The Slave-Making Ant Genus Chalepoxenus (Hymenoptera, Formicidae)

I. Review of Literature, Range, Slave Species

ALFRED BUSCHINGER, WERNER EHRRHARDT, 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) reecedens they all belong to the subgenus Myrafant. Unlike other leptotheoracine 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 reecedens 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 inquilinous 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>
<thead>
<tr>
<th>Year</th>
<th>Authors</th>
<th>&quot;Species&quot;</th>
<th>Localities</th>
<th>Main contents</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1921</td>
<td>Finzi</td>
<td><em>Leptothorax</em> (Temnotherax) <em>muellerianus</em> n. sp.</td>
<td>S. Canziano, Istria (Yugoslavia)</td>
<td>found 4 ♀♀ without host-species under moss on a rock</td>
<td>description of the species <em>muellerianus</em></td>
</tr>
<tr>
<td>1922</td>
<td>Menozzi</td>
<td><em>Chalepozenus</em> (n. gen.) <em>gribodoi</em> (n. sp.)</td>
<td>Cuceglio Northern Italy</td>
<td>1 ♂, 12 ♀♀ with ♀♀ of host-species <em>Leptothorax tuberum</em>, in a blackberry stem</td>
<td>description of the genus <em>Chalepozenus</em></td>
</tr>
<tr>
<td>1923</td>
<td>Müller</td>
<td><em>L. muellerianus</em> = <em>Chalepozenus muellerianus</em></td>
<td>(S. Canziano)</td>
<td>transfer of <em>muellerianus</em> into genus <em>Chalepozenus</em></td>
<td></td>
</tr>
<tr>
<td>1924</td>
<td>Finzi</td>
<td><em>Chalepozenus muellerianus</em></td>
<td>(S. Canziano)</td>
<td>details minor differences between <em>C. muellerianus</em> and <em>C. gribodoi</em></td>
<td></td>
</tr>
<tr>
<td>1925</td>
<td>Menozzi</td>
<td><em>Chalepozenus gribodoi</em></td>
<td>(Cuceglio)</td>
<td>description of the male</td>
<td></td>
</tr>
<tr>
<td>1946</td>
<td>Bernard</td>
<td><em>Chalepozenus gribodoi</em></td>
<td>Vercors, Dept. Drôme, France</td>
<td>found 10 colonies with &quot;L. nylanderi typiques&quot; as host-species, suggests slavemaking host-species, suggests slavemaking</td>
<td>The host-species very probably was misidentified (see text) misidentities (see text)</td>
</tr>
<tr>
<td>1950</td>
<td>Kutter</td>
<td><em>Chalepozenus insubricus</em> n. sp.</td>
<td>Ticino, Switzerland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>Arnoldi</td>
<td><em>Leonomyrma</em> n. gen. <em>spinosa</em> n. sp.</td>
<td>lower course of Ural River, Soviet Union</td>
<td>description of ♂ and ♀</td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>Bernard</td>
<td><em>Chalepozenus gribodoi</em></td>
<td>Vercors, France South of the FRG</td>
<td>host-species <em>L. nylanderi</em>, interrupted, <em>muscorum</em> and mixed; host queen &quot;generally coexisting with the <em>C.</em> queen&quot;</td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>Cagniant</td>
<td><em>Chalepozenus spec.</em> (C. tramieri Cagniant 1983)</td>
<td>Algeria</td>
<td>1 ♀ with <em>Leptothorax spinosus</em></td>
<td></td>
</tr>
</tbody>
</table>

Table 1. Survey of relevant literature on taxonomy and biology of the genus *Chalepozenus*.
<table>
<thead>
<tr>
<th>Year</th>
<th>Author</th>
<th>Species</th>
<th>Location</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1970a, b</td>
<td>Le Masne</td>
<td><em>Chalepozenus</em> spec.</td>
<td>Banyuls-sur-Mer (France, eastern Pyrenees)</td>
<td>Certain behaviours indicate slavemaking habits.</td>
</tr>
<tr>
<td>1973</td>
<td>Cagniant</td>
<td><em>Chalepozenus kutteri</em> n. sp.</td>
<td>Banyuls-sur-Mer (France)</td>
<td>Description of ♀, ♂, ♀; host-species <em>L. massiliensis, racoviitzae berlandi, niger</em>. Host-species queen always lacking.</td>
</tr>
<tr>
<td>1973</td>
<td>Kutter</td>
<td><em>Chalepozenus muellerianus</em>, <em>insubricus, kutteri</em></td>
<td>(Known localities, see above)</td>
<td>Morphological comparison; synonymizes <em>C. gribodoi</em> = <em>C. muellerianus</em>.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>C. siciliensis</em> n. sp.</td>
<td>Mount Etna, Sicily</td>
<td>Description of ♀ and ♀ of <em>C. siciliensis</em></td>
</tr>
<tr>
<td>1976</td>
<td>Collingwood</td>
<td><em>Chalepozenus</em> spec.</td>
<td>Northern Spain</td>
<td>List of Iberian <em>Formicidae</em> species undetermined</td>
</tr>
<tr>
<td>1982</td>
<td>Ehrhardt</td>
<td><em>Chalepozenus muellerianus</em></td>
<td>Northern Italy</td>
<td>Describes slave-raiding and laboratory culture</td>
</tr>
<tr>
<td>1983</td>
<td>Espadaler</td>
<td><em>Chalepozenus muellerianus</em></td>
<td>Spain</td>
<td>List of localities in Spain.</td>
</tr>
<tr>
<td>and Restrepo</td>
<td></td>
<td>and <em>C. kutteri</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>Cagniant</td>
<td><em>Chalepozenus tramieri</em> n. sp.</td>
<td>Morocco and Algeria</td>
<td>Description of ♀♀♀ with host-species <em>L. spinosus f. nivalis</em>. ♀ of <em>C. muellerianus</em>. <em>♀</em> of Cagniant 1968 presumably belonging to this species.</td>
</tr>
<tr>
<td>1985</td>
<td>Cagniant</td>
<td><em>Chalepozenus brunneas</em> n. sp.</td>
<td>Morocco</td>
<td>Description of ♂, ♀</td>
</tr>
<tr>
<td>1987</td>
<td>Buschinger</td>
<td><em>Leonomyrma</em> Arnoldi 1968 = <em>Chalepozenus</em></td>
<td>Soviet Union (see Arnoldi 1968)</td>
<td>Synonymy of <em>Leonomyrma</em> with <em>Chalepozenus</em></td>
</tr>
<tr>
<td>1987</td>
<td>Ehrhardt</td>
<td><em>C. muellerianus, insubricus, kutteri, siciliensis</em></td>
<td>(Known localities, see above)</td>
<td>Abstract on biologically relevant new behavioral and karyological data.</td>
</tr>
</tbody>
</table>
ant genus *Formicoxenus* (Francœur et al. 1985), or the slave-maker genus *Epipyrrma* (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. trumieri* 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, *Leonymyrma 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 *Leonymyrma 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
species and populations investigated by us exhibit this behavior (EHRHARDT 1987). CAGNIANT (1985) described C. brunnus 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 Cheilia (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 nivealis, 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 Leptothenax cf. marocanus 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.


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).


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, berlandii, 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 Chaelpoxenus "close to gibbodai" 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. Perin in litt., det. Perin, 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.


3: Surroundings of Madrid (Spain). One colony C. kutteri with L. rabaudi (?), one colony with L. exilis (Acosta Salmerón 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. Martínez 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.


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). Perp (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. "gibbodai" at elevations of 450—1,400 m with host species L. interruptus, nigriceps, pyrenaenus, 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. nigriceps*, near Vassieux-en-Vercors (1,060 m). Two of the colonies in addition contained *L. interruptus* slaves. No Chalepzenus 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, Ormea, and Chiappa. Nests were found in dry walls. A record of Le Masne (1970a) of a Chalepzenus "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. tuberum* ♀♀. 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 Chalepzenus 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) (1; CH), 78 colonies of Chalepzenus 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, Bargo) (Italy). 134 colonies of *Chalepzenus 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 Chalepzenus 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 Chalepzenus muellerianus (?) colonies all containing exclusively *L. (T.) recedens* as host-species (leg. det. Buschinger et al., IX. 1983).

12: Ljubač (near Zadar, Yugoslavia). 4 Chalepzenus muellerianus (?) colonies, all with exclusively *L. flavicornis* as host-species (leg. det. Buschinger et al., IX. 1983). *L. exilis*, *lichtensteinii*, 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 Chalepzenus muellerianus (?) colonies in the vicinity of Dubrovnik in 1977, one of them with *L. flavicornis*, the other with *L. affinis* as host-species.


14d: Perachora (N of Korinthos, Greece). 17 Chalepozenus 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 Chalepozenus 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 Chalepozenus muellerianus (?) colony with L. exilis, and one incipient colony (only C.-queen) with L. (T.) recedens (leg. det. Buschinger, IV. 1980).


16: Mount Etna (Sicilia, Italy). Type-locality of C. siciliensis Kutter 1973. W. Paarmann had collected 1 θ 6 θ 7 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. triarius (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 Tschwerwenta Siena, ca. 1,500 m. In a karst area beneath a stone. 1 θ 42 θ 43 C. muellerianus (?), host species near L. tuberum (leg. det. B. Seifert, IX. 1982, in litt.).

18: (Not on the map) — E-Kazakhstan, close to Peremetriaia, USSR: Type-locality of C. spinosus (Arnoldi 1968). θ 2 described, no θ 7 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 Chalepozenus 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 Chalepozenus 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 Chalepozenus 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 Epimyrma ravouri. 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. muellerianus (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, Epimyrma 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. marocanus Santschi which he had collected in Morocco. L. marocanus 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. racovitzae, one a worker of racovitzae 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.) racovitzaei* 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. racovitzaei* 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

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

*) 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 (1974a) 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. sicutiensis. 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 evaluated. 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 Chalepozenus 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 Chalepozenus. In the Tignale site, and in some others, only Epimyrma kraussei parasitizes L. recedens (Buschinger and Winter 1983); none were found in Chalepozenus nests.

Leptothorax (T.) recedens: In Liguria (pop. 7), we collected 18 C. muellerianus colonies with L. unifasciatus, and one incipient colony with a Chalepozenus queen in a L. recedens nest. Farther to the east, L. recedens is more frequently a host-species of Chalepozenus. 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. nylanderi 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 Myrafant 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 Chalepozenus 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 Epimyrma corsica), L. lichtensteini and L. recedens, but no free-living L. flavicornis colony. On the other hand, no Chalepozenus colony with any other host-species was collected there.

All the other host-species mentioned in Table 2, L. (M.) exilis Emery, L. (M.) tuberum (Fabricius), L. (M.) affinis Mayr, and two undetermined L. (M.) species from Greece and Turkey, respectively, only were found in up to 4 Chalepozenus colonies each. In addition Du Merle (1978) recorded L. (M.) racovitzaei 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 Chalepozenus colonies (calculated from Du Merle 1978, where only percentages of species are given).

Mixed slave populations were recorded in a total of 13 Chalepozenus 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 im-
possible, however, to determine whether or not these colonies belong to the same sam-
ple of 10 colonies recorded in Bernard (1946), with only *L. "nylanderi"*. From pop. 4b) Pyrenées 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. unifasii-
ciatus*. 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*, *flavi-
cornis*, and *lichtensteinii* 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 taxo-
nomic 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 Medi-
terranean, through the northern adjacent countries east to Turkey and to east Ka-
zakhstan (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 (*Lepto-
thorax*, subgenus *Myraptant*) also occurs throughout continental Asia to Japan (Chap-
man 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 ravouxi* (Busching and Winter 1983). In a site near Ossuccio (pop. 9a) we found *Chalepoxenus* and *E. ravouxi*, 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 (Busching 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. "gribodot"*, 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. Mexi (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. grederi*, 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 (Busching 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. grederi*, and 2 *L. acervorum* and *L. grederi* 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 *Epimyrmia* species. In our pop. 9b, Tignale, where *L. unifasciatus* and *L. recedens* occur in about equal densities, this explanation seemingly is correct, in that *Epimyrmia 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 were 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 *Leptothetaox* (*Leptothetaox*) 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. (Temnothetaox) 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 *Leptothetaox*.

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.


398 Zool. JB. Syst. 115 (1988) 3
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 sicilienis, konzuspezifisch 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. Perè, B. Seifert, X. Espadaler, H. Cagniant, M. Mei and M. D. Martinez Ibáñez 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


— A social parasite and its slaves. Reports of the DFG, German Research, 2/79 (1979), 10—12.


—and Alloway, T. M.: Sexual behaviour in the slave-making ant, Harpagozenus 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.

---


---


---


---

Description et représentation des trois castes de *Chalepoxenus kutteri* (nov. sp.) (Hyménoptères Formicidae-Myrmicinae). Ins. Soc. 20 (1973), 145—156.

---


---


---


---

**Collingwood, C. A.:** A provisional key to the worker caste. Eos, Rev. Espan. Ent. 52 (1976), 65—95.

---


---

**Du Merle, P.:** Les peuplements de Fourmis et les peuplements d’Arachnides du Mont Ventoux. II. — Les peuplements de Fourmis. La Terre et la Vie, Suppl. 1 (1978), 161—218.

---


---


---


---

**Finzi, B.:** Primo contributo alla conoscenza della fauna mirmecologica delle Venezia Giulia. Boll. Soc. Ent. Ital. 53 (1921), 118—120.

---


---


---

**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* Forest.). Behaviour 52 (1975), 1—37.

---


---


---


---


---


---


---


Received: June 2, 1987

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