

## **A survey of the socially parasitic ant genera *Epimyrma* Emery, 1915 and *Chalepoxenus* Menozzi, 1922 in Italy (Hymenoptera, Formicidae, Myrmicinae)**

M. Mei

*Dipartimento di Biologia Animale e dell' Uomo, Università di Roma "La Sapienza",  
Viale dell' Università, 32, 00185 Roma, Italy*

**Key words:** Formicidae, Leptothoracini, social parasitism, faunistics.

### **Summary**

An up-to-date synthesis is presented of the available faunistic and biological data concerning the Italian species belonging to the socially parasitic ant genera *Epimyrma* Emery and *Chalepoxenus* Menozzi.

The first known populations of *E. corsica* (Emery) and *E. stumperi* (Kutter) in Italy were discovered in the Lucretili mountains (Latium) and in Alto Adige, the former species being previously recorded only in Corsica and Dalmatia (Yugoslavia), the latter in the French and Swiss Alps.

The first records of *E. ravouxi* (André), *E. kraussei* (Emery) and *C. muellerianus* (Finzi) in central Italy are presented. Since no species of either genera has ever been collected in Italy in the area between the Po valley and Calabria, these new records are of great interest.

Maps, showing the currently known distribution of each taxon in Italy, are provided.

### **Introduction**

The closely related leptothoracine ant genera *Epimyrma* (Emery, 1915) and *Chalepoxenus* (Menozzi, 1922) are distributed, in about ten and five species respectively, in central and southern Europe, North Africa and central Asia. All species in both genera are parasites of *Leptothorax* (Mayr, 1855) species belonging to the subgenera *Myrafant* (Smith, 1950) and *Temnothorax* (Mayr, 1861).\*

In *Epimyrma*, an evolutionary trend from slave-making species to workerless forms has been noted (Buschinger and Winter, 1982; Buschinger, 1989a). Several species have true dulotic life habits, and conduct organized slave raids, with group recruitment and sting fighting, on neighbouring colonies of the host species (Winter, 1979; Buschinger and Winter, 1982, 1983; Buschinger, 1989a; Buschinger et al., 1990).

One species, *E. kraussei* (Emery, 1915), with a much reduced worker number, is not able to conduct effective slave raids, although the workers still exhibit all raiding behaviour (Buschinger and Winter, 1983; Buschinger, 1989a, 1989b). Finally,

workerless permanent parasitism has been documented in a population of *E. kraussei* from Crete, in *E. corsica* (Emery, 1985) and in *E. adlerzi* (Douwes et al., 1988).

Such workerless parasitism differs from true inquilinism in that the young *Epimyрма* queen, as is usual in the genus, strangles the host queen during colony foundation instead of co-existing with her (Buschinger and Winter, 1985; Douwes et al., 1988; Buschinger, 1989 a, 1989 b).

In parallel with the reduction of the worker number, a trend has been observed in this genus leading from normal swarming behaviour (soon followed by colony foundation) to intranidal mating (with young queens overwintering in the mother nest and dispersing on foot for colony foundation in the spring) (Buschinger and Winter, 1982; Buschinger, 1989).

*Chalepoxenus* is also a slave-making genus; however, it differs from *Epimyрма* in some behavioural features. The young *Chalepoxenus* queen does not strangle the host queen during colony foundation, but manages to eliminate all adults from the host colony in order to take possession of the brood; recruitment to raid is also different from *Epimyрма*, being performed by tandem-running (Buschinger et al., 1980; Ehrhardt, 1982, 1987).

Recently, a North African species, *C. brunneus* (Cagniant, 1985), has been proved to be a truly workerless parasite (Buschinger et al., 1988).

Four *Epimyрма* and at least one *Chalepoxenus* species, as well as *Myrmoxenus gordiagini* (Ruzsky, 1902) from Istria (Baroni Urbani, 1971), a slave-maker ant very closely related to and probably congeneric with *Epimyрма* (Buschinger et al., 1983), have so far been recorded with certainty for the Italian myrmecofauna.

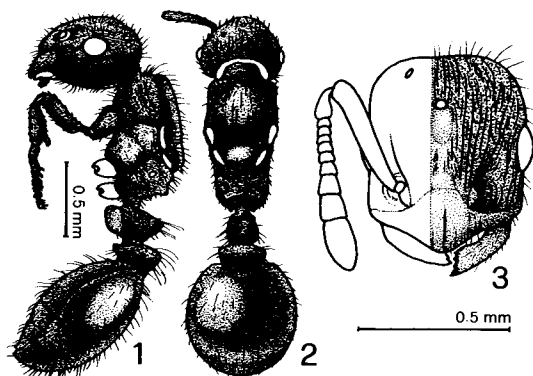
In this paper, a synthesis of available faunistic and biological data concerning the Italian *Epimyрма* and *Chalepoxenus* species is presented, in order to provide an up-to-date standpoint to support further studies on these ants.

New records from my recent collectings and several important, unpublished faunistic data kindly communicated by Prof. A. Buschinger of the Technische Hochschule of Darmstadt (Germany) are presented, contributing to fill large gaps in the known distribution of both genera.

### *Epimyрма corsica* (Emery, 1895) (Figs. 1–3)

The original description of this species (Emery, 1895) was based on a single dealate female from an unspecified locality of Corsica. This was the only known *E. corsica* specimen until recently, when Buschinger and Winter (1985) discovered a population of this species in Corsica and a few others on the island of Krk and along the Dalmatian coast (Yugoslavia). These, together with the two that are recorded here, are so far the only known populations of this parasitic ant.

*E. corsica* is a workerless parasite of *Leptothorax* (M.) *exilis* (Emery, 1869) (Buschinger and Winter, 1985). As in the other "degenerate slave-maker" *Epimyрма*, young sexuals do not exhibit normal swarming behaviour (Buschinger, 1989 a). Mating occurs inside the mother nest, and the dealate females overwinter there. In early spring, the young queens leave the nest on foot in search of new host colonies (Buschinger and Winter, 1985).



Figures 1–3. *E. corsica*, dealate female, from Valle del Fosso di Castiglione (Latium)

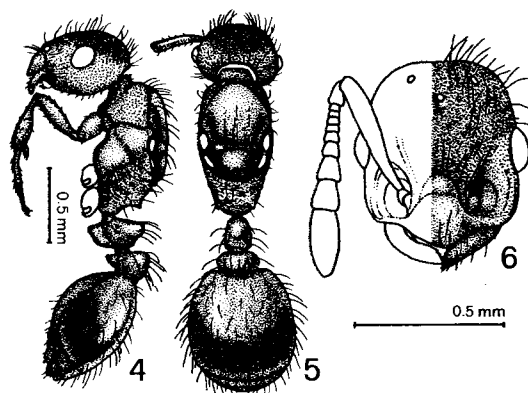
*E. corsica* was discovered in two different sites in the Lucretili mountains, about 40 km NE of Rome (Latium).

The site of Valle del Fosso di Castiglione, 1.5 km N of the village of Civitella (RM), is a steep, rocky slope at an elevation of 700 m. The slope is covered by low, sparse vegetation, with bushes of *Crataegus* sp., *Spartium* sp. and *Rosa* sp., and isolated oak trees. The nests were located in crevices of the hard limestone rock, and were quite difficult to find. The host species was *L. exilis*. Three colonies, found in June 1984, consisted of 1 *Epimyrma* queen, 3 to 12 *Leptothorax* workers and brood. Another two larger colonies, collected in early October 1990, both contained several dealate parasitic females, many host workers and brood.

The other site is located 1 km N of the village of Percile (RM) (about 3 km from Civitella), along the road S.S. 314 "Licinese" at an elevation of 550 m; the nests were found on the border of a small clearing a few meters from the bridge on the stream called Fosso Pisciarelli. The vegetation is similar to the other site's, although higher and denser, and the stones are scattered on the ground. This site is very rich in *Leptothorax* species, and *Epimyrma ravouxi* (André, 1896) is also present (see below).

Several *E. corsica* colonies were discovered in the crevices and under small stone chips on the rocks. Six colonies were collected in January 1989. One consisted of 5 *Epimyrma* dealate females, several *L. exilis* workers and brood; the remaining five contained 1 parasitic queen only, together with host workers and brood, and had been probably newly founded. New colonies of this ant, both in Corsica and in Dalmatia, are founded in March (Buschinger, pers. comm., 1989). Early colony foundation can be induced by an exceptionally dry and warm winter (which was the case in 1988/89), and can also result from biological differences of a particular population, as observed in other *Epimyrma* species (Buschinger, pers. comm., 1989).

An unusual production of *L. exilis* sexuals in a parasitized colony from this site was observed. In the field, in early May 1989, the colony consisted of 1 *E. corsica* queen, 75 *Leptothorax* workers and brood; the colony was reared until mid-August, when I had to stop my observations. At that time, 22 *Leptothorax* females and 4 males has been produced as a whole; only 4 *Epimyrma* males hatched, but 2 *Epimyrma* male



Figures 4–6. *E. kraussei*, dealate female, from Gizzeria (Calabria)

and 5 female pupae were still present in the nest. The parasitic queen died (was killed?) during the first days of August.

Buschinger (1989b) observed the same unusual production of host sexuals in several *Leptothorax* (*T.*) *recedens* (Nylander, 1856) colonies parasitized by *E. kraussei*.

#### *Epimyrmica kraussei* (Emery, 1915) (Figs. 4–6)

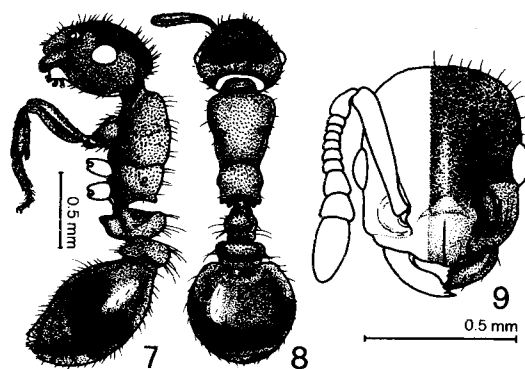
The range of *E. kraussei* (= *E. vandeli* (Santschi, 1927), = *E. foreli* (Menozzi, 1921)) (Buschinger et al., 1986) extends around the Mediterranean Basin. So far, this species has been recorded in Morocco (Buschinger and Douwes, 1991) Algeria, Spain, southern France, Switzerland, northern Italy, Yugoslavia (Buschinger et al., 1986), Greece (Buschinger, 1989a) and Turkey (Heinze, 1987). It is known also from southern Italy, Sardinia, Corsica (Buschinger et al., 1986) and Crete (Buschinger, 1989b).

In northern Italy *E. kraussei* is known from the Valle d'Aosta (Aosta), Liguria (Albenga, Alassio, Pornassio, Ranzo, Toirano, Ventimiglia, Zuccarello) (Chiavari, Baroni Urbani, 1971), Lombardy (Biolo, Lovere, Ossuccio, Tignale), Trentino (Rovere della Luna) and Alto Adige (Salorno) (Buschinger et al., 1986; Buschinger, 1987, pers. comm.).

Furthermore, this species has been recorded in Sambiasi in Calabria (= *E. foreli*, type locality; Menozzi, 1921) and in the neighbouring localities of Gizzeria, Rogliano and Serrastretta (Buschinger et al., 1986; Buschinger, 1987, pers. comm.).

The type locality of this species is Sorgono in Sardinia (Emery, 1915); however, this species has not been found again there, nor anywhere else on the island (Buschinger et al., 1986).

The host species of this *Epimyrmica* is *Leptothorax* (*T.*) *recedens* (Nylander, 1856). *E. kraussei* is a "degenerate slave-maker" (Buschinger and Winter, 1983), representing an intermediate stage between the slave-making *Epimyrmica* species, with a high worker number, and the workerless forms such as *E. corsica* and *E. adlerzi*



Figures 7–9. *E. ravouxi*, worker, from Percile (Latium)

(Buschinger, 1989a; Buschinger et al., 1986). The number of workers is reduced; recently a completely workerless population of this species was found in Crete (Buschinger, 1989b). Slave-raids in nature are generally thought to be an exception (Buschinger et al., 1986), although the workers can conduct normal slave-raids under favourable laboratory conditions, as described by Buschinger and Winter (1983).

Intranidal mating occurs in early autumn, and mated females overwinter in the mother nest until they disperse on foot for colony foundation in spring (Winter and Buschinger, 1983).

Recently (October 1990), *E. kraussei* was collected by Buschinger et al. from several sites in central and southern Italy. Populations were found in the Gargano promontory (Apulia), in the Abruzzi National Park and in Latium near the city of Sora (FR) (Buschinger, 1990, pers. comm.).

#### *Epimyrma ravouxi* (André, 1896) (Figs. 7–9)

*Epimyrma ravouxi* (= *E. goesswaldi* (Menozzi, 1931)) (Buschinger, 1982) is one of the most widespread species of the genus. It is distributed all over southern Europe, from the Spanish Pyrenees (Espadaler and Restrepo, 1983) to Greece (Agosti and Collingwood, 1987); within this area, the species has been collected from several localities in France, Switzerland, Austria, northern Italy and Yugoslavia (Buschinger et al., 1981) as well as from the islands of Corsica (Buschinger, 1985a) and Sardinia (Buschinger, 1988, pers. comm.). It is the only *Epimyrma* species with a distribution extending northward as far as southern Germany (Buschinger, 1985).

So far, *E. ravouxi* is known only from a few Italian localities: in the Valle d'Aosta (Vollon; Villair), Lombardy (Ossuccio, near Lake Como), Trentino (Rovere della Luna) and Sardinia (Sorgono) (Buschinger, 1988, pers. comm.).

*E. ravouxi* is a slave-making ant (Winter, 1979; Buschinger and Winter, 1983). It is known to exploit several *Leptothorax* (*Myrafant*) host species such as *L. unifasciatus* (Latreille, 1798), *L. nigriceps* (Mayr, 1855), *L. affinis* (Mayr, 1855), *L. interruptus* (Schenck, 1852) and others (Buschinger, 1989a). Two host species may be present together in the same *ravouxi* colony (Buschinger, 1989a).

Young sexuals hatch in late summer; they engage in a mating flight, after which mated queens soon start colony foundation, entering a host species colony and strangling the host queen (Winter and Buschinger, 1983). The strangling can last for months, and may be completed in the following spring after hibernation (Winter and Buschinger, 1983). The raiding behaviour of this *Epimyrma* has been described by Winter (1979).

I found a population of *E. ravouxi* in the Lucretili mountains, near the village of Percile (RM). Several colonies were collected N of the village, on the slopes of the hills named Colle Catosciano and Colle Piglioni (elevation 650–700 m) as well as at the site of Fosso Pisciarelli (see above). The host species was *L. unifasciatus*.

The site of Colle Catosciano is a slope covered by a thin wood of young oak trees with scattered *Spartium* sp. bushes; the wood is periodically logged. A declining colony was discovered in a cynipid gall on an oak shrub. It consisted of 5 *Epimyrma* and 11 *Leptothorax* workers, and a few larvae. In spite of further intensive searching, no other *Epimyrma* colony was found at this site.

In January 1989, a founding *E. ravouxi* queen was collected in an *L. unifasciatus* nest on the western slope of Colle Piglioni. The nest, containing about 80 *Leptothorax* workers and brood, was located in a cynipid gall on an oak tree. The paralysed *unifasciatus* queen was still present in the nest.

Finally, four colonies of this species were collected of the Fosso Pisciarelli site. The nests were located in the crevices of the rocks and under moss. In late September 1990, a colony from this site consisted of a queen, 10 winged, unmated females and 40 *Epimyrma* workers, together with about 50 *L. unifasciatus* workers and brood.

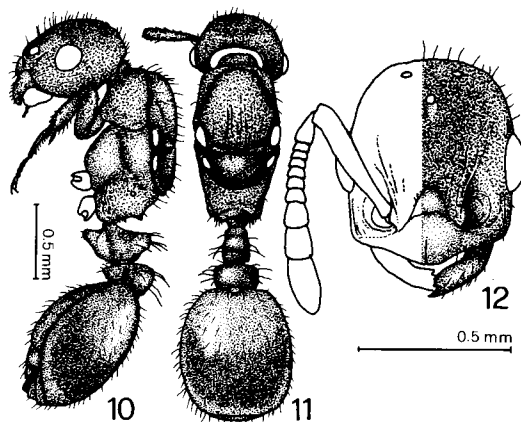
Very recently (July 1991), this ant was collected by Buschinger in Alto Adige, in a locality named "Steinwand" in the Martello valley (elevation 1450 m), with *L. unifasciatus* as the host species (Buschinger, 1991, pers. comm.).

### *Epimyrma* cf. *ravouxi* (André, 1896) (Figs. 10–12)

In December 1984 I collected a single dealate female of this species in a locality named Prati di S. Elia, a wide grassland surrounded by beech woods at an elevation of 1400 m, near the village of Collelongo (AQ) in the Abruzzi Apennines. The host was an undetermined species of *Leptothorax*. The nest was discovered in a rotten twig on the ground, in a rocky area with sparse *Fagus sylvatica* trees; the colony consisted of the parasitic queen, about 60 *Leptothorax* workers and brood. No *Epimyrma* worker was found; however, the presence of a worker caste cannot be excluded, as the colony could have been newly founded.

In morphology, sculpture, colour and pilosity, this *Epimyrma* is very similar to *E. ravouxi*. The biometrics also coincide with the dimensional range of this species; however, since *Epimyrma* species differ more in eco-ethological characters than in morphology (Buschinger, 1987, pers. comm.; Douwes et al., 1988), it is impossible to identify with certainty a species by a single specimen only.

The identification of the *Leptothorax* host species is also problematic; according to Buschinger (1987, pers. comm.) it "apparently belongs to the *nylanderi* group (meso-epinotal suture, yellow antennal clubs). The petiole looks like the one in



Figures 10–12. *E. cf. ravouxi*, queen, from Collelongo (Abruzzi)

*L. parvulus*, however the ants are too big and too dark in colouring. Herein they are more like *L. nylanderii*”.

Host specificity is a distinctive feature among *Epimyrma* species. *E. ravouxi* exploits several host species; however no *Leptothorax* species belonging to the *nylanderii* group has been so far recorded among its hosts.

From the present evidence, the specimen from Collelongo could be either *E. ravouxi* (with an unusual host) or a new species.

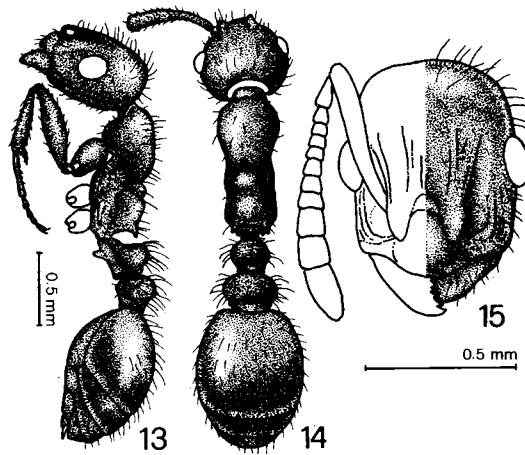
More samples of both this *Epimyrma* and its host are needed. Last year A. Buschinger, U. Winter, P. Douwes and I went to Collelongo in order to look for other colonies of this parasite, but we had no success. I am hoping that further research will enable us to rediscover this interesting ant.

### *Epimyrma stumperi* (Kutter, 1950)

This *Epimyrma* has a very restricted range, being so far known only from a very few localities at high altitude in the French and Swiss Alps (Kutter, 1950, 1951; Buschinger et al., 1981; Buschinger, 1985b). It is a slave-making species parasitizing *Leptothorax (M.) tuberum* (Fabricius, 1775) (Buschinger, 1989), which is usually polygynous in the areas where *E. stumperi* occurs. During colony foundation, the *stumperi* female strangles all the host queens, as described by Kutter (1951).

Very recently, Buschinger collected this ant from a locality in the surroundings of Silandro, in Alto Adige (Buschinger, 1991, pers. comm.). This is the first known record of *E. stumperi* in Italy, and the easternmost of this species, the nearest locality being Val Müstair, near Il Fuorn, Swiss National Park (Switzerland).

A newly founded colony was discovered in July 1991 at a site named Forna, near the village of Corzes, at an elevation of 1800 m. The host species was *L. tuberum*, which is polygynous there (Buschinger, 1991, pers. comm.).



Figures 13–15. *C. muellerianus*, worker, from Sperone (Abruzzi)

*Chalepoxenus muellerianus* (Finzi, 1921) (Figs. 13–15)

*Chalepoxenus muellerianus* (= *C. gribodoi* (Menozzi, 1922)) (Kutter, 1973) is a species widely distributed in southern Europe. It is known from central Spain, the Spanish Pyrenees, southern France, northern Italy, Yugoslavia, Greece and Bulgaria (Buschinger et al., 1988); the species has also been recorded in Turkey (Heinze, 1987).

There is morphological, ethological and biochemical evidence suggesting that *C. insubricus* (Kutter, 1950) from Switzerland and northern Italy and *C. siciliensis* (Kutter, 1973) from Mt. Etna in Sicily, may be conspecific with *C. muellerianus* (Buschinger et al., 1988; Ehrhardt, 1987).

In Italy, *C. muellerianus*/*insubricus* is known from Piedmont (Cuveglio, type locality of *C. gribodoi*; Ormea), Liguria (Andora; Ranzo; Chiappa), Lombardy (Ossuccio; Valtellina; Val Bregaglia; Loverè; Tignale), Trentino (Novaledo; Borgo), Alto Adige (Salorno) and Istria (S. Canziano, type locality of *C. muellerianus*) (Buschinger et al., 1988). *C. siciliensis* is known only from Mt. Etna (Nicolosi; Pineta di Linguaglossa) (Buschinger et al., 1988).

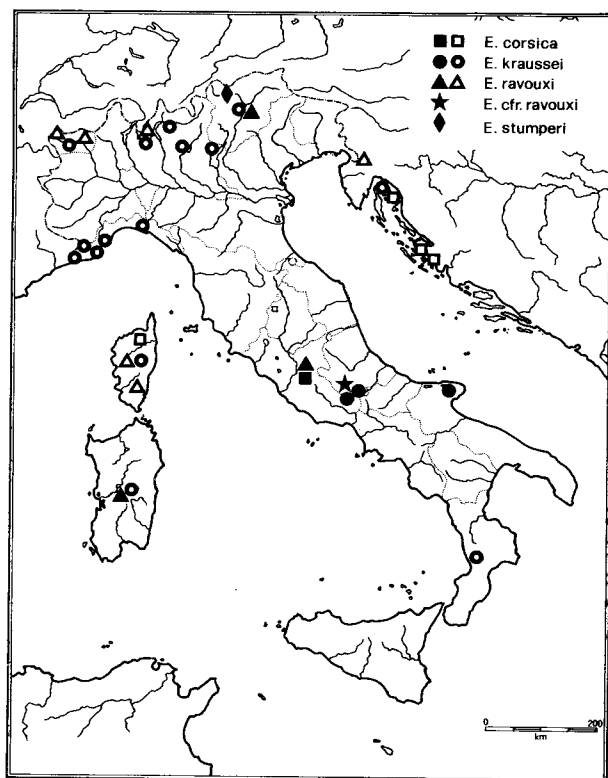
As with all other species of the genus investigated so far, (apart from the workerless *C. brunneus* from Morocco) *C. muellerianus* is a slavemaking ant; it enslaves several *Leptothorax* species belonging to both the *Myrafant* and *Temnothorax* subgenera, the most frequent host species being *L. (M.) unifasciatus* (Buschinger et al., 1988).

This species has been collected from several localities in Latium and Abruzzi (central Italy).

In Latium, stray workers and females were caught in pitfall traps in the mixed woodland of Castelporziano, near Rome. Winged and dealate females were collected in the summer, from mid-July until mid-August 1986.

A population was discovered in the Lucretili mountains, at a locality named Fosso della Scarpellata (elevation 1000 m) near the village of Marcellina (RM). The



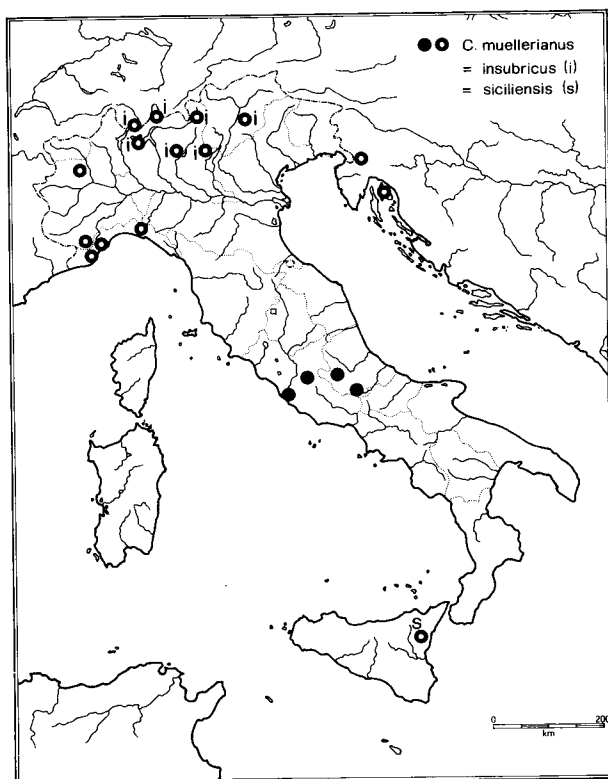


**Figure 16.** Present known distribution of the *Epimyrmica* species in Italy (open symbols: literature data; solid symbols: original data)

site is a stony pasture with scattered bushes of *Crataegus* sp. In late April 1988, two newly founded colonies were collected, each consisting of a *Chalepoxenus* queen, 2–3 *Leptothorax* (*M.*) *exilis* workers and brood. As is usual in this *Leptothorax* species, the nests were located in the crevices of limestone rocks. Two other interesting social parasitic ants, *Bothriomyrmex* sp. and *Plagiolepis* cf. *xene* (Staercke 1936), were collected at the same site.

Another large population has been located in the Abruzzi Apennines, in the clearings along the dirt road leading to the deserted village of Sperone (AQ), at an elevation of nearly 1200 m. The main host species was *L. unifasciatus*. Two colonies with *L. (M.) racovitzai* Bondroit, 1918 and three others with both *L. unifasciatus* and *L. racovitzai* slaves were also observed (Buschinger, 1990, pers. comm.). This is the first record of *L. racovitzai* in the Abruzzi. Several queenright *muellerianus* colonies as well as queenless colony fragments were collected. Sexuals were produced in July under laboratory conditions.

*C. muellerianus* has also been collected in the Abruzzi, by Buschinger et al., from several sites surrounding Civitella Alfedena in the Abruzzi National Park (Buschinger, 1990, pers. comm.).



**Figure 17.** Present known distribution of *Chalepoxenus muellerianus* in Italy (circles: literature data; dots: original data)

## Discussion

Socially parasitic ants, which depend strictly upon large populations of their host species, and which often have reduced dispersal abilities, are usually very rare and patchily distributed. Aimed sampling is needed in order to find such ants; this is especially true for parasitic Leptothoracini and their host species, which constitute small inconspicuous colonies in unusual nest sites such as rock crevices, hollow stems, rotten twigs, acorns etc., which are often neglected by generalist collectors.

Because of this, the actual range of many parasitic ants is poorly known, being largely influenced by the uneven collectings in the various countries (Hölldobler and Wilson, 1990).

This is also the case for the present known distribution of *Epimyrma* and *Chalepoxenus* in Italy (Figs. 16–17). Twenty years ago, all but one of the species known to occur in Italy up to that time were still recorded only from the type locality (Baroni Urbani, 1971). The important research of Buschinger and his co-workers, leading to the discovery of several new Italian sites (Buschinger et al., 1981; Buschinger, 1985; Buschinger and Winter, 1985; Buschinger et al., 1986, 1988), as

well as my own recent, successful collectings in central Italy, an area in which parasitic Leptothoracini had previously not been searched for, clearly show that gaps in the known range of such rare species are largely caused by inadequate research.

However, since most of central and southern Italy still remains unexplored as regards parasitic Leptothoracini, a great deal of further research is needed in order to increase our knowledge of the distribution of these ants. New populations, and even undescribed species, are likely to be discovered in areas such as the southern Apennines, where the myrmecofauna is still barely known.

## Acknowledgements

I am indebted to Alfred Buschinger, who generously gave me so much important, unpublished data concerning Italian parasitic ants, and who contributed to this paper with comments and suggestions; I wish to thank also Louise Taylor who revised the English text, and Roberto Argano and Augusto Vigna Taglianti for their suggestions.

## References

- Agosti, D. and C. A. Collingwood, 1987. A provisional list of the Balkan ants (Hym. Formicidae) and a key to the worker caste. I. Synonymic list. *Mitt. Schweiz. Ent. Ges.* 60:51–62.
- Baroni Urbani, C., 1971. Catalogo delle specie di Formicidae d'Italia (Studi sulla mirmecofauna d'Italia – X). *Mem. Soc. ent. ital., Genova* 50:5–287.
- Buschinger, A., 1982. *Epimyrmica goesswaldi* Menozzi, 1931 = *Epimyrmica ravouxi* (André, 1896) – Morphologischer und biologischer Nachweis der Synonymie (Hym., Formicidae). *Zool. Anz.* 208:352–358.
- Buschinger, A., 1985a. The *Epimyrmica* species of Corsica (Hymenoptera, Formicidae). *Spixiana* 8:277–280.
- Buschinger, A., 1985b. New records of rare parasitic ants (Hym., Form.) in the French Alps. *Ins. Soc.* 32:321–324.
- Buschinger, A., 1987. Synonymy of *Leonomyrmica* Arnoldi, 1968 with *Chalepoxenus* Menozzi, 1922 (Hymenoptera: Formicidae). *Psyche* 94:117–126.
- Buschinger, A., 1989a. Evolution, speciation and inbreeding in the parasitic ant genus *Epimyrmica* (Hymenoptera, Formicidae). *J. evol. Biol.* 2:265–283.
- Buschinger, A., 1989b. Workerless *Epimyrmica kraussei* Emery, 1915, the first parasitic ant of Crete. *Psyche* 96:69–74.
- Buschinger, A. and P. Douwes, 1991. Socially parasitic ants of Greece. *Biologia gallo-hellenica*, in press.
- Buschinger, A., W. Ehrhardt and K. Fischer, 1981. *Doronomyrmex pacis*, *Epimyrmica stumperi* und *E. goesswaldi* (Hym., Formicidae) neu für Frankreich. *Ins. Soc.* 28:67–70.
- Buschinger, A., W. Ehrhardt, K. Fischer and J. Ofer, 1988. The slave-making ant genus *Chalepoxenus* (Hymenoptera, Formicidae). I. Review of literature, range, slave species. *Zool. Jb. Syst.* 115:383–401.
- Buschinger, A., W. Ehrhardt and U. Winter, 1980. The organization of slave raids in dulotic ants – a comparative study (Hymenoptera, Formicidae). *Z. Tierpsychol.* 53:245–264.
- Buschinger, A., K. Fischer, H.-P. Guthy, K. Jessen and U. Winter, 1986. Biosystematic revision of *Epimyrmica kraussei*, *E. vandeli* and *E. foreli* (Hymenoptera: Formicidae). *Psyche* 93:253–276.
- Buschinger, A., K. Jessen and H. Cagniant, 1990. The life history of *Epimyrmica algeriana*, a slave-making ant with facultative polygyny (Hymenoptera, Formicidae). *Zool. Beitr. N. F.* 33:23–49.
- Buschinger, A. and U. Winter, 1982. Evolutionary trends in the parasitic ant genus *Epimyrmica*, 266–269. In: Breed M. D., Michener C. D., Evans H. E. (eds.), *The biology of Social Insects*, Proc. 9th Congr. IUSSI, Boulder, Colorado.

- Buschinger, A. and U. Winter, 1983. Population studies of the dulotic ant, *Epimyrma ravouxi*, and the degenerate slave-maker, *Epimyrma kraussei* (Hymenoptera: Formicidae). *Ent. Gener.* 8:251–266.
- Buschinger, A. and U. Winter, 1985. Life history and male morphology of the workerless parasitic ant *Epimyrma corsica* (Hymenoptera: Formicidae). *Ent. Gener.* 10:65–75.
- Buschinger, A., U. Winter and W. Faber, 1983. The biology of *Myrmoxenus gordiagini* Ruzsky, a slave-making ant (Hymenoptera, Formicidae). *Psyche* 90:335–342.
- Douwes, P., K. Jessen and A. Buschinger, 1988. *Epimyrma adlerzi* sp. n. (Hymenoptera: Formicidae) from Greece: morphology and life history. *Ent. scand.* 19:239–249.
- Ehrhardt, W., 1982. Untersuchungen zum Raubzugverhalten der sozialparasitischen Ameise *Chalepoxenus muellerianus* (Finzi) (Hym., Formicidae). *Zool. Anz.* 208:145–160.
- Ehrhardt, W., 1987. Biosystematics of the slavemaking ant genus *Chalepoxenus*, 39–40. In: Eder J. and Rembold H. (eds.), *Chemistry and Biology of Social Insects*, Peperny, München.
- Emery, C., 1895. Sopra alcune formiche della fauna mediterranea. *Mem. R. Acad. Sci. Bologna, Ser.* 5, 5:291–307.
- Emery, C., 1915. Contributo alla conoscenza delle formiche delle isole italiane. *Ann. Mus. Civ. Stor. Nat. Genova, Ser.* 3 a, 46:244–270.
- Espadaler, X. and C. Restrepo, 1983. Els generes *Epimyrma* Emery i *Chalepoxenus* Menozzi, formigues parasites socials (Hymenoptera: Formicidae), a la península iberica. Estat actual del coneixement. *Bull. Inst. Cat. Hist. Nat.* 49 (Sec. Zool., 5):123–126.
- Heinze, J., 1987. Three species of social parasitic ants new to Turkey. *Ins. Soc.* 34:65–68.
- Hölldobler, B. and E. O. Wilson, 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Mass., 732 pp.
- Kutter, H., 1950. Über zwei neue Ameisen. *Mitt. Schweiz. Ent. Ges.* 23:337–346.
- Kutter, H., 1951. *Epimyrma stumperi* Kutter (Hym. Form.), 2. Mitteilung. *Mitt. Schweiz. Ent. Ges.* 24:153–174.
- Kutter, H., 1973. Zur Taxonomie der Gattung *Chalepoxenus* (Hymenoptera, Formicidae, Myrmicinae). *Mitt. Schweiz. Ent. Ges.* 46:269–280.
- Menozzi, C., 1921. Formiche dei dintorni di Sambiasi di Calabria. *Boll. Lab. Zool. gener. Agr. Portici* 15:24–32.
- Winter, U., *Epimyrma goesswaldi* Menozzi, eine sklavenhaltende Ameise. *Naturwissenschaften* 66:581.
- Winter, U. and A. Buschinger, 1983. The reproductive biology of a slave-maker ant, *Epimyrma ravouxi*, and a degenerate slave-maker, *E. kraussei* (Hymenoptera: Formicidae). *Entomol. Gener.* 9:1–15.

Received 7 October 1991;  
 revised 15 November 1991;  
 accepted 17 January 1992.