

Best regards,
A. BuschingerAus dem Institut für Zoologie, Fachbereich Biologie der
Technischen Hochschule Darmstadt, BRDThe Slave-Making Ant Genus *Chalepoxenus*
(Hymenoptera, Formicidae)

I. Review of Literature, Range, Slave Species

ALFRED BUSCHINGER, WERNER EHRLHARDT, KARL FISCHER and JACOB OFER

With 1 Figure

Abstract

A survey of literature on the obligatory slave-making ant genus *Chalepoxenus* is presented (Tab. 1). The genus at present comprises seven taxa, *C. muellerianus*, *insubricus*, *siciliensis*, *kutteri*, *tramieri*, *brunneus*, and *spinosus*. Their range, which extends from the western Mediterranean through Yugoslavia and Greece to Turkey, Bulgaria and Kazakhstan (USSR), is depicted in Fig. 1. A total of about 485 colonies, predominantly ascribed to *muellerianus/insubricus* (which may represent a single species-level taxon), *kutteri*, and *siciliensis* have been collected to the present time. Very little material is available of *C. tramieri*, *brunneus* and *spinosus*.

With respect to the slave-species spectra a main host-species, *Leptothorax unifasciatus*, can be determined for *C. muellerianus/insubricus*, and *L. massiliensis* is the main host of *C. kutteri*. Several other *Leptothorax* species are also occasionally enslaved. Apart from *L. (Temnothorax) recedens* they all belong to the subgenus *Myrafant*. Unlike other leptothoracine slavemakers, e.g., *Harpagoxenus sublaevis*, *Chalepoxenus* colonies only very rarely contain two slave-species simultaneously. Certain *Chalepoxenus* populations apparently specialize in enslaving one particular host-species, which in other populations is an accessory host only, e.g., *Leptothorax recedens* or *L. flavicornis*.

Host species recognition in *Chalepoxenus* presumably relies on a blend of innate and learned characters, which renders possible the formation of traditions with respect to host-species choice.

The present data suggest conspecificity of *C. muellerianus* with *insubricus* and perhaps *siciliensis*. Morphological and ethological studies and a formal taxonomic revision of the genus will be presented in following papers.

✱

1. Introduction

Slave-making and otherwise parasitic ants are much rarer than most independent species. Often only a few specimens, or one or two colonies of a given species, have become known to science. Consequently, our knowledge of the life history, range, morphological variation etc., of a large proportion of inquiline or dulotic ant taxa is quite restricted, and sometimes the sparse available data has been considerably misinterpreted.

During the past two decades some parasitic ant genera have been investigated more extensively, both in field and laboratory studies. In the myrmicine tribe Leptothoracini, which is particularly rich in socially parasitic species (BUSCHINGER 1981), recent work has brought about substantial changes in the systematics of the guest

Table 1. Survey of relevant literature on taxonomy and biology of the genus *Chalepoxenus*

Year	Authors	"Species"	Localities	Main contents	Remarks
1921	FINZI	<i>Leptothorax (Temnothorax) muellerianus</i> n. sp.	S. Canziano, Istria (Yugoslavia)	found 4 ♂♂ without host-species under moss on a rock	description of the species <i>muellerianus</i>
1922	MENOZZI	<i>Chalepoxenus</i> (n. gen.) <i>gribodoi</i> (n. sp.)	Cuceglia Northern Italy	1 ♀, 12 ♂♂ with ♂♂ of host-species <i>Leptothorax tuberum</i> , in a blackberry stem	description of the genus <i>Chalepoxenus</i>
1923	MÜLLER	<i>L. muellerianus</i> = <i>Chalepoxenus muellerianus</i>	(S. Canziano)	transfer of <i>muellerianus</i> into genus <i>Chalepoxenus</i>	
1924	FINZI	<i>Chalepoxenus muellerianus</i>	(S. Canziano)	details minor differences between <i>C. muellerianus</i> and <i>C. gribodoi</i>	
1925	MENOZZI	<i>Chalepoxenus gribodoi</i>	(Cuceglia)	description of the male	
1946	BERNARD	<i>Chalepoxenus gribodoi</i>	Vercors, Dept. Drôme, France	found 10 colonies with " <i>L. nylanderii typiques</i> " as host-species, suggests slavenaking host-species, suggests slavenaking	The host-species very probably was misidentified (see text) misidentified (see text)
1950	KUTTER	<i>Chalepoxenus insubricus</i> n. sp.	Ticino, Switzerland	description of ♂	
1968	ARNOLDI	<i>Leonomyrma</i> n. gen. <i>spinosa</i> n. sp.	lower course of Ural River, Soviet Union	description of ♂ and ♀	junior synonym of <i>Chalepoxenus</i> (see BUSCHINGER 1987)
1968	BERNARD	<i>Chalepoxenus gribodoi</i>	Vercors, France South of the FRG	host-species <i>L. nylanderii</i> , <i>inter-raptus</i> , <i>muscorum</i> and mixed; host queen "generally coexisting with the <i>C. queen</i> "	Errors: <i>Chalepoxenus</i> does not occur in Germany, <i>L. muscorum</i> is never a host-species and the host queens are eliminated.
1968	CAGNIANT	<i>Chalepoxenus</i> spec. (<i>C. tramieri</i> CAGNIANT 1983)	Algeria	1 ♀ with <i>Leptothorax spinosus</i>	

1970a, b	LE MASNE	<i>Chalepoxenus</i> spec.	Banyuls-sur-Mer (France, eastern Pyrenees)	certain behaviours indicate slavemaking habits	observations refer to <i>C. kutteri</i>
1973	CAGNIANT	<i>Chalepoxenus kutteri</i> n. sp.	Banyuls-sur-Mer (France)	description ♂, ♀, ♀; host-species <i>L. massiliensis</i> , <i>racovitzai</i> <i>berlandi</i> , <i>niger</i> . Host-species queen always lacking.	for host-species see text
1973	KUTTER	<i>Chalepoxenus muellerianus</i> , <i>insubricus</i> , <i>kutteri</i> <i>C. siciliensis</i> n. sp.	(known localities, see above) Mount Etna, Sicily	morphological comparison; synonymizes <i>C. gribovdoi</i> = <i>C. muellerianus</i> . description of ♀ and ♂ of <i>C. siciliensis</i>	
1976	COLLINGWOOD	<i>Chalepoxenus</i> spec.	Northern Spain	list of Iberian Formicidae	species undetermined
1982	EHRHARDT	<i>Chalepoxenus muellerianus</i>	Northern Italy	describes slave-raiding and laboratory culture	
1983	ESPADALER and RESTREPO	<i>Chalepoxenus muellerianus</i> and <i>C. kutteri</i>	Spain	list of localities in Spain.	
1983	CAGNIANT	<i>Chalepoxenus tramieri</i> n. sp.	Morocco and Algeria	description of 4 ♂♂ with host-species <i>L. spinosus</i> f. <i>nivalis</i> . ♀ of CAGNIANT 1968 presumably belonging to this species.	
1985	CAGNIANT	<i>Chalepoxenus brunneus</i> n. sp.	Morocco	Description of ♂, ♀	
1987	BUSCHINGER	<i>Leonomyrma</i> ARNOLDI 1968 = <i>Chalepoxenus</i>	Soviet Union (see ARNOLDI 1968)	Synonymy of <i>Leonomyrma</i> with <i>Chalepoxenus</i>	
1987	EHRHARDT	<i>C. muellerianus</i> , <i>insubricus</i> , <i>kutteri</i> , <i>siciliensis</i>	(known localities, see above)	Abstract on biosystematically relevant new behavioral and karyological data	

ant genus *Formicoxenus* (FRANCOEUR et al. 1985), or the slave-maker genus *Epimyrma* (BUSCHINGER 1981, 1982; BUSCHINGER et al. 1986). The life histories of *Harpagoxenus sublaevis* (BUSCHINGER 1966, 1974, 1979; WINTER 1979a), *H. canadensis* (BUSCHINGER and ALLOWAY 1978, 1979; STUART 1984), and *H. americanus* (BUSCHINGER and ALLOWAY 1977; ALLOWAY 1979) have been established, revealing that *H. americanus* has probably evolved convergently to the other two species (BUSCHINGER 1981).

Chalepoxenus (Greek: The nasty guest) is another genus of parasitic ants belonging to the tribe Leptothoracini, with several rarely found and poorly known taxa. Presently it comprises seven described species, six of them from the Mediterranean area: *C. muellerianus* (FINZI 1921) from Yugoslavia, *C. insubricus* KUTTER (1950) from southern Switzerland and northern Italy, *C. kutteri* CAGNIANT (1973) from southern France, *C. siciliensis* KUTTER (1973) from Sicily, *C. tramieri* CAGNIANT (1983) from Algeria and Morocco, and *C. brunneus* CAGNIANT (1985) from Morocco. The former species *C. gribodoi* MENOZZI (1922) from North Italy has been synonymized with *muellerianus* by KUTTER (1973). The last species, *Leonomyrma spinosa* ARNOLDI (1968) from USSR, was transferred to *Chalepoxenus* by BUSCHINGER (1987).

We have collected numerous colonies of *Chalepoxenus* in the type-localities of *C. kutteri*, *muellerianus*, *insubricus*, "*gribodoi*", and *siciliensis*, and in many other places (Fig. 1). We are studying the morphology of workers and sexuals, the karyotypes, the sexual behavior including crossbreeding experiments, and slave raiding behavior of material from representative populations. The results are already indicating that major taxonomic corrections will be necessary. With respect to morphology and life history the taxa belonging to *Chalepoxenus* appear quite uniform. Interesting peculiarities refer to their host choice and specificity. In this present, first part of our studies we provide a literature survey, then deal with the range of the genus, and finally analyze the host species spectra of the various populations. Other aspects such as comparative morphology, karyotypes, ethology, and the formal systematic revision of the genus will be detailed in subsequent papers.

2. Survey of literature on *Chalepoxenus*

In Table 1 we have listed in chronological order, for swift and convenient reference, the papers describing or revising the genus and its species, and the few publications providing biological data. FINZI (1921) described the first species, *C. muellerianus*, as belonging to the independent genus *Leptothorax*, subgenus *Temnothorax*. However, MENOZZI (1922) was the first to report on the socially parasitic relations of *C. "gribodoi"* (later synonymized with *muellerianus*; KUTTER 1973) with a host-species of the genus *Leptothorax*.

With the exception of *C. spinosus* (originally described as *Leonomyrma spinosa* ARNOLDI; BUSCHINGER 1987), where only alate sexuals have been collected, all *Chalepoxenus* species described later on were found to live as social parasites together with one or more host-species. LE MASNE (1970a, b) presented some evidence for slave-maker habits in a *Chalepoxenus* population (later described as *C. kutteri*; CAGNIANT 1973) from Banyuls-sur-Mer, France. Finally EHRHARDT (1982) demonstrated that *C. muellerianus* (from North Italy) is a slave-making species, and all other

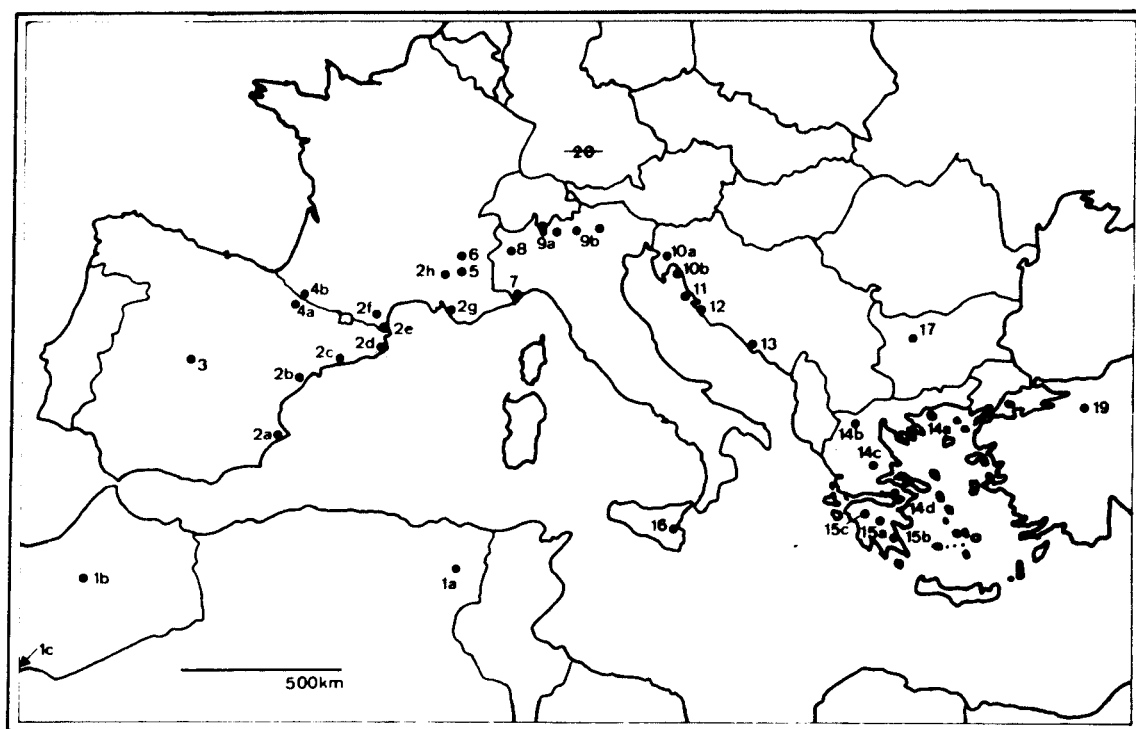


Fig. 1. Range of *Chalepoxenus*. For detailed description of the numbered sites see text. Population 18 (Kazakhstan) not in the map. No. 20, south of the Federal Republic of Germany: Erroneous indication from BERNARD (1968).

Abb. 1. Verbreitung von *Chalepoxenus*. Detaillierte Beschreibung der nummerierten Fundorte im Text. Die Population 18 (Kasachstan) ist nicht im Bereich der Karte. Nr. 20, Süden der BRD: Irrtümliche Angabe aus BERNARD (1968).

species and populations investigated by us exhibit this behavior (EHRHARDT 1987). CAGNIANT (1985) described *C. brunneus* from Morocco based on sexuals alone, which were reared from a host-species nest. No workers have been found and it is likely that they are truly lacking in this species (see 3, 1c).

3. The geographical distribution of *Chalepoxenus*

In the map (Fig. 1) the location of all *Chalepoxenus* populations mentioned in the literature or detected by us is roughly indicated, except for that of *C. spinosus* in east-Kazakhstan. The populations are numbered, and in the following section a brief comment on each is provided, including collecting data, host-species, nesting sites, sample sizes and other information which is currently available. Question marks indicate doubtful data or indentifications most of which will be discussed later.

1a: Djebel Chelia (Algeria). One *Chalepoxenus* female found with *Leptothorax spinosus*, at 1,200—1,500 m (CAGNIANT 1968). Following CAGNIANT (1983) this specimen belongs to *C. tramieri* described from Morocco (see 1b).

1b: Djebel Hebri (Morocco). Type-locality of *C. tramieri* CAGNIANT 1983. 4 workers found with *Leptothorax spinosus nivalis*, at 2,000 m, underneath a basaltic rock. An intensive search in the area in May, 1987, did not reveal any additional material (BUSCHINGER, CAGNIANT, ESPADALER, HEINZE).

- 1c: Tizi n'Test (Great Atlas, Morocco), type-locality of *C. brunneus* CAGNIANT 1985. Males and females emerged in the laboratory from a colony of *Leptothorax* cf. *maroccanus* which had been collected at 2,000 m, on a west-exposed slope with limestone rocks. In May, 1987, we (BUSCHINGER, HEINZE) collected 11 colonies in the type locality. None contained workers of the parasitic species.
- 2a: Calpe (Alacant, Spain). 12 colonies of *C. kutteri* (leg. det. BUSCHINGER, VII. 1981) with *L. massiliensis*. Nests in crevices of limestone rocks at 100—600 m (ESPADALER and RESTREPO 1983).
- 2b: Gandesa (Tarragona, Spain). One (?) colony of *C. kutteri* (leg. det. COLLINGWOOD, VIII. 1977) with *L. unifasciatus* (?) (ESPADALER and RESTREPO 1983).
- 2c: Sitges (Barcelona, Spain). Several colonies of *C. kutteri* with *L. specularis* (?) (leg. RESTREPO, det. ESPADALER), at 100 m (ESPADALER and RESTREPO 1983).
- 2d: Llansa, Cadaquès, Figueras, Embalse de Boadella (Spain). Eight colonies of *C. kutteri* with *L. massiliensis*. Nests in crevices of limestone rocks or dry walls, at 10—250 m (leg. det. BUSCHINGER et al., IV. 1984).
- 2e: Banyuls-sur-Mer (P.-O., France). Type-locality of *C. kutteri* CAGNIANT 1973. Following this author, 43 colonies had been collected by LE MASNE since 1950, and 5 by himself and L. PASSERA, 1965 to 1970, at 100—250 m. The host-species were *L. massiliensis*, *berlandi*, *racovitzae*, and *niger*. Twice 2 host species were found in one nest. Own samples: 7 colonies, all with *L. massiliensis*, (leg. det. BUSCHINGER et al. III 1981). LE MASNE (1970a) briefly, mentions a colony of *Chalepoxenus* "close to *gribodoi*" from the vicinity, Pyrénées-Orientales, at 600 m.
- 2f: Between Durban and Tuchan (Aude, France). One colony of *C. kutteri* collected VI. 1982 by Mme. LE MAIRE (L. Peru in litt., det. PERU, BUSCHINGER), with *L. racovitzae* (?).
- 2g: La Couronne (near Marseille, France). One colony *C. kutteri* with *L. massiliensis* (leg. det. BUSCHINGER, VII. 1975); 2 colonies with *L. massiliensis* (leg. det. BUSCHINGER et al., III. 1981). In crevices in limestone rocks, ca. 30 m.
- 2h: La Borie, near Bollène (Drôme, France). 2 colonies of *C. kutteri* with *L. massiliensis* (leg. det. FISCHER, IV. 1981).
- 3: Surroundings of Madrid (Spain). One colony *C. kutteri* with *L. rabaudi* (?), one colony with *L. exilis* (ACOSTA SALMÉRON et al. 1983). Following these authors the second sample might represent an undescribed species. However, a direct comparison revealed that it also belongs to *C. kutteri* (det. MARTINEZ IBAÑEZ, BUSCHINGER). One colony *C. muellerianus* with *L. unifasciatus* (leg. det. M. D. MARTINEZ IBAÑEZ, IV. 1978, in litt.), Canencia (Madrid), Guadarrama mountains, 1,200 m.
- 4a: Huesca (Spain) and from there to the French border in the Pyrenees. One colony *C. kutteri* (?) with *L. (Temnothorax) recedens* (leg. det. COLLINGWOOD, V. 1958), at Canfranc (ESPADALER and RESTREPO 1983). *C. muellerianus*: Monte Lalana, with *L. tuberum* (leg. Mas, VIII. 1978, det. ESPADALER). San Juan de la Peña, 1,130 m with *L. unifasciatus* (leg. det. ESPADALER, VIII. 1982). Labati, 1,800 m, with *L. tuberum* (leg. det. ESPADALER, VIII. 1982) (ESPADALER and RESTREPO 1983). Own samples: 5 colonies *C. muellerianus* with *L. unifasciatus* at Biescas (leg. det. BUSCHINGER et al., IV. 1984). In dry walls. One colony *C. muellerianus* near San Juan de la Peña, VII. 1986, with *L. unifasciatus* (leg. det. BUSCHINGER).
- 4b: Bielle (Pyrenees-Atlantiques, France). One colony of *C. muellerianus* with *L. unifasciatus*, 300 m (leg. det. BUSCHINGER et al., IV. 1984), in a dry wall. One colony *C. muellerianus* with *L. tuberum*, VII. 1986, about 1.5 km south of Lac de Fabrèges, 1,300 m (leg. det. BUSCHINGER). PERU (in litt.) reported 2 colonies of *C. muellerianus* with *L. unifasciatus* and 2 other species of the *tuberum*-group which he had collected IV. 1982, "au dessus du Lac de Fabrèges (1,400 m)".
- 5: Mont Ventoux (Vaucluse, France). DU MERLE (1978) found ca. 6 colonies of *C. "gribodoi"* at elevations of 450—1,400 m with host species *L. interruptus*, *nigrices*, *pyrenaeus*, *racovitzae*, *tuberum*, *unifasciatus*.

- 6: Le Vercors (Drôme, France). BERNARD (1946) reported the occurrence of *C. "gribodoi"* in the Forêt de Lente (1,100–1,300 m). He collected 10 colonies with "*L. nylanderi* FÖRST. typique" as host-species. Own samples: 12 colonies X. 1978 (leg. BUSCHINGER et al.), and 3 colonies VIII. 1985 (leg. BUSCHINGER), all with *L. nigrices*, near Vassieux-en-Vercors (1,050 m). Two of the colonies in addition contained *L. interruptus* slaves. No *Chalepoxenus* could be found in the adjacent Forêt de Lente, and BERNARD's identification of the host-species as *L. nylanderi* presumably was erroneous since we did not find any *L. nylanderi* in that area.
- 7: Between Albenga, Ormea and Imperia (Liguria, Italy). 19 colonies of *C. muellerianus*, mostly with *L. unifasciatus*, at elevations of 100–700 m (leg. det. BUSCHINGER et al., V. 1983). Only one incipient colony had *L. (T.) recedens* as host-species. The localities are close to Andora (Marino, S. Pietro), Ranzo, Ormeo, and Chiappa. Nests were found in dry walls. A record of LE MASNE (1970a) of a *Chalepoxenus* "close to *gribodoi*" from the Alpes-Maritimes at 1,000 m may be mentioned here.
- 8: Cuceglio near Ivrea (Piemont, Italy). Type locality of *C. gribodoi* MENOZZI 1922. 1 ♀ and 12 ♂♂ were found in a *Rubus* stem, with *L. tuberosum* ♂♂. Own samples: 3 colonies with *L. unifasciatus* from a dry wall at the western border of the village of Cuceglio, ca. 300 m (leg. BUSCHINGER et al., X. 1978). A few host-species colonies, but no further *Chalepoxenus* were found in dry *Rubus* stems there.
- 9a: Monte Gambarogno (Ticino, Switzerland). Type-locality of *C. insubricus* KUTTER 1950. 1 ♂ at the top of the mountain (1683 m). KUTTER (1973) ascribed our material from Salorno (pop. 9b) to this species. Own samples: Lago di Como (Ossuccio), Valtellina (Biolo, Tirano, Val Masino), Val Bregaglia (Villa di Chiavenna, Promontogno) (I; CH), 78 colonies of *Chalepoxenus* with exclusively *L. unifasciatus*, in elevations of 200–950 m (leg. BUSCHINGER et al., IV. 1978–X. 1980). Nests were usually collected in dry walls of terraced vineyards and olive orchards.
- 9b: Lago d'Iseo (Lovere), Lago di Garda (Tignale), Trento (Salorno, Novaledo, Borgo) (Italy). 134 colonies of *Chalepoxenus insubricus/muellerianus* with *L. unifasciatus*, at elevations of 100–500 m (leg. det. BUSCHINGER et al., VIII. 1968–X. 1982). The population of Tignale is particularly large and dense.
- 10a: Škocjan (= San Canziano, Istria, Yugoslavia). Type locality of *C. muellerianus* (FINZI 1921). 4 ♂♂ under moss, collected without host-species. In the close vicinity of Škocjan (400 m) we found only one small colony with 1 ♀ 3 ♂♂ of the parasite, and *L. nigriceps* as host-species (leg. det. BUSCHINGER et al., IV. 1979).
- 10b: Krk (Dalmatian island, Yugoslavia). W. FABER had collected 16 colonies of *C. muellerianus* (?) there between 1966 and 1972 (KUTTER 1973 and FABER, pers. comm.). He recorded *L. unifasciatus* as the main host-species, but also *L. affinis*, *nylanderi*, and *flavicornis* in one *Chalepoxenus* colony each, and always together with *L. unifasciatus*. In 2 of his colonies *L. exilis* was present together with *L. unifasciatus*, and one colony contained *L. exilis* only. Own samples: 27 colonies from around Baška/Krk (100–300 m). 25 colonies had *L. unifasciatus* as the only host-species, 1 had only *L. (T.) recedens*, and one *L. unifasciatus* together with *L. recedens* (leg. det. BUSCHINGER et al., IX. 1981 and X. 1985).
- 11: Pag (Dalmatian island, Yugoslavia): In an old pine stand on the west-coast near Kolan, ca. 20–50 m, we found a population of 11 *Chalepoxenus muellerianus* (?) colonies all containing exclusively *L. (T.) recedens* as host-species (leg. det. BUSCHINGER et al., IX. 1983).
- 12: Ljubač (near Zadar, Yugoslavia). 4 *Chalepoxenus muellerianus* (?) colonies, all with exclusively *L. flavicornis* as host-species (leg. det. BUSCHINGER et al., IX. 1983). *L. exilis*, *lichtensteini*, and *L. (T.) recedens* were present in the same locality, in comparatively high densities, whereas we could not find any free-living *L. flavicornis* colony there.
- 13: Dubrovnik (Yugoslavia). W. FABER (pers. comm.) found 2 *Chalepoxenus muellerianus* (?) colonies in the vicinity of Dubrovnik in 1977, one of them with *L. flavicornis*, the other with *L. affinis* as host-species.

- 14a: Thássos (Greek island). U. WINTER (pers. comm.) collected 2 *Chalepoxenus muellerianus* (?) colonies with *L. unifasciatus* near Kastro and Prinos, and 2 with *L. (T.) recedens* near Panagia and Potomia (X. 1984).
- 14b: Klidion (W of Florina, Greece). One *Chalepoxenus muellerianus* (?) colony with *L. (T.) recedens* (leg. det. BUSCHINGER et al., X. 1985).
- 14c: Meteora monasteries, near Kalambaka (Greece). Three *Chalepoxenus muellerianus* (?) colonies with *L. (T.) recedens*, two with *L. (T.) recedens* and *L. interruptus* (leg. det. BUSCHINGER et al., X. 1985).
- 14d: Perachora (N of Korinthos, Greece). 17 *Chalepoxenus muellerianus* (?) colonies with *L. (T.) recedens*, one with *L. exilis*, one with both host-species (leg. det. BUSCHINGER et al., X. 1985).
- 15a: L. Takka (Takka Lake, Peloponnissos, Greece). One *Chalepoxenus muellerianus* (?) colony with an undetermined *Leptothorax* species, in a limestone rock close to the bank of the lake (leg. BUSCHINGER, IV. 1980).
- 15b: Paralia Tirou (east-coast of Peloponnissos, Greece). One *Chalepoxenus muellerianus* (?) colony with *L. exilis*, and one incipient colony (only C.-queen) with *L. (T.) recedens* (leg. det. BUSCHINGER, IV. 1980).
- 15c: Bassai (near Andritsená, Peloponnissos, Greece). One *Chalepoxenus muellerianus* (?) colony with *L. (T.) recedens* (leg. det. BUSCHINGER et al., X. 1985).
- 16: Mount Etna (Sicilia, Italy). Type-locality of *C. siciliensis* KUTTER 1973. W. PAARMANN had collected 1 ♀ 6 ♂♂ at about 1,800 m on the southern slope of the volcano in 1970. (KUTTER 1973, and PAARMANN, pers. comm.). The host-species resembles *L. tristis* (L. PLATEAUX in litt.), but a definitive identification was not yet possible. Own samples: 10 colonies, all with the same host species, on the southern slope of Mt. Etna along the road from Nicolosi to the observatory, between 1,450 and 1,700 m, and on the northern slope, in the Pineta di Linguaglossa (ca. 1,600 m). Nests were found underneath and within lava rocks (leg. det. BUSCHINGER et al., X. 1982).
- 17: Rhodopen (Bulgaria), Dobrosten mountains, near Tschervenata Stena, ca. 1,500 m. In a karst area beneath a stone. 1 ♀ 42 ♂♂ *C. muellerianus* (?), host species near *L. tuberum* (leg. det. B. SEIFERT, IX. 1982, in litt.).
- 18: (Not on the map) — E-Kazakhstan, close to Peremetrija, USSR: Type-locality of *C. spinosus* (ARNOLDI 1968). ♂♀ described, no ♂♂ found and no host-species mentioned.
- 19: Turkey, near Tarakli, north-west-Turkey, ca. 650 m, in a dry stick of wood in a dense mixed forest. One *C. muellerianus* (?) colony with a host-species near *L. unifasciatus* (HEINZE 1987).
- 20: Southern FRG. Erroneous indication of BERNARD (1968, p. 222). Also cited in BARONI URBANI 1971, p. 129, and in ESPADALER and RESTREPO 1983. No *Chalepoxenus* has ever been found in the Southern FRG, and from our experiences with numerous mediterranean sites we may conclude that this genus is absent north of the Alps.

The total number of *Chalepoxenus* samples collected to the present is approximately 485. Our own material consists of 375 samples, which comprise 7 colonies from the type-locality of *C. kutteri* (pop. 2e), 3 from that of *C. "gribodoi"* (pop. 8), 212 of *C. insubricus* (pop. 9a, 9b), 1 of *C. muellerianus* (pop. 10a), and 10 of *C. siciliensis* (pop. 16).

The known range of the genus extends around the western Mediterranean Sea from Algeria and Morocco through Spain, Southern France, Italy, Yugoslavia, Bulgaria, Greece and Turkey, with one record from the lower Ural area of the USSR. It may be expected that *Chalepoxenus* also occurs much farther to the east, but without detailed collecting this remains speculation.

4. The host- or slave-species of *Chalepoxenus*

Slave-making ant species usually have more than one host-species, which, however, are closely related to one another (BUSCHINGER 1981; WILSON 1971). In areas where several potential host-species occur sympatrically, the slave-maker colonies may contain one or the other host-species, or sometimes have slaves of two or three different species together in one nest (BUSCHINGER 1966, for *Harpagoxenus sublaevis*. GÖSSWALD 1930; WINTER 1979b; BUSCHINGER and WINTER 1983, for *Epimyrmica ravourei*. BUSCHINGER and ALLOWAY 1977, for *Harpagoxenus americanus*. Further examples in WILSON 1971).

For *Chalepoxenus* this same phenomenon has been observed. A number of different slave-species have been recorded for *C. kutteri* (CAGNIANT 1973), and for *C. muelle-rianus* (ESPADALER and RESTREPO 1983), or *C. "gribodoi"* (DU MERLE 1978). Most colonies, however, contain only one slave-species, and in several large populations we found but one host-species as slaves, despite other potential host-species being present in the vicinity.

In the following, we provide a detailed analysis of our own material and of the literature records as far as possible. Some identifications of host-species are quite uncertain, due to the generally poor condition of leptothoracine taxonomy (BOLTON 1982; BUSCHINGER 1981), and to the overlapping variation of many species.

- a) *Chalepoxenus tramieri* (pop. 1a, 1b): According to CAGNIANT (1983), one female of *C. tramieri* has been found with *Leptothorax spinosus* (FOREL) in Algeria, and 4 workers have been collected in Morocco, with *L. spinosus nivalis* (FOREL). The host-species clearly belongs to the subgenus *Myrafant* (SMITH 1950). It is remarkable that another dulotic ant, *Epimyrmica algeriana* CAGNIANT, also enslaves *L. spinosus* (BUSCHINGER et al., in prep.), in the same localities.
- b) *Chalepoxenus brunneus* (pop. 1c): CAGNIANT (1985) obtained some males and females from a colony of *Leptothorax* cf. *maroccanus* SANTSCHI which he had collected in Morocco. *L. maroccanus* belongs to the subgenus *Myrafant*. All our 11 samples from the type-locality, collected in May, 1987, contained only this same host species.
- c) *Chalepoxenus kutteri* (pop. 2a—h, 3, 4a, from Spain and southern France). Under this name we include all populations corresponding to the original description, and the material from the type-locality. Our own material consists of 32 colonies, and from the literature we calculate that another 53 colonies have been collected (ACOSTA SALMÉRON et al. 1983; CAGNIANT 1973; ESPADALER and RESTREPO 1983; LE MASNE 1970a). In addition, ESPADALER and RESTREPO (1983) mentioned "several colonies with *L. specularis*" without giving numbers.

The following host-species were recorded:

- *Leptothorax (Myrafant) massiliensis* BONDROIT: Apparently the main host-species of *C. kutteri*, since 76 or 77 of the total of 85 colonies had slaves belonging to this species. In all our 32 colonies we found only *L. massiliensis*. LE MASNE (1970a) reported the same host-species for 43 colonies which he had collected. However, among 13 samples which LE MASNE had sent to H. KUTTER, one contained a worker of *L. racovitzai*, one a worker of *racovitzai* and 4 *massiliensis*, and in one sample a *L. berlandi* worker was found alongside 3 *massiliensis* slaves (CAGNIANT 1973).

- *Leptothorax (M.) niger* FOREL: The only host-species in 3 *C. kutteri* colonies (CAGNIANT 1973). Due to its black coloration *L. niger* is easily distinguished from *L. massiliensis* and other yellow to brownish species. *L. niger*, thus, surely represents a second, although rare, host of *C. kutteri*.
- *Leptothorax (M.) exilis* EMERY: Once found as host-species in a *C. kutteri* colony from the vicinity of Madrid (ACOSTA SALMÉRON et al. 1983). *L. exilis* is quite a variable species. Many subspecies and varieties have been described, but these were synonymized by BARONI URBANI (1971). *L. exilis* is also one of the host-species of *C. muellerianus* (see below).
- *Leptothorax (M.) specularis* EMERY: According to ESPADALER and RESTREPO (1983) several *C. kutteri* colonies with this host-species were found near Sitges (Barcelona). The species was originally described as a variety of *L. exilis*, and hence is a synonym of this species according to BARONI URBANI (1971). ESPADALER and RESTREPO (1983) refer to COLLINGWOOD (1976) for *L. specularis*.
- *Leptothorax (M.) rabaudi* BONDROIT: Recorded once as host of *C. kutteri*, from the vicinity of Madrid (ACOSTA SALMÉRON et al. 1983).
- *Leptothorax (M.) unifasciatus* (LATREILLE): One colony *C. kutteri* with this host-species, from Gandesa (Tarragona) (ESPADALER and RESTREPO 1983). *L. unifasciatus* is the main host-species of *C. muellerianus* (see below).
- *Leptothorax (M.) racovitzai* BONDROIT: Found as host-species of *C. kutteri* in one colony from Banyuls, and in one other together with *L. massiliensis* (CAGNIANT 1973). In a third colony, pop. 2f (Aude), the host-species may have been confused with *L. massiliensis* (PERU, in litt.).
- *Leptothorax (M.) berlandi* BONDROIT: One worker was identified in a *C. kutteri* colony with *L. massiliensis* slaves (CAGNIANT 1973). More material would be necessary to confirm *berlandi* as a regular host of *C. kutteri*. According to PLATEAUX (in litt.) *berlandi* is also very similar to *rabaudi*, which itself varies quite a lot.
- *Leptothorax (Temnothorax) recedens* (NYLANDER): Once recorded as host-species of *C. kutteri* from Canfranc (pop. 4a). The *Chalepoxenus* had originally been misidentified as *Epimyrma vandeli* by COLLINGWOOD and YARROW (1969) (ESPADALER and RESTREPO 1983). *L. recedens* is morphologically quite different from usual *Myrafant* species. *Temnothorax*, therefore, has been treated as a separate genus, or a subgenus of *Leptothorax*, by various authors. However, BOLTON (1982) states that *Temnothorax* grades into *Leptothorax*, and thus is not valid. *L. recedens* is also one of the more frequent host species of *C. muellerianus* (see below).

In conclusion, we may state that the majority of *C. kutteri* colonies have *L. massiliensis* as host-species, which was the only slave-species in 74 or 75 out of 85 colonies evaluated. In the remaining colonies some 7 or 8 *Leptothorax* species were found as slaves, however, usually only once or twice each. Only *L. exilis* (including *specularis*) might be a somewhat more important second host-species. In most instances *C. kutteri* colonies contain but one host-species each. Only in two samples where *L. massiliensis* was the main host-species was a second host-species recorded, one worker each of *L. racovitzai* and *L. berlandi*. A mixed slave population is thus extremely rare in *C. kutteri*.

Table 2. The host-species of *Chalepoxenus muellerianus*, including “*gribodoi*”, *insubricus*, and allied populations

Host species	Own material		Foreign material		Total	
	n col.	(%)	n col.	(%)	n col.	(%)
<i>L. unifasciatus</i>	267	(80.2)	12	(26.1)	279	(73.6)
<i>L. recedens</i>	38	(11.4)	—	—	38	(10.0)
<i>L. nigriceps</i>	14	(4.2)	10*)	(21.7)	24	(6.3)
<i>L. flavicornis</i>	4	(1.2)	1	(2.2)	5	(1.3)
<i>L. exilis</i>	2	(0.6)	1	(2.2)	3	(0.8)
<i>L. tuberum</i>	1	(0.3)	3	(6.5)	4	(1.0)
<i>L. affinis</i>	—	—	1	(2.2)	1	(0.3)
<i>L. species</i>	1	(0.3)	2	(4.3)	3	(0.8)
mixed slave stock**)	6	(1.8)	7	(15.2)	13	(3.4)
Total	333	(100)	37	(80.4)	370	(97.5)
Footnote***)			(46	(100))	(379	(100))

*) The colonies of BERNARD (1946), pop. 6, with “*L. nylanderi*”
**) Detailed in the text
***) One sample, type material of *muellerianus* without host workers, two colonies of LE MASNE (1970a) without indication of a host-species, and 6 colonies of DU MERLE (1978) (pop. 5) not evaluated because it is not possible to derive from the paper the numbers of colonies with one or the other of the 6 host-species mentioned. Percentage, however was calculated from the totals of 46 and 379 colonies respectively.

d) *Chalepoxenus muellerianus* (= *gribodoi*), *insubricus*, and allied populations (“*muellerianus*?”).

Because of great similarities in morphology, colony size, and other characters we here examine together all the remaining material except for that of *C. siciliensis*. The material from Spain (pop. 3, 4a), France (pop. 4b, 5, 6), Italy (pop. 7, 8, 9a, b), Yugoslavia (pop. 10a, b, 11, 12, 13), Greece (pop. 14a—d, 15a—c) and Bulgaria (pop. 17) comprises a total of 333 samples collected by us, mostly complete colonies, and 46 samples mentioned in the literature or sent to us for identification. The predominant host-species are listed in Table 2.

As in *C. kutteri*, in this group of “species” and populations also one very frequent host-species, *Leptothorax unifasciatus* (LATREILLE), can be recognized. *L. unifasciatus* was the only host-species in 73.6 % of all colonies evalued. The second most frequent slave-species was *L. (Temnothorax) recedens*, present in 10.0 % of the material; and *L. (M.) nigriceps* MAYR represents a third important species, found in 6.3 % of all *Chalepoxenus* colonies of this group. Five other *Leptothorax (Myrafant)* species were found in 1 to 5 (0.3 to 1.3 %) *Chalepoxenus* colonies, and a total of 13 (3.4 %) of the colonies contained a mixture of two different host-species, including several not mentioned in Table 2.

The occurrence of these host-species in the various populations is discussed in more detail in the following section.

— *Leptothorax (M.) unifasciatus* is a widespread and easily recognizable species. It is by far the most frequent host-species in the western parts of the range of

C. muellerianus (including *insubricus* etc.), in spite of the presence of several other potential host-species in many of the populations investigated. Thus, in pop. 9a and b, we collected a total of 78 and 134 *Chalepoxenus* colonies respectively, all exclusively with *L. unifasciatus*. In some localities, particularly in the large population of Tignale (9b), we also found numerous colonies of *L. recedens*, which in other populations is apparently quite a usual host of *Chalepoxenus*. In the Tignale site, and in some others, only *Epimyrmica kraussei* parasitizes *L. recedens* (BUSCHINGER and WINTER 1983); none were found in *Chalepoxenus* nests.

- *Leptothorax* (*T.*) *recedens*: In Liguria (pop. 7), we collected 18 *C. muellerianus* colonies with *L. unifasciatus*, and one incipient colony with a *Chalepoxenus* queen in a *L. recedens* nest. Farther to the east, *L. recedens* is more frequently a host-species of *Chalepoxenus*. Thus, in the Dalmatian island of Krk (pop. 10b), W. FABER and the authors have collected a total of 43 colonies, one of which had *L. recedens* as slaves, and one *L. recedens* together with *L. unifasciatus*. In Greece (pop. 14a—d, 15a—c), a total of 32 colonies was found, 25 of which had *L. recedens* as the only host-species, and three had a mixed slave population of *L. recedens* and one other species each (once *exilis*, twice *L. interruptus*). Particularly remarkable is a population from Pag (pop. 11), where 11 colonies exclusively contained *L. recedens*.
- *Leptothorax* (*M.*) *nigriceps* MAYR is the most frequent host-species in the *C. muellerianus* population no. 6 (Vercors, France). Of the 15 colonies collected by us, all contained *L. nigriceps*, and two had some *interruptus* slaves in addition. We assume that the 10 colonies recorded by BERNARD (1946) also contained *L. nigriceps*, not *L. nylanderii* as originally stated. *L. nigriceps* was the host-species in only one other of all our samples, a small colony of *C. muellerianus* from its type locality (pop. 10a) in Istria.
- *Leptothorax* (*M.*) *flavicornis* EMERY: The only European *Myrmica* with 11-jointed antennae in females and workers, it quite rarely serves as a host-species. On the island of Krk (pop. 10b) it was found once together with *L. unifasciatus*; near Dubrovnik (pop. 13), FABER had collected one *Chalepoxenus* colony which contained only *L. flavicornis*; and near Zadar (pop. 12) we found 4 colonies with this host-species. The latter samples are most remarkable, as in this area we found numerous colonies of *L. exilis* (some parasitized by *Epimyrmica corsica*), *L. lichtensteini* and *L. recedens*, but no free-living *L. flavicornis* colony. On the other hand, no *Chalepoxenus* colony with any other host-species was collected there.
- All the other host-species mentioned in Table 2, *L. (M.) exilis* EMERY, *L. (M.) tuberosum* (FABRICIUS), *L. (M.) affinis* MAYR, and two undetermined *L. (M.) species* from Greece and Turkey, respectively, only were found in up to 4 *Chalepoxenus* colonies each. In addition DU MERLE (1978) recorded *L. (M.) racovitzai* BONDROIT, and *L. (M.) pyrenaicus* BONDROIT as host-species in the Mont Ventoux area (pop. 5). It is remarkable that he observed no less than 6 host-species in a total of about 6 *Chalepoxenus* colonies (calculated from DU MERLE 1978, where only percentages of species are given).
- Mixed slave populations were recorded in a total of 13 *Chalepoxenus* colonies, always with one of the more frequent host-species, and one other species. Thus, in

the Vercors (pop. 6), we found two colonies with *L. nigriceps* and *L. interruptus* (SCHENCK) together. BERNARD (1968) lists one colony with only *L. interruptus*, and one with a mixed slave population of *interruptus* and *nylanderi*. It is impossible, however, to determine whether or not these colonies belong to the same sample of 10 colonies recorded in BERNARD (1946), with only *L. "nylanderi"*.

From pop. 4b) Pyrénées Atlantiques, PERU reported two colonies with *L. unifasciatus* and two other, related species (not identified). In Krk (pop. 10b) FABER collected 5 colonies, all containing *L. unifasciatus*, and in addition *L. exilis* occurred in two, *L. affinis*, *L. flavicornis*, and *L. "nylanderi"* in one each of these colonies. *L. "nylanderi"* probably was confused with *L. (M.) lichtensteini* BONDROIT, since this is a frequent species in the island, whereas *L. nylanderi* is apparently absent there. In the same area we found one *Chalepoxenus* colony with *L. recedens* and *L. unifasciatus*. Finally, *L. recedens* with *L. interruptus* was observed in two *Chalepoxenus* colonies from pop. 14c (Greece), and in one colony (pop. 14d) *L. recedens* was combined with *L. exilis*.

- e) *Chalepoxenus siciliensis* (pop. 16): This species closely resembles the preceding group and may have to be synonymized with *C. muellerianus*. We discuss the only known population (from Mt. Etna) separately, because it is situated at quite a distance from the other ones. Our 10 colonies, and apparently also the type material, all contained one host-species which was identified as close to *L. (M.) tristis* BONDROIT. Free-living colonies of this species were most frequent in the area investigated by us, but we also found *L. recedens*, *unifasciatus*, *exilis*, *flavicornis*, and *lichtensteini* there. As in some other localities, *Chalepoxenus* pop. 16 apparently has specialized in parasitizing, exclusively or preferably, only one of the potential host-species.
- f) *Chalepoxenus spinosus* (pop. 18): Nothing is known of the host-species since only alate sexuals have been collected and described.

5. Discussion and conclusions

In this first of a proposed series of papers on *Chalepoxenus* we provide a survey of literature on the genus. It reveals quite a typical scientific fate of a genus of rare parasitic ants, with some errors mainly due to insufficient material, others due to collecting deficiencies and misidentifications. It also clearly shows that a reasonable number of samples taken from several localities is necessary to determine the taxonomic position of a population, and to find out a minimum of biological data. After the first description of a species (FINZI 1921) and the first observation of parasitic habits (MENOZZI 1922), 60 years elapsed until EHRHARDT (1982) finally demonstrated the obligatory slave-making habits of a *Chalepoxenus* species.

The range of *Chalepoxenus*, as stated above, extends around the western Mediterranean, through the northern adjacent countries east to Turkey and to east Kazakhstan (Soviet Union). From this known area we may conclude that the range of the genus extends much farther to the east, since the host species group (*Leptothorax*, subgenus *Myrafant*) also occurs throughout continental Asia to Japan (CHAPMAN and CAPCO 1951).

The known range of *Chalepoxenus* is widely coincident with that of *Epimyrma*, another genus of active or degenerate slave-maker species which often parasitize the same host-species as *Chalepoxenus*. Thus the main host of *C. muellerianus* (and *insubricus*) is *L. unifasciatus*, and this is also the most important slave-species of *Epimyrma ravousxi* (BUSCHINGER and WINTER 1983). In a site near Ossuccio (pop. 9a) we found *Chalepoxenus* and *E. ravousxi*, both with *L. unifasciatus*. In Algeria, *C. tramieri* was found with *L. spinosus*, which in the same area is the slave-species of *Epimyrma algeriana* (CAGNIANT 1968; JESSEN 1987). In many sites in Spain, France, North Italy, Yugoslavia and Greece, *Chalepoxenus* occurs in the same localities as *Epimyrma kraussei*, the latter being restricted to *L. (T.) recedens* as host-species (BUSCHINGER et al. 1987).

With respect to the various *Chalepoxenus* "species" it is remarkable that the populations ascribed to *C. kutteri* (2a—h) inhabit a comparatively continuous area which only slightly overlaps that of *C. muellerianus* and related forms. Only two *C. kutteri* colonies were found in some isolation, one near Madrid (pop. 3), and one at Canfranc (pop. 4a), in proximity to *C. muellerianus* sites. *C. kutteri* is also usually found quite close to the coast, and at elevations up to 250 m, rarely 600 m. East of Marseille it is apparently absent, and on the Ligurian coast *C. muellerianus* reaches down nearly to sea level.

C. muellerianus, together with *C. insubricus* and the former *C. "gribodoi"*, forms a series of populations with partly overlapping areas along the western and southern slopes of the Alps, from southern France through Italy to Yugoslavia and Greece. Gaps in the map (Fig. 1) are presumably more often due to lack of information than to absence of the genus. One branch population, apparently belonging to the *muellerianus* group, reaches from the Pyrenees south, presumably through great parts of northern and central Spain. Other branches may be represented by the two colonies from Bulgaria (pop. 17), and Turkey (pop. 19), respectively.

The population of *C. siciliensis* is perhaps a more isolated deme, despite being morphologically similar to *muellerianus*. In Calabria we have not found any *Chalepoxenus*, and in central Italy and northward to the Po valley the genus has not yet been detected¹⁾. *C. siciliensis*, like the two North African species, has only been found at high altitudes (1,200—2,000 m). *C. tramieri* is morphologically similar to *C. kutteri*. Presumably it documents a former faunal connection between Spain and North Africa via Gibraltar.

Most interesting are the relations between *Chalepoxenus* and its host-species. In chapter 4 we have already explained that the two *Chalepoxenus* groups which are most easily distinguished, *C. kutteri* on the one hand, and *C. muellerianus* and related taxa on the other hand, have one predominant host-species each, namely *L. massiliensis* for *C. kutteri*, and *L. unifasciatus* for *C. muellerianus* and allies. Both groups comparatively rarely utilize other potential host-species which nevertheless are usually at accessible distances from their nests in the respective populations. And very rarely we found two slave-species together in one *Chalepoxenus* nest.

¹⁾ Recently, after submission of this paper, M. MEI (in litt.) has reported *C. muellerianus* from the Italian Abruzzi (5 colonies with host species close to *L. unifasciatus*).

This is remarkably different when compared with *Harpagoxenus sublaevis* for example: This species has three slave-species, two of which, *L. acervorum* and *L. muscorum*, usually occur sympatrically and in similar frequencies. The third host-species, *L. gredleri*, has somewhat different ecological requirements and therefore is comparatively rare in the sites where the other two species, and *Harpagoxenus*, are frequent. In an evaluation of 54 *Harpagoxenus* colonies (BUSCHINGER 1966), and of additional 64 colonies (WINTER unpubl.), 41 colonies had exclusively *L. acervorum*, 9 colonies only *L. muscorum*, 62 colonies both *L. acervorum* and *L. muscorum*, 4 colonies *L. acervorum*, *L. muscorum* and *L. gredleri*, and 2 *L. acervorum* and *L. gredleri* as slaves. Slaves of only one species were thus found in only 42.4 % and a mixed slave stock of 2 or 3 species in 57.6 % of the 118 colonies. In *Chalepoxenus*, mixed slave stocks were found in only two (2.4 %) of the *C. kutteri* colonies, and in 13 (3.4 %) of the *C. muellerianus* nests.

Such a difference may have several causes. One would be that the potential slave-species of *Chalepoxenus* are less tolerant towards each other in mixed nests than those of *Harpagoxenus*. However, the existence of colonies with quite variable combinations of host-species speaks against incompatibilities. Some of these colonies were kept for more than a year in laboratory conditions, and the two slave-species cooperated without any visible problems.

Another reason for *Chalepoxenus* to have but one host-species in each colony might be a certain competitive exclusion, for example in areas where potential host-species are also parasitized by *Epimyrma* species. In our pop. 9b, Tignale, where *L. unifasciatus* and *L. recedens* occur in about equal densities, this explanation seemingly is correct, in that *Epimyrma kraussei* parasitizes *L. recedens*, and *C. muellerianus* exclusively enslaves *L. unifasciatus*. However, in other populations no such niche segregation is observed.

Finally, we may consider a certain learning effect being involved. In ants, the newly enclosed specimens usually have to learn the nest and species odors of the colony in which they are born (JAISSON 1975). This "imprinting" is surely one of the most important of all preconditions for the functioning of ant slavery.

We assume that a young *Chalepoxenus* female may also somehow learn the characteristics of the slaves present in the nest where she ecloses. After mating, when she is in search of a host-colony to invade, in which to found her own colony, she may prefer a nest belonging to the slave-species she had already met with in her mother colony. And the slave-maker workers which develop later on may again be more or less imprinted on the slave-species already present in the young colony; they may prefer to raid on neighboring nests only of this host-species.

Such a slave-recognition system with a restricted innate knowledge of suitable host-species, and a good deal of acquired information on slave-species characters, would certainly be able to explain some of our observations. A tradition with respect to utilization of a particular slave-species in a given population could easily develop and be maintained, especially when this slave-species is the most frequent, or has the most easily accessible nests in the area. On the other hand, *Chalepoxenus* workers trying to conduct a raid may sometimes fail to find their familiar host-species. They may then rely on the innate compound nature of their host recognition system and

attack another, related, host-species. A colony with two slave-species will thus be formed, and the young queens reared in that nest will be attracted by host nests belonging to the two slave-species. A rapid and easy switch from one host-species to another thus seems possible.

Never the less, *Chalepoxenus* surely has an innate "filter" for differentiation between suitable and unsuitable host-species. Thus, in all of the approximately 485 *Chalepoxenus* colonies examined a slave belonging to one of the *Leptothorax* (*Leptothorax*) species was never found. On the other hand, we never found a member of the subgenus *Myrafant* as slaves in any of the approximately 900 *Harpagoxenus sublaevis* colonies which we have checked over the years. (The record of one *Chalepoxenus* colony with *L. muscorum* in BERNARD (1968) is very probably due to a misidentification).

The remarkable fact that *Chalepoxenus*, apart from the *Myrafant* species, also enslaves *L. (Temnothorax) recedens* thus speaks in favor of a very close relationship between these two subgenera (cf. BOLTON 1982), closer than that between them and the subgenus *Leptothorax*.

In summary then, *Chalepoxenus* comprises at least two distinct taxa, *C. kutteri* and *C. muellerianus*. There is little overlap in their ranges, and they are specialized in enslaving two different main host-species, *L. massiliensis* and *L. unifasciatus*, respectively. However, some overlapping occurs in the spectra of accessory host-species. The taxon *C. muellerianus* apparently should include *C. insubricus*, *C. siciliensis*, and most or all of the populations in Yugoslavia, Greece, Bulgaria and Turkey. Our ethological and morphological studies, which will be presented in subsequent contributions, corroborate this assumption. For *C. tramieri* and *C. brunneus*, as well as for *C. spinosus*, more material will be necessary to determine their relationships and taxonomic positions.

Zusammenfassung

Die Sklavenhalter-Ameisen der Gattung *Chalepoxenus* (Hymenoptera, Formicidae). I. Literaturübersicht, Verbreitung, Sklavenarten

Die Literatur über *Chalepoxenus*, eine Gattung obligatorisch sklavenhaltender Ameisen, wird in einer Übersicht dargestellt (Tab. 1). Die Gattung umfaßt sieben Taxa, *C. muellerianus*, *insubricus*, *siciliensis*, *kutteri*, *tramieri*, *brunneus* und *spinosus*. Ihr Verbreitungsgebiet erstreckt sich vom westlichen Mittelmeerraum über Jugoslawien und Griechenland bis in die Türkei, nach Bulgarien und Kasachstan (Abb. 1). Bisher wurden insgesamt etwa 485 Völker gesammelt, die hauptsächlich den Arten *muellerianus/insubricus* (die wahrscheinlich nur ein Taxon auf dem Artniveau darstellen), sowie *kutteri* und *siciliensis* zuzuordnen sind. Von *tramieri*, *brunneus* und *spinosus* steht sehr wenig Material zur Verfügung.

Aus jeweils einem Spektrum von Sklavenarten konnte für *C. muellerianus/insubricus* als Hauptwirtsart *Leptothorax unifasciatus*, für *C. kutteri* *Leptothorax massiliensis* bestimmt werden. Daneben werden mehrere andere *Leptothorax*-Arten gelegentlich als Sklaven benutzt. Außer *L. (Temnothorax) recedens* gehören sie alle der Untergattung *Myrafant* an. Im Gegensatz zu anderen Sklavenhaltern der Tribus Leptothoracini, z. B. *Harpagoxenus sublaevis*, enthalten *Chalepoxenus* Völker nur sehr selten gleichzeitig Sklaven zweier Arten. Offenbar spezialisieren sich bestimmte *Chalepoxenus*-Populationen auf die Versklavung jeweils einer Wirtsart, auch solcher, die andernorts nur gelegentlich als Wirtsart dienen, so *L. recedens* oder *L. flavicornis*.

Das Erkennen der Wirtsarten beruht bei *Chalepoxenus* wahrscheinlich auf einer Mischung von angeborenen und erlernten Merkmalen, womit sich Traditionen hinsichtlich der Wirtswahl entwickeln können.

Das vorliegende Material läßt vermuten, daß *C. muellerianis*, *insubricus*, vielleicht auch *siciliensis*, konspezifisch sind. Morphologische und ethologische Untersuchungen dazu sowie eine formale Revision der Gattung werden in nachfolgenden Arbeiten dargestellt.

Acknowledgements

Our work was supported by grants of the Deutsche Forschungsgemeinschaft to A. B., and a grant of the Minerva Funds to J. O. We are grateful to LUC PLATEAUX for identification of some of the host-species. L. PERU, B. SEIFERT, X. ESPADALER, H. CAGNIANT, M. MEI and M. D. MARTINEZ IBAÑEZ have generously sent us *Chalepoxenus* material for study and comparison. U. WINTER, K. GROH, J. HEINZE and P. DOUWES have helped to collect material during several of our excursions. Valuable informations on *Chalepoxenus* sites in Yugoslavia were drawn from the papers of the late W. FABER. B. BOLTON has commented on the manuscript, and helped to improve the English.

Literature

- ACOSTA SALMERÓN, F. J., MARTINEZ IBAÑEZ, M. D., y MORALES, M.: Contribución al conocimiento de la mirmecofauna del Encinar Peninsular (1). (Hym. Formicidae). Boletín Asoc. esp. Entom. **6** (1983), 379—381.
- ARNOLDI, K. V.: Wichtige Ergänzungen zur Myrmecofauna (Hymenoptera, Formicidae) der USSR, mit einigen Neubeschreibungen (in Russian, German Summary). Zool. Zh. **47** (1968), 1800—1822.
- BARONI URBANI, C.: Studien zur Ameisenfauna Italiens XI. Rev. Suisse Zool. **78** (1971), 1037 bis 1067.
- BERNARD, F.: Notes sur les Fourmis de France. II. Peuplement des Montagnes Méridionales. Ann. Soc. Ent. France **115** (1946), 1—36.
- Les Fourmis. Paris 1968.
- BOLTON, B.: Afrotropical species of the myrmicine ant genera *Cardicondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). Bull. Br. Mus. nat. Hist. (Ent.) **45** (1982), 307 to 370.
- BUSCHINGER, A.: Untersuchungen an *Harpagoxenus sublaevis* NYL. (Hym. Formicidae) I. Freilandbeobachtungen zu Verbreitung und Lebensweise. Ins. Soc. **13** (1966), 5—16.
- Experimente und Beobachtungen zur Gründung und Entwicklung neuer Sozietäten der sklavenhaltenden Ameise *Harpagoxenus sublaevis* (NYL.). Ins. Soc. **21** (1974), 381—406.
- A social parasite and its slaves. Reports of the DFG, German Research, **2/79** (1979), 10—12.
- Biological and systematic relationships of social parasitic Leptothoracini from Europe and North America. In: Biosystematics of Social Insects, P.E. HOWSE and J.-L. CLEMENT, eds., London and New York 1981.
- *Epimyrmica goesswaldi* MENOZZI 1931 = *Epimyrmica ravouxi* (ANDRÉ, 1896) — Morphologischer und biologischer Nachweis der Synonymie (Hym., Formicidae). Zool. Anz. **208** (1982), 352 bis 358.
- Synonymy of *Leonomyrma* ARNOLDI, 1968 with *Chalepoxenus* MENOZZI, 1922 (Hymenoptera: Formicidae). Psyche **94** (1987), 117—126.
- and ALLOWAY, T. M.: Population structure and polymorphism in the slave-making ant *Harpagoxenus americanus* (EMERY) (Hymenoptera: Formicidae). Psyche **83** (1977), 233—242.
- and ALLOWAY, T. M.: Caste polymorphism in *Harpagoxenus canadensis* M. R. SMITH (Hym., Formicidae). Ins. Soc. **25** (1978), 339—350.
- and ALLOWAY, T. M.: Sexual behaviour in the slave-making ant, *Harpagoxenus canadensis* M. R. SMITH, and sexual pheromone experiments with *H. canadensis*, *H. americanus* (EMERY),

- and *H. sublaevis* (NYLANDER) (Hymenoptera; Formicidae). Z. Tierpsychol. **49** (1979), 113 bis 119.
- EHRHARDT, W., and WINTER, U.: The organization of slave raids in dulotic ants — a comparative study (Hymenoptera; Formicidae). Z. Tierpsychol. **53** (1980), 245—264.
- FISCHER, K., GUTHY, H.-P., JESSEN, K., and WINTER, U.: Biosystematic revision of *Epimyrma kraussei*, *E. vandeli*, and *E. foreli* (Hymenoptera: Formicidae). Psyche **93** (1986), 253—276.
- und WINTER, U.: Population studies of the dulotic ant, *Epimyrma ravouxi*, and the degenerate slave-maker, *E. kraussei* (Hymenoptera: Formicidae). Entomol. Gener. **8** (1983), 251—266.
- CAGNIANT, H.: Liste préliminaire de fourmis forestières d'Algérie. Résultats obtenus de 1963 à 1966. Bull. Soc. Hist. Nat. Toulouse **104** (1968), 138—147.
- Description et représentation des trois castes de *Chalepoxenus kutteri* (nov. sp.) (Hyménoptères Formicidae-Myrmicidae). Ins. Soc. **20** (1973), 145—156.
- Contribution à la connaissance des fourmis marocaines. *Chalepoxenus tramieri*, nov. sp. Nouv. Rev. Ent. **13** (1983), 319—322.
- Contribution à la connaissance des fourmis marocaines: *Chalepoxenus brunneus* n. sp. (Hymenoptera, Myrmicidae). Nouv. Revue Ent. (N.S.) **2** (1985), 141—146.
- CHAPMAN, J. W., and CAPCO, S. R.: Check list of the ants (Hymenoptera: Formicidae) of Asia. Manila 1951.
- COLLINGWOOD, C. A.: A provisional list of Iberian Formicidae with a key to the worker caste. Eos, Rev. Espan. Ent. **52** (1976), 65—95.
- and YARROW, J. H. H.: A survey of Iberian Formicidae. Eos, Rev. Espan. Ent. **44** (1969), 53—101.
- DU MERLE, P.: Les peuplements de Fourmis et les peuplements d'Acridiens du Mont Ventoux. II. — Les peuplements de Fourmis. La Terre et la Vie, Suppl. **1** (1978), 161—218.
- EHRHARDT, W.: Untersuchungen zum Raubzugverhalten der sozialparasitischen Ameise *Chalepoxenus muellerianus* (FINZI) (Hym., Formicidae). Zool. Anz. **208** (1982), 145—160.
- — Biosystematics of the slavemaking ant genus *Chalepoxenus*. In: Chemistry and Biology of Social Insects, J. EDER and H. REMBOLD, eds., München 1987, 39—40.
- ESPADALER, X., and RESTREPO, C.: Els gèneres *Epimyrma* EMERY i *Chalepoxenus* MENOZZI, formigues paràsites socials (Hymenoptera: Formicidae), a la península Ibèrica. Estat actual del coneixement. Bull. Inst. Cat. Hist. Nat. **49** (Sec. Zool., 5) (1983), 123—126.
- FINZI, B.: Primo contributo alla conoscenza della fauna mirmecologica delle Venezia Giulia. Boll. Soc. Ent. Ital. **53** (1921), 118—120.
- Secondo contributo alla conoscenza della fauna mirmecologica della Venezia Giulia. Boll. Soc. Ent. Ital. **56** (1924), 120—123.
- GÖSSWALD, K.: Die Biologie einer neuen *Epimyrma*-Art aus dem mittleren Maingebiet. Z. wiss. Zool. **136** (1930), 464—484.
- HEINZE, J.: Three species of social parasitic ants new to Turkey. Ins. Soc. **34** (1987), 65—68.
- JAISSON, P.: L'imprégnation dans l'ontogenèse des comportements de soins aux cocons chez la jeune Fourmi Rousse (*Formica polyctena* FOERST.). Behaviour **52** (1975), 1—37.
- JESSEN, K.: Biosystematic revision of the parasitic ant genus *Epimyrma*. In: Chemistry and Biology of Social Insects, J. EDER and H. REMBOLD, eds., München 1987, 41—42.
- KUTTER, H.: Über zwei neue Ameisen. Mitt. Schweiz. Ent. Ges. **23** (1950), 337—346.
- Zur Taxonomie der Gattung *Chalepoxenus* (Hymenoptera, Formicidae, Myrmicinae). Mitt. Schweiz. Ent. Ges. **46** (1973), 269—280.
- LE MASNE, G.: Recherches sur la biologie des fourmis parasites. Les relations des ouvrières de *Chalepoxenus* avec leurs hôtes. C. R. Acad. Sc. Paris **271** (1970a), 1038—1041.
- Recherches sur la biologie des fourmis parasites. Le comportement agressif des ouvrières de *Chalepoxenus*. C.R. Acad. Sci. Paris **271** (1970b), 1119—1121.
- MENOZZI, C.: Nota su un genere e nuova specie die Formica parassita. Atti Soc. Ital. Sci. Nat. **61** (1922), 256—260.
- Note staccate di Mirmecologia. Boll. Soc. Ent. Ital. **57** (1925), 17—22.

- MÜLLER, G.: Le formiche della Venezia Giulia e della Dalmazia. *Boll. Soc. Adriat. Sci. Nat. Trieste* **28—29** (1923/24), 11—180.
- SMITH, M. R.: On the status of *Leptothorax* MAYR and some of its subgenera. *Psyche* **57** (1950), 29—30.
- STUART, R. J.: Experiments on colony foundation in the slave-making ant *Harpagoxenus canadensis* M. R. SMITH (Hymenoptera; Formicidae). *Can. J. Zool.* **62** (1984), 1995—2001.
- WILSON, E. O.: *The Insect Societies*. Cambridge, Mass. 1971.
- WINTER, U.: Untersuchungen zum Raubzugverhalten der dulotischen Ameise *Harpagoxenus sublaevis* (NYL.). *Ins. Soc.* **26** (1979a), 123—135.
- *Epimyrma goesswaldi* MENOZZI, eine sklavenhaltende Ameise. *Naturwissenschaften* **66** (1979b), 581.

Received: June 2, 1987

Authors' address: ALFRED BUSCHINGER, WERNER EHRHARDT and KARL FISCHER, Institut für Zoologie der THD, Schnittpahnstraße 3, D - 6100 Darmstadt; JACOB OFER, 11 Hapoel Str., Nof-Jam, Herzlia 46625, Israel.

Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere
 Verlag: VEB Verlage für Medizin und Biologie Berlin-Jena-Leipzig, VEB Gustav Fischer Verlag
 Jena, Villengang 2, Jena, DDR - 6900; Telefon 2 73 32; Verlagsdirektor: Dr. Dolf Künzel
 Verantwortlich für die Redaktion: Prof. Dr. Hans Joachim Müller, Prof.-Ibrahim-Straße 16,
 Jena, DDR - 6900

Redaktioneller Mitarbeiter im Verlag: Isolde Schneider

Veröffentlicht unter der Lizenznummer 1072 des Presseamtes beim Vorsitzenden des Ministerrates
 der Deutschen Demokratischen Republik

Redaktionsschluß für Karten: September 1987 (Topp), November 1987 (Buschinger)

Satz, Druck und Buchbinderei: Druckerei „Magnus Poser“ Jena, Betrieb des Graphischen Groß-
 betriebes INTERDRUCK Leipzig, Betrieb der ausgezeichneten Qualitätsarbeit

Alle Rechte beim Verlag. Nachdruck (auch auszugsweise) nur mit Genehmigung des Verlages und
 des Verfassers sowie mit Quellenangabe gestattet.

Printed in the German Democratic Republic

Artikel-Nr. (EDV) 77213; Artikel-Nr. (ZV) 1118003839

Erscheinungsweise: 4mal jährlich

03250