

BIOSYSTEMATIC REVISION OF *EPIMYRMA KRAUSSEI*,
E. VANDELI, AND *E. FORELI*
(HYMENOPTERA: FORMICIDAE)

BY ALFRED BUSCHINGER¹, KARL FISCHER¹, HANS-PETER GUTHY¹,
KARLA JESSEN¹, AND URSULA WINTER²

INTRODUCTION

The myrmicine genus *Epimyрма* Emery 1915 presently comprises 11 described species, inhabiting central and southern Europe and North Africa. They all are living as social parasites together with host species of the genus *Leptothorax* (subgenera *Myrafant* Smith 1950 and *Temnothorax* Mayr 1861), some as active slavemakers, e.g. *E. ravouxi* (André 1896) (Winter 1979), others as "degenerate slavemakers" (*E. kraussei* Emery 1915 (Buschinger & Winter 1982)), and *E. corsica* (Emery 1895) as a workerless permanent parasite (Buschinger & Winter 1985).

The taxonomy of the genus is not yet completely consolidated. Thus, in the most recent revision, Kutter (1973) comes to the conclusion that *E. kraussei*, *E. vandeli* Santschi 1927, and *E. foreli* Menozzi 1921, are so similar that a future comparison of larger series presumably would reveal their synonymy. It is the object of this paper to provide evidence for the accuracy of Kutter's prediction. *E. kraussei* was described by 2 ♂♂ and 1 ♀ (Emery 1915) from Sorgono, Sardegna. Menozzi (1921) established *E. foreli* on the basis of 4 colonies from the vicinity of Sambiasi di Calabria, S'Italy, and *E. vandeli* was described after 6 colonies collected by A. Vandel near Miramont-de-Quercy and Touffailles, Dept. Tarn-et-Garonne, in S'France (Santschi 1927, Vandel 1927). The most distinctive characters of the 3 species were slightly different shapes of the petioli, different grades of coloration from light, yellow-brown in *E. foreli* to a nearly black in *E. vandeli*, and the lack of ♀♀ in the latter as opposed to *E. foreli* and *E. kraussei*.

¹FB Biologie, Institut für Zoologie, der Technischen Hochschule, Schnittpahnstr. 3, D-6100 Darmstadt, FRG

²FB 2 (Biologie), Universität Bremen, Postfach 330440, D-2800 Bremen, FRG
Manuscript received by the editor December 23, 1985.

During the past years, we have collected *E. kraussei* from numerous localities in the mediterranean area, including the type localities of *E. vandeli* and *E. foreli*. We were studying their populations, ♂♀ ♀-production in the lab and in the field, their reproductive behavior, colony foundation behavior, and karotypes. Crossbreeding of several populations including *E. vandeli* and *E. foreli* was possible. All observations pointed towards a synonymy of the 3 species. Finally, the types were examined, and morphological studies including the ♂♂ of the 3 species were carried out. This considerable body of evidence now clearly demonstrates that *E. foreli* and *E. vandeli* represent but junior synonyms of *E. kraussei*.

MATERIAL COLLECTED AND RANGE OF
EPIMYRMA KRAUSSEI

A total of 337 colonies of *E. kraussei* (including *E.v.* and *E.f.*) have been collected between 1975 and 1984 (table 1). Populations are numbered for an easier identification in the following text. Fig. 1 may provide a visual impression of the range of *E. kraussei*; it also contains a few additional localities from the literature, mainly those from North Africa (Cagniant 1968). Nests usually are found in crevices between flat stones, most easily in old dry walls of terraced vineyards and olive orchards, but also in rocky slopes underneath shrubs (Buschinger & Winter 1983). Colonies are small and can thus be aspirated almost completely. In the type locality of *E. vandeli*, we did not find the species in the exact sites of Vandel; however, we could collect a sample of 11 colonies near Lauzerte, only 5 km W of the original site, in the limestone slopes of the Barguelonne valley (table 1, no 5). *E. foreli* had been found near Sambiasse di Calabria, in moss covering the bark of olive trees (Menozzi 1921). We tried in vain to find Leptothoracini in such sites, presumably because the ants have been decimated there by pesticide treatment of the trees. However, in several localities around Sambiasse (table 1, no 19), we found 22 colonies of a yellowish *Epimyrma* with *Temnothorax* hosts, again in terrace walls. We are convinced that they represent members of the same population as that studied by Menozzi. Unfortunately, the search for *E. kraussei* in its type locality, Sorgono in Sardegna, Italy, in April 1985, remained unsuccessful. Even the host species was quite rare in this area. From the map (Fig. 1) we may conclude that both the type localities of *E. vandeli* and *E. foreli* are situated well within the area of *E. kraussei*.

Table 1. Localities and numbers of colonies collected of *Epimyrra kraussei* Emery 1915 (no 5a: Type locality of *E. vandeli* Santschi 1927, no 19: Type locality of *E. foreli* Menozzi 1921).

population no.		locality	n colonies
1	1981/07/14-30	Calpe (Spain, E'coast)	16
2 a	1981/03/30	Banyuls (S'France)	36
b	1984/04/03	Puig de Pani (NE'Spain)	2
c	1984/04/03	Selva de Mar (NE'Spain)	5
d	1984/04/03	Faro de Sarnella (NE'Spain)	16
3 a	1984/04/05	Pont de Bar/Seo de Urgel (Span. Pyrenees)	8
b	1984/04/05	Tremp/Tolva (Span. Pyr.)	6
c	1984/04/06	Ainsa (Span. Pyr.)	1
d	1984/04/06	Broto (Span. Pyr.)	5
4	1984/04/10	Chapelle St. Pons (S Bouleterne, French Pyrenees)	2
5 a	1981/03/31 1981/04/01	Lauzerte/Quercy (S'France)	11
b	1978/08/10	Cabrespine/Aude (S'France)	1
6	1981/03/23	La Couronne/Bouches-du-Rhône (S'France)	1
7	1981/04/02	Nyons/Drôme (S'France)	4
	1984/04/11	Suze-la-Rousse/Vaucluse (S'France)	5
8	1983/05/07-08	Ste. Maxime, Puget Ville/Alpes Maritimes (S'France)	10
9	1982/03/25	Venaco/Haute Corse (France)	5
10	1983/05/03-06	Alassio, Albenga, Ranzo, Toirano Ventimiglia/Prov. Imperia and Savona (N'Italy)	45
11	1975/05/29	Aosta (N'Italy)	2
12 a	1978/05/02	Ossuccio/Lago di Como (N'Italy)	1
b	1978/10/14 1980/10/13	Biolo/Valtellino (N'Italy)	11
13	1980/10/12	Lovere (Lago d'Iseo, N'Italy)	2
14	1979/04/09 1980/05/05-06 1980/10/11	Tignale (Lago di Garda, N'Italy)	113

Table 1, continued.

population no.		locality	n colonies
	1981/03/26		
	1982/10/12		
15	1974/06/15	Salorno (Adige, N'Italy)	1
16	1981/09/23-26	Krk (Dalmatia, Yugoslavia)	4
17	1983/09/29	Pag (Dalmatia, Yugoslavia)	1
18	1978/08/22	Nacionalni park Paklenica (Dalmatia, Yugoslavia)	1
19	1982/10/03-10	Gizzeria, Rogliano, near Sambiasè (Calabria, S'Italy)	22

337

MORPHOLOGICAL STUDIES

Comparison of the type material of *E. kraussei*, *E. vandeli*, and *E. foreli* with new material

The types of *E.v.* and *E.f.* are deposited in the Naturhistorisches Museum Basel, Switzerland. We could study 1♀ *E. foreli*, and 1♀ *E. vandeli*, both from the type series. The Museo Civico di Storia Naturale "Giacomo Doria" in Genova, Italy, has provided us with the types (1♀, 1♂) of *E. kraussei*.

With a close examination of these types we could only confirm the similarity of all 3 "species" as was already stated by Kutter (1973). We therefore refrain from a detailed presentation of measurements and structures compared. We also did not find any constant differences between the types and specimens from our newly collected material, with respect to size, shape of petioli, head and thorax, length of body hairs etc.; just the coloration was slightly variable between different populations. Thus, the population from Calabria (*E. foreli*), and one from Spain (pop. no. 3) exhibit a quite light, yellowish brown coloration of ♀ and ♂. Other *E.k.* populations appear brownish, whereas a dark brown or nearly black is typical for ♀ *E. vandeli* (pop. no. 5), for a colony from La Couronne (no. 6), and for population no. 9 from Corsica. Young ♀ ♀ are darker in coloration than old queens, and callow ♀ ♀ usually exhibit some darker spots in the thorax, and a yellow base of the gaster,

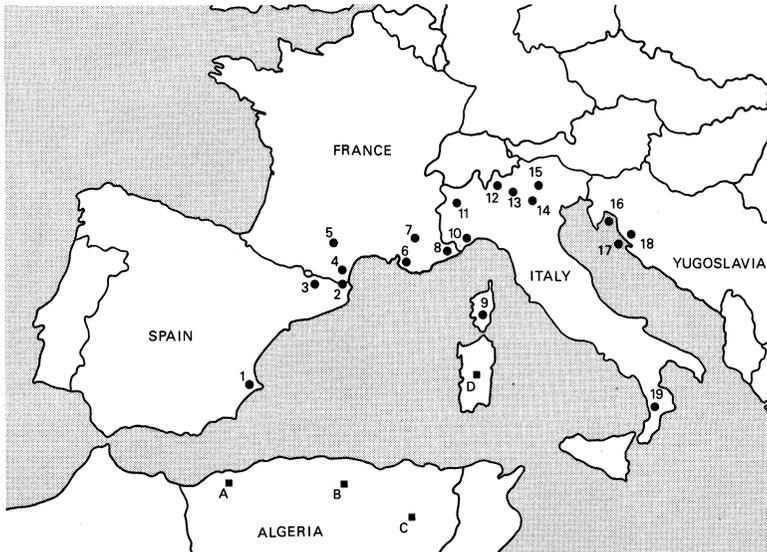


Fig. 1. Distribution of *Epimyrra kraussei* Emery 1915. ●: Our collecting sites listed in Table 1. No. 5: Type locality of *E. vandeli* Santschi 1927; no. 19: Type locality of *E. foreli* Menozzi 1921. A and C: Localities of *E. vandeli* in N'Africa cf. Cagniant (1968), B: Locality of *E. kraussei* cf. Cagniant (1968); D: Type locality of *E. kraussei* in Sardegna.

whereas the coloration in old queens is usually uniform. This age-dependent color variation is also typical for *E. ravouxi* (André 1896) (Buschinger 1982).

Male genitalia, wing venation, and shape of ♀♀ petioli

We studied wing venation and genitalia of *E.k.* ♂♂, and the outlines of the ♀ and ♀♀ petioli of specimens from Tignale and Biolo (Italian Alps), Calpe (Spanish Mediterranean coast), Calabria (S'Italy, *E. foreli*), and Lauzerte (S'France, *E. vandeli*). The same characters were investigated in *E. ravouxi* from several distant populations [Taubertal: Bavaria (D), Swiss Valley (CH), S'France, Corsica (F)], in order to compare their variation within and between the species. *E.r.* is clearly distinct from *E.k.* (Buschinger & Winter 1983, Winter and Buschinger 1983), and thus may serve as a reference species. Males preserved in alcohol were dissected, and permanent

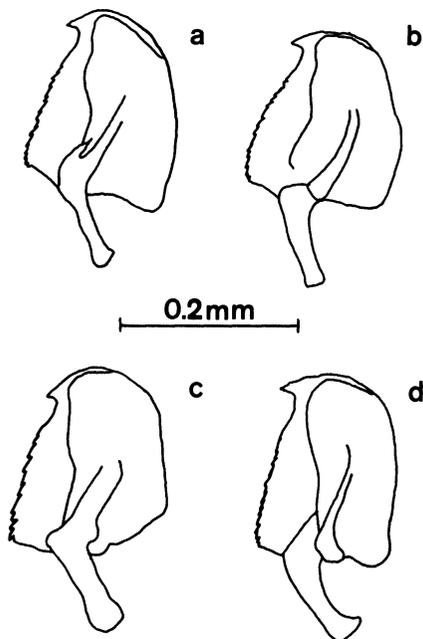


Fig. 2: Sagittae of *Epimyrma* ♂♂. a: Pop. no. 19 (*E. foreli*); b: Pop. no. 14 (*E. kraussei*); c: *E. ravouxi* from Corsica; d: Pop. no. 5a (*E. vandeli*).

mounds were made of the subgenital plate, the sagittae, and volsellae with laciniae, as well as the forewings and antennae. The outlines of ♀ and ♀ petioli were drawn and superimposed following a slightly modified method of Wehner (1983). As far as possible we always studied 10 ♂♀♀ from each of the populations mentioned above.

Male genitalia

Table 2 reveals that the numbers of sagittal teeth (Fig. 2) vary both within *E.k.* and *E.r.*, but with higher mean values in *E.k.*, including the populations of *E.v.* and *E.f.*.

The volsellae and laciniae (Fig. 3, table 3) exhibit a high conformity in *E.k.* and the two populations of *E.v.* and *E.f.*, in that the cuspis (tip of lacinia) rarely reaches, and never overlaps the digitus (terminology following Bitsch 1979). In *E. ravouxi*, on the contrary,

Table 2. Numbers of sagittal teeth in ♂♂ of *Epimyрма kraussei* Emery 1915 (= *E. vandeli* Santschi 1927, = *E. foreli* Menozzi 1921), and of *E. ravouxi* André 1896) from different populations.

species/population	<i>n teeth</i>			n sagittae checked
	min	\bar{x}	max	
<i>E. kraussei</i>				
no 14 Tignale	11	13.9	16	19
no 12b Biolo	10	13.6	16	18
no 1 Calpe	10	14.3	19	20
no 19 Calabria (<i>E.f.</i>)	12	14.4	18	19
no 5a Lauzerte (<i>E.v.</i>)	11	13.7	17	20
<i>E. ravouxi</i>				
Bavaria (D)	8	11.5	15	19
Nyons (F)	10	12.6	15	18
Corsica (F)	7	10.3	13	18
Swiss Valley (CH)	10	12.4	18	21

the cuspis usually overlaps or at least reaches the digitus, with very few exceptions.

The subgenital plates did not differ between populations or species.

Male wing venation

Wing venation in *Epimyрма* ♀♀ is quite variable (André 1896, Kutter 1973). In ♂ forewings the radial cell is short and open, the cubital cell long and usually closed, the discoidal cell may be closed, open, or nearly lacking, and the recurrens can be complete, incomplete, or absent. Reductions of wing venation need not be symmetrical in the two forewings of a specimen. We compared mainly the shape of the discoidal cells, which exhibits sizable differences between the species, but varies also within *E.k.* and *E.r.* considerably (Fig. 4).

Thus, table 4 shows the numbers of wings with open or closed discoidal cell. This character apparently is not appropriate for a differentiation of species or populations. A slightly better distinction is possible with the shape of the discoidal cell (table 4). In *E. ravouxi* this cell is near to quadratic, with a slightly shorter anterior border. This is also true for a good deal of the N'Italian and the Spanish populations of *E.k.*, but already in these populations, and more in the Calabrian (no 19, *E.f.*) and the Lauzerte (no 5, *E.v.*)

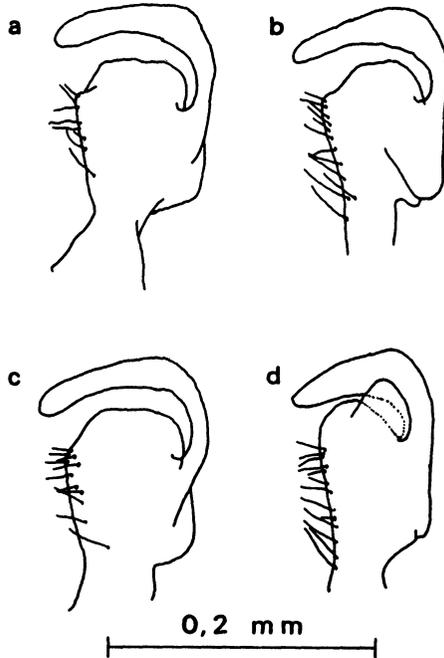


Fig. 3: Volsellae and laciniae of *Epimyrma* ♂♂. a: Population no. 14 (*E. krausseii*); b: Pop. no. 19 (*E. foreli*); c: Pop. no. 5a (*E. vandeli*); d: *E. ravouxi* from Corsica.

populations the anterior border becomes shorter until the discoidal cell is triangular.

Shape of the petioli in ♀♀ and ♂♂

In several publications (e.g. Menozzi 1931, Sadil 1953) the profiles of ♀ and ♂ petioli and postpetioli were used as the most important characters for the determination of *Epimyrma* species. Kutter (1973), however, clearly demonstrated with ♀♀ from a single *E. ravouxi* colony that these profiles may vary to such an extent that they are useless for species discrimination.

Nevertheless, we again studied this character, using a slightly modified method of Wehner (1983). The outlines of the petioli of 10 ♀♀ and 10 ♂♂ (exceptions: Population 12b: 5 ♂♂, and population 5a: 3 ♂♂) per population were drawn with the aid of a Wild M5

Table 3. Morphological comparison of the shape of volsella and lacinia in ♂♂ of *Epimyрма kraussei* Emery 1915 (= *E. vandeli* Santschi 1927, = *E. foreli* Menozzi 1921), and of *E. ravouxi* (André 1896) from different populations

species/population	<i>n volsellae and laciniae where</i>			n ♂♂ checked
	antrum open	cusps reaches digitus	c. overlaps digitus	
<i>E. kraussei</i>				
no 14 Tignale	16	2	—	10
no 12b Biolo	17	1	—	10
no 1 Calpe	19	—	—	10
no 19 Calabria (<i>E.f.</i>)	20	—	—	10
no 5a Lauzerte (<i>E.v.</i>)	21	1	—	11
<i>E. ravouxi</i>				
Bavaria (D)	—	—	20	11
Nyons (F)	1	3	12	9
Corsica (F)	2	4	12	10
Swiss Valley (CH)	1	3	17	11

dissecting microscope and a drawing tube at about $\times 88$. The drawings then were superimposed in such a way that they all were of the same size and overlapped to a maximal degree (Fig. 5). However, sizes and profiles of the petioli are varying within each population so much that a clear distinction of populations by this character is impossible. Even between *E. kraussei* and *E. ravouxi* we could not find any reliable differences in the petiolar outlines. The character, therefore, is useless for taxonomical purposes in the *Epimyрма* species investigated, and it can neither support nor contradict a synonymization of *E.f.* and *E.v.* with *E. kraussei*.

KARYOLOGY

Karyotypes were studied using the air-drying technique of Imai et al. (1977). Usually we made preparations from testes of ♂ pupae, and a few from cerebral ganglia of prepupae. *E. kraussei* from several populations (pop. no. 1, 5b, 6, 7, 9, 12a) and *E. vandeli* (pop. no. 5a) were checked, whereas no preparations of *E. foreli* could be made.

A total of 215 metaphase cells of 16 *E. kraussei*-♂ pupae from 8 colonies of 6 different localities showed 10 chromosomes each (Fig. 6). 6 cells had 9 chromosomes, and 5 cells had the diploid number of

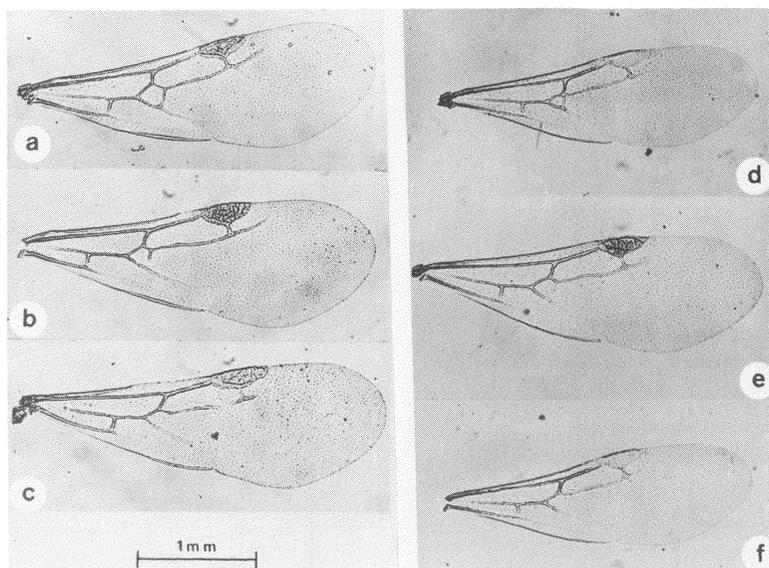


Fig. 4: Forewings of *Epimyrmica* ♂♂. Left: Variation of wing venation of *E. ravouxi* from 3 populations; reduction of the subrectangular discoidal cell. a: Corsica, b: Swiss Valley, c: Taubertal, Bavaria. Right: Variation of wing venation within one *E. krausseii*-population (no. 1, Calpe, Spain). d,e,f: Reduction of the subtriangular discoidal cell.

$2n = 20$. 9 cells of 2 additional, apparently ♀, prepupae contained 20 chromosomes, 2 others had 17 and 15, respectively. Chromosome numbers of less than the haploid ($n = 10$) or diploid ($2n = 20$) number are probably due to loss of chromosomes during preparation. Single diploid cells in haploid ♂♂ were occasionally found in other species, too (e.g. Hauschteck 1962, 1965).

In 2 *E. vandeli* ♂ pupae from a colony from the type locality (pop. 5a), 26 and 15 cells, respectively, were checked. They all had 10 chromosomes each.

The karyotypes of *E. krausseii* and *E. vandeli* with $n = 10$ chromosomes are apparently identical. They consist of 6 small to medium-sized metacentrics, 3 medium-sized submetacentrics and 1 large subtelocentric. *E.k.* and *E.v.* share this karyotype with all the species of this genus so far studied [*E. bernardi* Espadaler 1982, *E. corsica* (Emery 1895), *E. ravouxi* (André 1896) and *E. stumperi* (Kutter

Table 4. Wing venation in forewings of ♂♂ of *Epimyrra kraussei* Emery 1915 (= *E. vandeli* Santschi 1927, = *E. foreli* Menozzi 1921), and of *E. ravouxi* (André 1896) from different populations. Total numbers of wings checked for open or closed discoidal cell (left part of the table) and those checked for the shape of this cell (right part) differ because characters could not always be surely defined.

species/population	n wings with discoidal cell		shape of discoidal cell			(total)	
	open	closed	(total)	subrectangular	subtriangular		triangular
<i>E. kraussei</i>							
no 14 Tignale	9	9	(18)	8	9	-	(17)
no 12b Biolo	16	1	(17)	15	1	-	(16)
no 1 Calpe	8	10	(18)	6	8	6	(20)
no 19 Calabria (<i>E.f.</i>)	2	18	(20)	-	10	8	(18)
no 5a Lauzerte (<i>E.v.</i>)	8	14	(22)	-	12	9	(21)
<i>E. ravouxi</i>							
Bavaria (D)	24	-	(24)	22	-	-	(22)
Nyons (F)	6	12	(18)	7	2	-	(9)
Corsica (F)	12	3	(15)	17	-	-	(17)
Swiss Valley (CH)	22	-	(22)	20	-	-	(20)

1950)], and with *Myrmoxenus gordiagini* Ruszky 1902, a species very closely related to *Epimyrma* (Buschinger et al. 1983, Fischer unpubl.). No host species of *Epimyrma* and no other Leptothoracine species having this particular karyotype could yet be found. Thus, we may suppose that *E. foreli* as well has the karyotype of the genus, and no arguments for or against the synonymization of the 3 species in question can be derived from our karyological studies.

BIOLOGICAL DATA

Host specificity

The host species of *E. kraussei* in all populations investigated, including those ascribed to *E. vandeli* and *E. foreli*, is invariably *Leptothorax (Temnothorax) recedens* (Nylander 1856). All other *Epimyrma* species have different host species belonging to the subgenus *Myrafant* (Kutter 1973, Espadaler 1982, Buschinger & Winter 1985), and no other *Epimyrma* species has ever been found with *Temnothorax* hosts. In or close to the localities where we have collected *E. kraussei* (table 1) we usually found several other *Leptothorax* species, particularly often *L. (Myrafant) unifasciatus* (Latreille 1798), which then was parasitized by the slavemaking ants, *E. ravouxi* or *Chalepoxenus sp.*, but never by *E. kraussei*. Host specificity, is thus apparently a good character for species discrimination in the genus *Epimyrma*, and the joint use of *Temnothorax* by *E.v.*, *E.f.*, and *E.k.* is an argument for their synonymization.

Population Data

Reproductive biology and colony foundation

Epimyrma species, as far as is known, may differ considerably with respect to their sex ratios. Thus, *E. ravouxi* has a sex ratio of about 1.5 (♂/♀); in *E. kraussei* from population no. 14 (Tignale) this ratio is about 0.3 in field colonies; and 0.2 in laboratory culture (Winter & Buschinger 1983), and in *E. corsica* it is 0.08 (Buschinger & Winter 1985). Sex ratios correspond well with the reproductive biology of the species concerned: *E. ravouxi* is characterized by extranidal mating, whereas *E. kraussei* (pop. no. 14 Tignale) and *E. corsica* mate inside the mother nests and thus continually inbreed. The inseminated, dealate ♀♀ of *E.k.* and *E.c.* remain in the mother

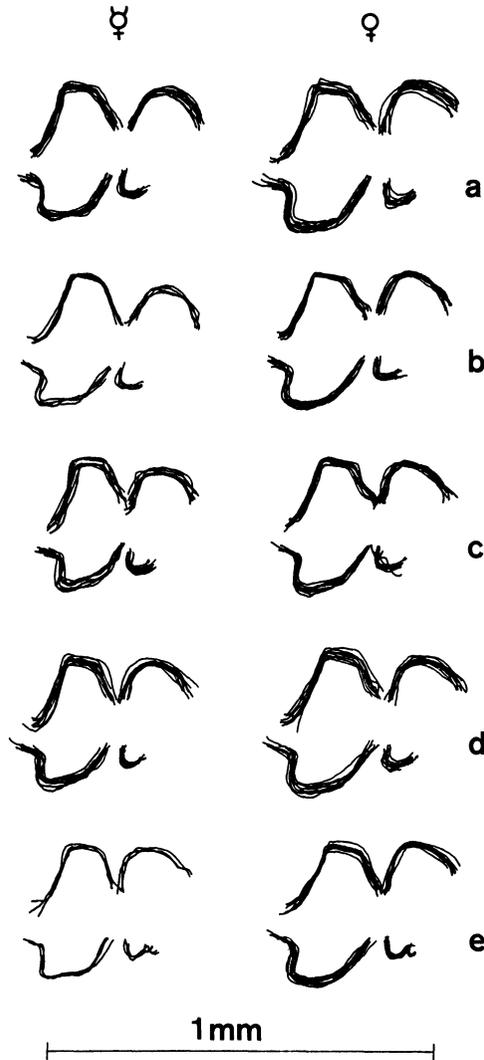


Fig. 5: Shape of petiolus and postpetiolus in *Epimyrma* ♀♀ and ♂♂. a, b, c: *E. kraussei* from populations no. 1 (a), 12b (b), 14 (c); d: no. 19 (*E. foreli*); e: no. 5a (*E. vandeli*). Usually the drawings of 10 specimens (b♀: 5, e♀: 3) were superimposed following the method of Wehner 1983.

Table 5. Production of sexuals and sex ratios in populations of *Epimyrma kraussei* (= *E. foreli*, = *E. vandeli*). Mean values in (.). (a, b): Sexuals found in field colonies in fall; (c, d, e): Sexuals produced in laboratory culture from colonies collected in spring. Colonies with relatively high numbers of host ♀♀ were selected from the field material for laboratory culture.

population	lab/field	n colonies	host ♀♀	production of		sex ratio ♂/♀
				♂♂	♀♀	
(a) no 14 Tignale (<i>E.k.</i>)	field	19	371 (19.5)	71 (3.7)	224 (11.8)	0.32
(b) no 19 Calabria (<i>E.f.</i>)	field	22	505 (22.9)	24 (1.1)	221 (10)	0.11
(c) no 14 Tignale (<i>E.k.</i>)	lab	23	1082 (47)	113 (4.9)	537 (23.3)	0.21
(d) no 19 Calabria (<i>E.f.</i>)	lab	12	298 (24.8)	16 (1.3)	140 (11.7)	0.11
(e) no 5a Lauzerte (<i>E.v.</i>)	lab	5	86 (17.2)	8 (1.6)	54 (10.8)	0.148

nests over winter, and colony foundation through invading of a host colony occurs in spring. *E.r.* young queens, on the other hand, begin with colony foundation immediately after swarming, in late summer.

In most of the populations of *E.k.*, *E.f.* and *E.v.*, we found evidence of a reproductive biology identical to that of *E.k.* pop. no 14 (Tignale), where we first have observed this kind of behavior (Winter & Buschinger 1983). 3 of the 11 colonies of *E.v.*, which were collected on 31 March and 1st April, contained young *Epimyrma*-♀♀ still engaged with throttling the host colony queens. The *E.f.*-population, on the other hand, was studied in fall, October 3–10, and most of the colonies contained dealate young ♀♀, a few alate ones, and some ♂♂. Reproductive behavior, thus, is identical in *E.k.*, *E.v.* and *E.f.*, with intranidal mating and colony foundation in spring. So far as it could be checked, also the production of sexuals and the sex ratios are quite similar (table 5), the sex ratios indicating a generally high ♀-bias.

Epimyrma worker-numbers

Slave-making ant species are characterized by the presence of a comparatively high number of ♀♀ in their nests, apart from incipient colonies. In the genus *Epimyrma*, we found a considerable variation of ♀ numbers in different species, dependent upon their respective type of parasitism. Thus, *E. ravouxi*, an active slave-maker, has up to 77 *E.*-♀♀ (mean 24.9) in a nest, whereas the “degenerate slavemaker”, *E. krausseii*, had an average of only 3.5 and a maximum of 10 *E.*-♀♀ (Buschinger & Winter 1983). *E. corsica* (Emery 1895) has lost the ♀-caste completely (Buschinger & Winter 1985). *E. vandeli* was originally said to be workerless, whereas ♀♀ had been described of *E. krausseii* and *E. foreli*. We therefore censused the *E.*-♀♀ in most of our field-collected colonies, and also the ♀-production of a representative number of colonies in laboratory culture.

In table 6 we compare the *Epimyrma* ♀-numbers of 4 larger populations including 2 ascribed to *E. krausseii* (no 14 and 2a), and the populations no 5a (*E.v.*) and no 19 (*E.f.*), and of 5 local populations of *E. krausseii* from the Spanish Pyrenees with nests always found in close vicinity.

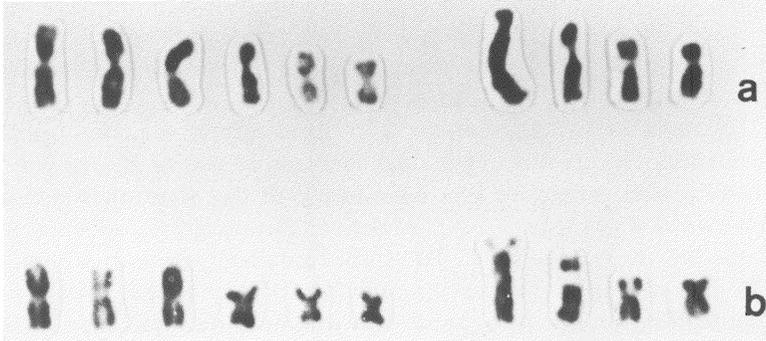


Fig. 6: Karyotypes of a: *Epimyrmex kraussei* from pop. no. 5b (Aude, S'France) and b: *Epimyrmex ravouxi* from pop. no. 12a (Lago di Como, N'Italy).

Most striking is the fact, that our 11 field colonies of *E. vandeli* did not contain any $E.-\text{♀}\text{♀}$. This corresponds to the original description of 6 colonies without $\text{♀}\text{♀}$ (Vandel 1927). In laboratory culture, however, we obtained a few $\text{♀}\text{♀}$ from colonies of this population (see below).

Workerlessness is also found in a certain amount of colonies in most populations of *E. kraussei*. In part, this is due to the fact the newly founded colonies do not yet contain $E.-\text{♀}\text{♀}$, and most of our collecting was done in spring during the time of colony foundation. Therefore, it is not surprising that the population of *E. foreli* is the only one where all colonies contained at least one $E. \text{♀}$: The sample was entirely collected in the fall. On the contrary, our material from the type locality of *E. vandeli* was collected in spring, and in 3 of the 11 colonies the $E.-\text{♀}$ was still engaged in throttling the *Temnothorax* queen. A few more colonies may as well have been incipient ones, where the host queen had already been eliminated. Furthermore, 3 colonies in the laboratory produced unusually high amounts of $E.-\text{♂}\text{♂}$, and when dissected, the queens proved to be poorly inseminated, having very few sperm cells in their receptacula. The lack of $E.-\text{♀}\text{♀}$ in our sample is thus at least in part explained by these facts.

The highly variable average and median values of ♀ -numbers as well as the maximum values in other populations are also very remarkable. In some populations, like that of *E. foreli*, but also at

Table 6. Numbers of *Epimyrma*-♂♂ in field populations of *E. kraussii* Emery 1915 (= *E. vandeli*, = *E. forelfi*).

population	n colonies censused	n Epimyrma ♂♂/colony	mean	median	range	% colonies lacking E.-♂♂	season
no 14 Tignale (<i>E.k.</i>)	82	2.07	1.5	0-10	46.3	spring & fall	
no 2a Banyuls (<i>E.k.</i>)	36	5.33	3.5	0-20	11.1	spring	
no 19 Calabria (<i>E.f.</i>)	22	6.64	5	1-26	0.0	fall	
no 5a Lauzerte (<i>E.v.</i>)	11	0	0	0	100.0	spring	
no 3a Pont de Bar (<i>E.k.</i>)	7	1.0	0	0-7	85.7	spring	
no 2d Faro de Sarnella (<i>E.k.</i>)	16	2.31	1	0-9	56.2	spring	
no 2c Selva de Mar (<i>E.k.</i>)	5	6.8	5	0-15	20.0	spring	
no 3d Broto (<i>E.k.</i>)	5	7	4	0-16	20.0	spring	
no 3b Tremp/Tolva (<i>E.k.</i>)	6	10.5	10.5	0-24	16.6	spring	

Banyuls (no 2a) and along the Spanish Pyrenees (no 2c, 3b, 3d), we found a few colonies with 15 to more than 20 *E.-♀♀*, which would be sufficient for an effective slave-raiding. As was suggested for *E. kraussei* from Tignale (Buschinger & Winter 1983), however, we believe that slave-raids do occur only exceptionally, if at all, in the other populations now studied: Most colonies comprise but very few *E.-♀♀*, and colonies with higher *E.-♀*-numbers on average do not contain more host species workers than those with few or no *E.-♀♀*. From table 6 we may conclude that *Epimyrma kraussei* has established numerous local populations in which the reduction of ♀-numbers has occurred to highly variable degrees. The population ascribed to *E. vandeli* then would be close to one end of the scale which is complete loss of the ♀-caste like in *E. corsica* (Buschinger & Winter 1985), and *E. foreli* is among the populations with highest *E.-♀*-numbers. It must be stated, however, that a geographical variation of ♀-numbers, e.g., in the sense of a cline, is lacking: Populations with low ♀-numbers have been found in S'France (no 5a, *E. vandeli*) and in N'Spain (no 3a), and high ♀-numbers occur close to the latter locality (no 3b) as well as in S'Italy (no 19, *E. foreli*).

In laboratory culture the ♀-production of *Epimyrma* colonies roughly corresponds to the field data. Table 7 provides a comparison of ♀-production in colonies from 3 populations. Most important is the fact that *E.-♀♀* appeared in 2 of the 5 laboratory-kept colonies from population no 5a (Lauzerte, *E. vandeli*).

Worker numbers, thus, are not contradictory to a synonymization of *E.v.* and *E.f.* with *E. kraussei*.

Crossbreeding experiments

Intranidal mating is an excellent condition for experimental crossbreeding of sexuals from different populations and even species. Colonies are kept in nearly natural annual cycles with a long hibernation of about 6 months at 10°C a "spring" and "fall" phase in daily temperature rhythms of 10°C (12h, dark) and 20°C (12h, light) for 2 weeks each, and a summer phase of 15°C (10h, dark) and 25°C (14h, light) for 2 weeks, followed by 2 months of 17°C (10h, dark) and 28°C (14h, light), and again 2 weeks of 15°C/25°C when pupation decreases. For details of formicaries, feeding etc. see Buschinger (1974). All ♂ pupae from colonies of 2 populations or species are exchanged. Further ♂ pupae arising newly from the

Table 7. Worker-production in colonies of *Epimyrra kraussei* Emery 1915 from 3 populations, in the first summer after collecting (including the populations of *E. foreli* Menozzi 1921 and *E. vandeli* Santschi 1927).

population	n colonies	Epimyrra ♀♀ produced			
		total	mean	median	range
no 14 Tignale (<i>E.k.</i>)	23	12	0.52	0	0- 2
no 19 Calabria (<i>E.f.</i>)	12	24	2.0	1	0-10
no 5a Lauzerte (<i>E.v.</i>)	5	5	1.0	0	0- 4

remaining brood are either removed or exchanged. Usually the foreign pupae are easily accepted, and also the sexuals hatching from them. After dealation of the young ♀♀ a few of them are dissected for control of insemination. In the following spring the ♀♀ leave the nest chambers and can be placed with host colonies, where they found their own colonies. The first sexual offspring usually develops from rapid brood in the year of colony foundation (Winter & Buschinger 1983).

It must be said, however, that the rate of successful colony foundations is generally low, both with cross-mated ♀♀ and those having normally mated with brothers. Quite often this is due to insufficient insemination, and perhaps to not yet optimal laboratory conditions. We therefore present only a preliminary survey of successful cross-breeding (table 8) without giving data on numbers of replicates or numbers of offspring produced. These experiments are being continued.

Table 8 clearly reveals that crossbreeding between different *E.k.* populations, and also between *E.k.* and *E.v.* or *E.f.*, is possible. This result, however, can only weakly support our supposition of the synonymy of the 3 species, since we also succeeded in crossbreeding *E.k.* with *E. corsica*, and with *E. bernardi*, both of which are morphologically and biologically distinct good and species.

DISCUSSION AND CONCLUSION

The meaning of the morphological and biological characters studied in *E. kraussei*, *E. vandeli* and *E. foreli*, has been discussed with reference to the question of synonymy of the 3 species already in the respective sections. We found no morphological characters which would allow a clear distinction between them. The karyotype is apparently homologous in all *Epimyrra* species. The 3 species

investigated have a common host species, *Leptothorax (T.) recedens*, which is not parasitized by any other *Epimyrma* species. The numbers of *Epimyrma*-♀ ♀ are variable, but low in all the 3 species, which therefore should represent "degenerate slavemakers" as was already stated for *E. krausseii* (Buschinger & Winter 1983). Field data and laboratory breeding results indicate that the 3 species have a highly ♀-biased sexual production, intranidal mating and inbreeding, that the young ♀♀ overwinter in their mother nests and invade own host colonies in spring. Crossbreeding experiments reveal that a strict genetical isolation is lacking. The 3 original samples, comprising only few specimens, were apparently described as separate species mainly because they were found in quite distant localities, and because the variability of their slight morphological differences could not be evaluated then.

We therefore synonymize *E. vandeli* Santschi 1927 and *E. foreli* Menozzi 1921 with *E. krausseii* Emery 1915.

Population structure and reproductive biology in this species, however, are highly remarkable (Winter & Buschinger 1983). The inbreeding system with young queens spreading on foot, and thus over only short distances, must result in an extremely restricted gene flow, even if a rare mating of sexuals from neighboring colonies might occur. The populations from different continents (northern Africa, southern Europe) and islands (Sardegna, Corsica), but also from more neighboring localities (southern France, northern Spain), must have been isolated for a very long time. This isolation, in our opinion, is responsible for the differences in coloration, morphology of wings and genitalia, and worker numbers, which we observed in certain populations. The replacement of one of these characters by another one can only occur through interdemec selection, through supplantation of a local population by another one which is somewhat more effective. Since *E. krausseii*, however, does not inhabit large, continuous habitats, but instead forms numerous small, patchily distributed populations, this process must be slow and rare. The reduction of worker numbers in favor of a higher ♀ production should be highly adaptive in this species. Since, however, the genetical basis for this evolution cannot spread, e.g., through flying ♂♂, we may speculate that different demes just have reached different degrees of worker reduction. Crossbreeding experiments have been started in order to find out whether or not

Table 8. Successful crossbreeding experiments with *Epimyrma krausei* from different populations, including *E. foreli* and *E. vandeli*. Numbers of colonies are given in which ♀ and/or ♂ offspring of crossmated ♀♀ was obtained. "Interspecific" crossbreedings underlined.

♂♂ from popul.	Calpe (<i>E.k.</i>)	Lauzerte (<i>E.v.</i>)	Nyons (<i>E.k.</i>)	Corsica (<i>E.k.</i>)	Tignale (<i>E.k.</i>)	Krk (<i>E.k.</i>)	Calabria (<i>E.f.</i>)
♀♀ from popul. no							
1		<u>1</u>		4		7	
Calpe (<i>E.k.</i>)						<u>1</u>	
5a							
Lauzerte (<i>E.v.</i>)						3	
7							
Nyons (<i>E.k.</i>)							
9	4						
Corsica (<i>E.k.</i>)							
14		<u>3</u>	1	1		6	<u>1</u>
Tignale (<i>E.k.</i>)							
16	1						
Krk (<i>E.k.</i>)							

worker number in *E. kraussei* populations is genetically determined. If so, we may predict that somewhere in the range of *E. kraussei*, populations will be found with high \checkmark -numbers, and still actively slave-raiding, and other perhaps truly workerless demes. The evolution from outbreeding and slave-raiding towards intranidal mating and reduction of worker numbers and slave-making behavior, is an apparently widespread trait in the genus *Epimyrma*. Intranidal mating has been found also in *E. bernardi* and in *E. corsica*, two species which are morphologically clearly separated from *E. kraussei*. Whereas *E. bernardi* "still" produces a considerable amount of $\checkmark\checkmark$, *E. corsica* has lost this caste completely (Buschinger & Winter 1985). Future studies will be necessary to find out whether worker reduction in *Epimyrma* is developing in several species or species groups independently, in parallel evolution, or whether the species with different worker numbers form a series of descent. The present study of *E. kraussei* evidently favors the first alternative.

SUMMARY

Epimyrma vandeli Santschi 1927 and *E. foreli* Menozzi 1921 are junior synonyms of *E. kraussei* Emery 1915. A comparison was made of the type specimens and of newly collected material from the type localities of *E.v.* and *E.f.*, and from numerous populations of *E.k.*. No reliable morphological differences could be found, despite a certain variation in \checkmark genitalia, wing venation and body coloration of different populations. Karyotypes are homologous in all *Epimyrma* species and populations yet studied. The host species is *Leptothorax (Temnothorax) recedens* (Nylander 1856) in all *E.k.* populations including *E.v.* and *E.f.*, whereas all other *Epimyrma* species have different host species. *Epimyrma* \checkmark -numbers vary between populations, *E.v.* having a particularly low, and *E.f.* quite a high one, both, however, remaining within the range of the other *E.k.* populations. Sexual production is similar in all populations with a remarkably low \checkmark -production. In all populations studied, sexuals mate within the mother nests, and inseminated, dealate young $\checkmark\checkmark$ remain there over winter until they leave for colony foundation in spring. *E.v.* and *E.f.* could be successfully crossbred with *E.k.*, and sexuals from several *E.k.* populations among each other. Differences between *E.k.* populations presumably are due to their

quasi-clonal structure with very restricted or lacking gene flow between colonies and demes.

ACKNOWLEDGEMENTS

This work was supported by grants of the Deutsche Forschungsgemeinschaft.

REFERENCES

- ANDRÉ, E. 1896: Description d'une nouvelle fourmi de France. - Bull. Soc. Ent France **2**: 367-368.
- BITSCH, J. 1979: Morphologie abdominale des Insectes. In: Grassé, P.-P., Traité de Zoologie, t. VIII, fasc. II, 290-578; Masson, Paris.
- BUSCHINGER, A. 1974: Experimente und Beobachtungen zur Gründung und Entwicklung neuer Sozietäten der sklavenhaltenden Ameise *Harpagoxenus sublaevis* (Nyl.). - Ins. soc. **21**: 381-406.
- BUSCHINGER, A. 1982: *Epimyrma goesswaldi* Menozzi 1931 = *Epimyrma ravouxi* (André 1896) - Morphologischer und biologischer Nachweis der Synonymie (Hym., Formicidae). - Zool. Anz. **208**: 352-358.
- BUSCHINGER, A. & WINTER, U. 1983: Population studies of the dulotic ant, *Epimyrma ravouxi*, and the degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). - Entomol. Gener. **8**: 251-266.
- BUSCHINGER, A. & WINTER, U. 1985: Life history and male morphology of the workerless parasitic ant *Epimyrma corsica* (Hymenoptera: Formicidae). - Entomol. Gener. **10**: 65-75.
- BUSCHINGER, A., WINTER, U. & FABER, W. 1983: The biology of *Myrmoxenus gordiagini* Ruzsky, a slave-making ant (Hymenoptera, Formicidae). - Psyche **90**: 335-342.
- CAGNIANT, H. 1968: Du nouveau sur la répartition des *Epimyrma* d'Algérie (Hymenoptères - Formicidae - Myrmicinae). - Bull. Soc. Hist. Nat. Toulouse **104**: 427-429.
- EMERY, C. 1915: Contributo alla conoscenza delle formiche delle isole italiane. - Ann. Mus. Civ. Stor. Nat. Genova, Ser. 3a, **46**: 244-270.
- ESPADALER, X. 1983: *Epimyrma bernardi* n.sp., a new parasitic ant. - Spixiana **5**: 1-6.
- HAUSCHTECK, E. 1962: Die Chromosomen einiger in der Schweiz vorkommender Ameisenarten. - Vierteljahresschr. Naturf. Ges. Zürich **107**: 213-220.
- HAUSCHTECK, E. 1965: Halbe haploide Chromosomenzahl im Hoden von *Myrmica sulcinodis* Nyl. (Formicidae). - Experientia **21**: 323-325.
- IMAI, H. T., CROZIER, R. H. & TAYLOR, R. W. 1977: Karyotype evolution in Australian ants. - Chromosoma **59**: 341-393.
- KUTTER, H. 1950. Über zwei neue Ameisen. - Mitt. Schweiz. Ent. Ges. **23**: 337-346.
- KUTTER, H. 1973: Beitrag zur Lösung taxonomischer Probleme in der Gattung *Epimyrma* (Hymenoptera Formicidae). Mitt. Schweiz. Ent. Ges. **46**: 281-289.

- MENOZZI, C. 1921: Formiche dei dintorni di Sambiasse di Calabria. - Boll. Lab. Zool. gener. Agr. Portici **15**: 24-32.
- MENOZZI, C. 1931: Revisione del genere *Epimyrma* Em. (Hymen. Formicidae) e descrizione di una specie inedita di questo genere. - Mem. Soc. Ent. Ital. **10**: 36-53.
- SADIL, J. 1953: *Epimyrma zaleskyi* nov. spec. (Hym., Formicoidea). - Casop. Cesk. Spol. ent. **50**: 188-196.
- SANTSCHI, F. 1927: Notes myrmecologiques. I. Sur quelques nouvelles fourmis de France. - Bull. Soc. Ent. France **1927**: 126-127.
- VANDEL, A. 1927: Observations sur les moeurs d'une Fourmi parasite: *Epimyrma vandeli* Santschi. - Bull. Soc. Ent. France **1927**: 289-295.
- WEHNER, R. 1983: Taxonomie, Funktionsmorphologie und Zoogeographie der saharischen Wüstenameise *Cataglyphis fortis* (Forel 1902) stat. nov. (Insecta: Hymenoptera: Formicidae). - Senckenbergiana biol. **64**: 89-132.
- WINTER, U. 1979: *Epimyrma goesswaldi* Menozzi, eine sklavenhaltende Ameise. - Naturwissenschaften **66**: 581.
- WINTER, U. & BUSCHINGER, A. 1983: The reproductive biology of a slavemaker ant, *Epimyrma ravouxi*, and a degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). - Entomol. Gener. **9**: 1-15.