, in several populations collected in Switzerland, Greece, Tunisia, as well as in Málaga (Spain), by Hauschteck-Jungen & Jungen (1983). In populations from Jaén (Spain) we found the same haploid number and karyotype (Fig. 5a), formed by 6 submetacentric and 4 metacentric chromosomes (Palomeque *et al.* 1987). Although in the papers of Hauschteck-Jungen & Jungen in 1983 n=10 is given as the haploid number, previously the author indicated that in this species the chromosome numbers were n=12, 2n=24 (Hauschteck 1961). The author explains this difference as a consequence of a polymorphism similar to that present in *P. nodus*. The species *P. nodus* has n=17 to 20 as a consequence of a process of centric fusion or fission, showing different karyotypes, n=17 (with 4M+0T), n=18 (3M+2T), n=19 (2M+4T) and n=20 (1M+6T) (Imai & Kubota 1972, 1975). We have found numerical variations in the chromosome numbers of this species with the presence to a B-chromosome (Fig. 5b) but not by Robertsonian process. Imai (1966), in Japanese populations, found n=12, but is not possible to carry out comparisons because in this paper the metaphase plate is not shown.

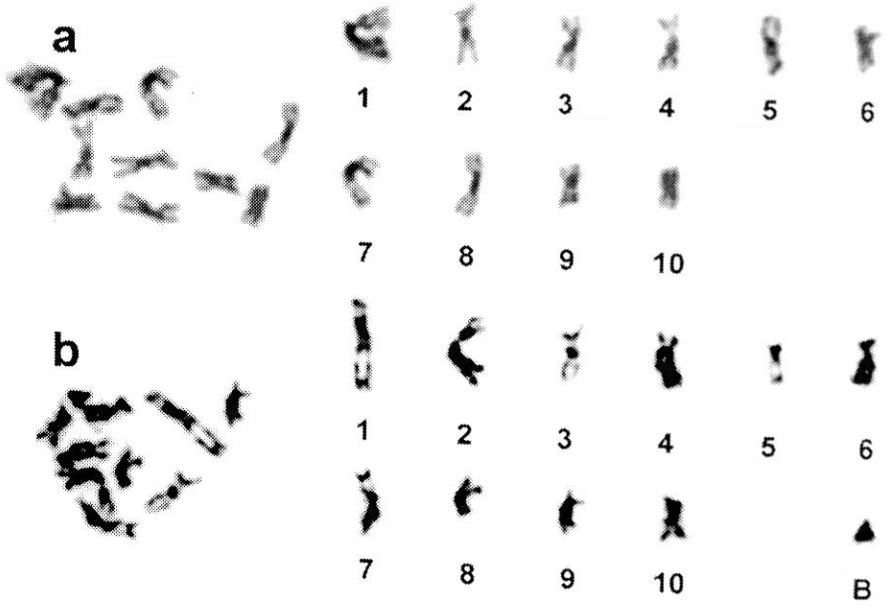

Fig. 5. *Pheidole pallidula*, standard karyotype (a), and with a B chromosome (b).

Genus *Stenamma*

Two species of this genus have been studied. These species present very different karyotypes, since *S. brevicorne* has n=4 (Imai 1966, Hauschteck 1962) and *S. westwoodi* has n=20. The last species has been cited in Spain.

Stenamma westwoodi: n=20, determined by Hauschteck-Jungen (in the revision carried out by Crozier 1975).

Genus *Strongylognathus*

Only one species of the genus has been studied. This species has been cited in Spain.

Strongylognathus huberi: n=14, in Japanese populations (Imai 1966).

Genus *Tetramorium*

The haploid chromosome numbers in this genus vary between n=7 in *T. kheperra* and n=18 in a non-determinated species (Imai 1969, Imai *et al.* 1984, 1985, Goñi *et al.* 1982, Tjan *et al.* 1986, Taber & Cokendolpher 1988). Only three Spanish species have been studied.

Tetramorium caespitum: n=14, in Swiss populations (Hauschteck 1961) as well as in several populations from Jaén (Spain) (Palomeque *et al.* 1987). The same haploid number was found in Japanese populations (Imai & Yosida 1964, Imai 1966, 1969).

Tetramorium hispanicum: n=14, in populations from Jaén (Spain)(Palomeque *et al.* 1987).

Tetramorium semilaeve: n=14, in populations from Jaén (Spain)(Palomeque *et al.* 1987).

The three species present the same karyotypic formula, 4SM+3ST+7T (Fig. 6). Differences between the karyotypes can be observed before C-banding or Ag-staining (Palomeque *et al.* 1987). Imai (1969) found for *T. caespitum* the same chromosome numbers but different karyotypic formula, 5M+3ST+6T. The differences may be due to growth or loss of heterochromatin, processes that are frequent in ant chromosome evolution (Imai *et al.* 1977, 1984, 1994, Palomeque *et al.* 1993a).

Other Spanish genera

Other genera of Myrmicinae cited in Spain are *Crematogaster* and *Smithistruma*, but no data is available from species cited in Spain. However, data is available for other species. For *Crematogaster* the haploid chromosome numbers found vary between n=10 to n=29 (Imai & Yosida 1964, Imai 1966, Goñi *et al.* 1982, Imai *et al.* 1983, 1984, 1985, Tjan *et al.* 1986). The species with low chromosome numbers have submetacentric to metacentric chromosomes, however in species with n=25 the majority of them are acrocentric (Imai *et al.* 1984). This could

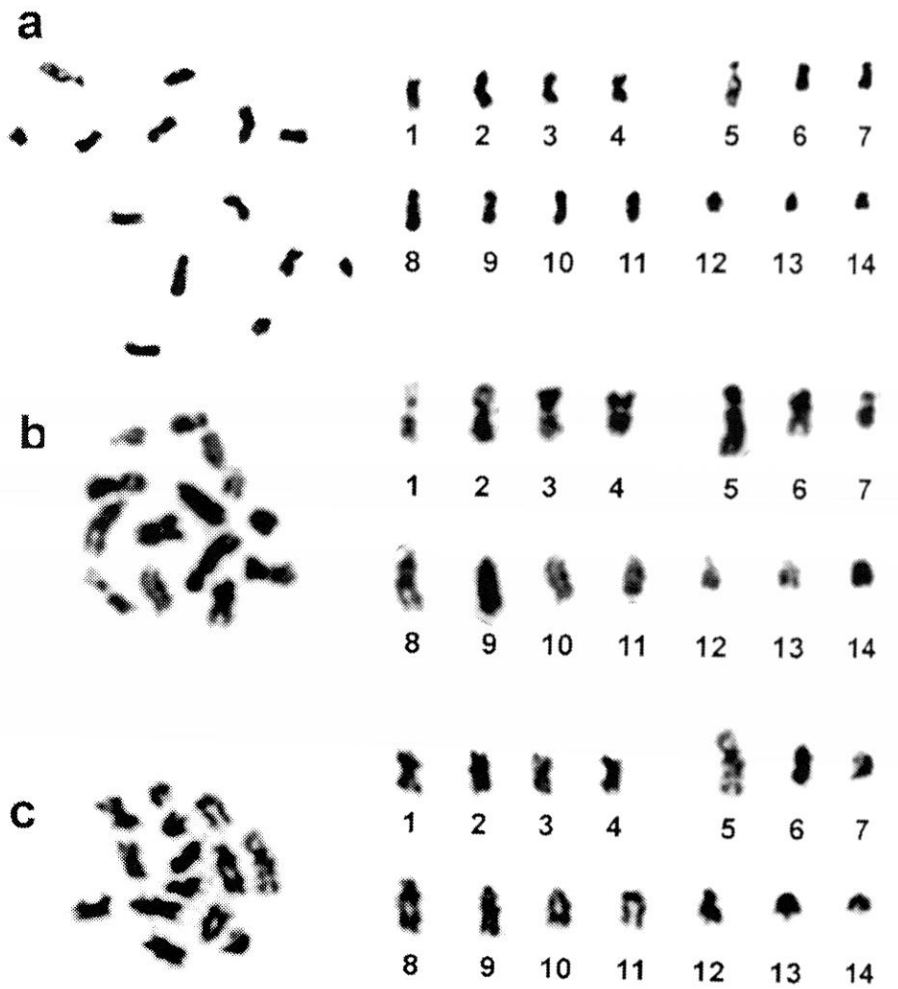

Fig.6. Standard kayotypes of the species *Tetramorium caespitum* (a), *Tetramorium hispanicum* (b) and *Tetramorium semilaeve* (c).

indicate that in this genus Robertsonian processes are very common, as in other genera (Imai *et al.* 1988, 1994). For *Diplorhoptrum* only the chromosome number of a undetermined species collected in Malaysia is known, with n=19 (Goñi *et al.* 1982). Only five species of *Smithistruma* have been studied, with n=8 to n=20 (Brown 1954, Crozier 1975, Goñi *et al.* 1982, Imai *et al.* 1983, 1985).

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