

Institut für Zoologie, Fachbereich Biologie, der Technischen Hochschule, Darmstadt, FRG

Sympatric speciation and radiative evolution of socially parasitic ants – Heretic hypotheses and their factual background

By A. BUSCHINGER

Abstract

According to current hypotheses the main types of social parasitism among ants, namely slavery, temporary parasitism, and inquilinism, arose from such features as predation on other ants, or territorial behavior, both presumed precursors of slavemaking, and polygyny, a presumed precursor of temporary parasitism and inquilinism. The latter is believed also to represent a final instar in several evolutionary pathways leading from slavery, temporary parasitism, and xenobiosis to this permanently parasitic, workerless condition. Speciation, the origin of parasitic species from their usually closely related host species, is suggested to occur due to temporary geographic isolation and subsequent transition of one of the newly formed daughter species to parasitism in the nests of the other.

Evidence is presented suggesting that the main types of social parasitism originated independently of each other. 15 ant genera are parasitized exclusively by inquilines, five other genera exclusively by temporary parasites. Only four groups of non-parasitic ant species (*Formica*, *Tetramorium*, *Leptothorax* subgenera *Leptothorax* and *Myrafant*) have parasites of several types each. Within these groups, however, there is little evidence of evolutionary transitions from one type to another. The few exceptions, mainly workerless species of the genera *Epimyrmica* and *Chalepoxenus*, represent parasites which clearly derive from slave-making congeners, but differ from ordinary inquilines in that they eliminate the host colony queens like their actively dulotic ancestors.

The new hypothesis suggests that all forms of interspecific true social parasitism (excluding xenobiosis) originated from a common "preparasitic" stage, a subpopulation of reproductives in polygynous colonies and species, with diverging sexual behavior (near-nest mating vs. swarming) and caste ratios (production of more sexuals vs. workers). Arguments for sympatric speciation are compiled. Various features of the ancestral, and then host species (colony sizes, population density and structure, transition from polygyny to monogyny, etc.), and of the "preparasite" (production of few, or no workers, etc.) may shape the developing parasite to become a slave-maker, inquiline, or temporary parasite. These features usually leave open only one, or in a few genera, several options. The different types of parasitism within one host species group thus may have developed in a radiative manner from the common, prepasitic stage, which explains that independent colony foundation is a common feature of all true social parasites among ants.

Key words: Formicidae – Social parasitism – Evolution – Sympatric speciation

Introduction

Since DARWIN (1859) presented a first hypothesis on the origin of slavery in ants, the evolution of dulosis and other forms of social parasitism between ant species has been discussed by numerous authors. For a recent review of the hypotheses hitherto published see BUSCHINGER (1986). Territorial raiding of conspecific, and later also heterospecific colonies as the basic behavior developing into slave-raiding, is the presently most favored idea, put forward by WILSON (1971, 1975), ALLOWAY (1980) and STUART and ALLOWAY (1982, 1983), whereas DARWIN (1859) had suggested that predation on other ants' brood be the first step leading to slave-making behavior. Both hypotheses, however, provide no explanation for the well-known fact that all true slavemaker species (i. e. those enslaving

foreign ant species) also establish new colonies in a parasitic manner, in colonies of their particular host species.

Other forms of parasitic behavior, mainly temporary parasitism, were believed to originate from polygyny with adoption of young queens in the colonies of the ancestral, free-living species (WASMANN 1908, 1909). Inquilinism or permanent parasitism without dulosis was supposed to evolve convergently from xenobiosis, degenerate dulosis, or via the temporary parasitic route (WASMANN 1908, 1909; EMERY 1909; WILSON 1971; HÖLLDOBLER and WILSON, 1990) (Fig. 1A).

Speciation, the splitting of a free-living species into a host- and a parasite species, according to WILSON (1971) occurred in the traditional way, the range of a given species being subdivided through a geographical barrier, and after subsequent overlapping of the ranges of the two newly formed daughter species one of them becomes the parasite of the other (Fig. 1B).

BUSCHINGER (1970) suggested a direct origin of all kinds of parasitic ants (except the xenobiotic or guest ants) from polygynous populations of independent (= non-parasite) species which then become the host species. This hypothesis involves sympatric speciation, the genetic isolation of a parasitic genotype from the gene-pool of the independent species, without prior geographic isolation. It was questioned therefore by several authors (ALLOWAY 1980; HÖLLDOBLER and WILSON 1990), but others agreed (ELMES 1978; PEARSON 1981; BOURKE and FRANKS 1987, in press) and similar ideas had been put forward already by former authors (WASMANN 1909; KUTTER 1969). WEST-EBERHARD (1986, 1987) discussed the possible origin of "novel phenotypes, such as social parasitism, as facultative intraspecific alternatives rather than new branches on a phylogenetic tree".

In this paper, I will provide some further empirical evidence speaking much in favor of the hypothesis of a sympatric speciation of socially parasitic ants, from their later host species. Both host and parasitic species, of course, then may undergo further speciation, and a change to additional host species is not always unlikely. In addition, I will consider the possibility of a "radiative" evolution of the various forms of social parasitism out of a common "preparasitic" stage. This hypothesis is partially reversing WILSON's (1971) scheme.

For convenience an annotated systematic survey of the ant taxa mentioned in this article is presented in the appendix.

The types of social parasitism among ants

Traditionally three or four different forms of parasitic relations between ants are distinguished. They shall be briefly characterized in the following.

Xenobiosis

The so-called guest-ants are living together with usually quite unrelated host species. The well investigated myrmicine genus *Formicoxenus* (FRANCOEUR et al. 1985), thus comprises a number of species living in nests of a different subfamily, the Formicinae, whereas others coexist with *Myrmica* species. They have to be mentioned here only because in WILSON's scheme (Fig. 1A) they form a possible intermediate stage to true inquilinism. The origin of xenobiosis from plesiobiosis, the frequent casual nesting of two species in close vicinity, is quite plausible.

Temporary parasitism

This term characterizes relations where the parasitic species is dependent upon its host species only during the time of colony foundation. A parasitic young queen enters a host

colony, kills or replaces by other means the host species queen, and is accepted by the host workers. From the parasitic queens' eggs a workforce of this species is reared, the host workers die out, and an independent, pure colony of the parasitic species is formed. This kind of parasitism has evolved, certainly convergently, in the subfamily Dolichoderinae, the Myrmicinae, and it is most frequent among the Formicinae. In the *Formica* group temporary parasitism in most species is combined with polygyny and polydomy.

For clarity I do not follow GAULD and BOLTON (1988), who define "temporary parasitism is where the worker caste is retained"; hereby the slave-makers are included within this group, though by far most of them are permanently dependent upon their host or slave species.

Dulosis or slavery

Together with the following group, the slave-making ants are parasitic during all their lifetime. With the exception of one group, *Raptiformica* spp., they are unable to survive without slaves. Typically the – often morphologically specialized – slavemaker workers raid upon neighboring nests of their hosts species, capture brood stages and carry them back to the own nest. From the foreign pupae, host- or slave-workers emerge which then care for their "masters", forage, feed the slavemakers' brood and so on. It is important to note that all slave-making species establish their colonies in a similar way as the temporary parasites, i. e. the young queens penetrate a slave species nest, kill or drive off the queen(s) and often also the adult workers, and obtain their first slaves from workers emerging from the brood of that nest.

Dulosis, like temporary parasitism, has evolved several times independently, at least once among the Formicinae and polyphyletically 5 to 6 times in the Myrmicinae (ALLOWAY 1980).

Permanent parasitism without dulosis

This group sometimes is also termed the "inquilines", however, it evidently comprises a variety of life habits which may have different phylogenetic origins. Clearly this inquilinism is the most frequent form of social parasitism. In the list of HÖLLDOBLER and WILSON (1990) about 80 inquiline species are noted, ca. 65 temporary parasites, 55 slavemakers, and 10 xenobiotic species. Exact numbers cannot be provided since in some cases the type of parasitism is not yet clearly documented, and in several groups a number of species will certainly fall into synonymy when carefully examined.

Characteristic for nearly all of the inquilines is their coexistence with the host species queens. Usually they also have the worker caste reduced, most species being workerless. Inquilinism is found in the primitive subfamily Myrmecinae, in several genera of Myrmicinae, and in the Formicinae.

Current hypotheses on the origin of slavery and social parasitism

An important trait of practically all temporary and permanent parasites including the slave-makers is their always close relationship to the respective host species. There are a few exceptions, such as *Rhoptromyrmex mayri*, a tetramoriine once found in a *Pheidole* nest (Pheidolini), and *R. schmitzi*, one female found in a *Tapinoma* colony (Dolichoderinae) (BOLTON 1986a). Both are supposed to be inquilines, but this appears quite questionable. EMERY (1909) formulated what was later (LE MASNE 1956) termed "Emery's rule": The dulotic and the temporarily as well as the permanently parasitic ants all descended from closely related forms which serve them as slaves or host species". This rule is not strictly applicable, particularly in such instances where a number of parasitic species evidently from a monophyletic genus, or where one dulotic species enslaves two or three

host species together. This restriction has been made already by WASMANN (1909, p. 702). However, EMERY was right insofar as for any group of interrelated parasitic species the most closely related outgroup of independent ants comprises their host species. We may conclude that generally a certain host species genus or subgenus gave rise to its particular parasite group.

The close relationships between parasitic ant species and their hosts, and the frequent convergent evolution of similar life habits in distant genera, tribes and even subfamilies, must mean that there exist certain widespread traits in the ordinary behavior of non-parasitic ants which time and again develop towards parasitic relations (BUSCHINGER 1970). Evidently the most favored of these behaviors are 1. predation on other ant species, 2. territoriality between conspecific colonies, and 3. polygyny, usually combined with polydomy. All three behaviors are quite common in the various subfamilies, and they all correspond to certain features of parasitic ants. Most of the serious hypotheses on the evolution of ant parasitism thus refer to one or the other of these fundamental behaviors, or a combination of them, as the basis for the development of parasitic life habits.

1. DARWIN (1859), with reference to the then known slavery of *Polyergus* and *Raptiformica*, hypothesized that the first step in the evolution of their dulotic behavior was predation of an ancestral *Formica* on nests of other ants. Pupae of other *Formica* species which by chance were not consumed could eclose to become workers. These were integrated into the predators' colonies, and became useful as additional workforce.

Selection would have favoured colonies gaining ever more slaves by this means, and apparently the facultative slavery of the subgenus *Raptiformica* was a nice intermediate stage in the evolution of the highly specialized genus *Polyergus* the species of which are absolutely dependent upon their slaves.

One major argument against this "predation hypothesis", however, is the fact that slavery did not evolve among those groups of ants which are particularly specialized predators of other ants, such as the tribe Cerapachyini, some *Myrmecia*, *Gnamptogenys*, and several army ant species (HÖLLDOBLER and WILSON 1990). *Cerapachys* (HÖLLDOBLER 1982) and *Sphinctomyrmex* (BUSCHINGER et al. 1990) store captured ant brood over days or weeks in their nests, but then consume them all.

2. Territoriality is often observed among neighboring conspecific colonies (HÖLLDOBLER 1979). A dominant colony may invade a weaker one, kill the adults and rob their brood. From such brood items again workers may develop which join the workforce of the dominant colony. HÖLLDOBLER (1976) describes in detail such "intraspecific slavery" in *Myrmecocystus*. WILSON (1975), ALLOWAY (1979, 1980) and STUART and ALLOWAY (1982, 1983) put forward the hypothesis that interspecific dulosis originated from such intraspecific slavery.

3. About one half of all ant species investigated for polygyny exhibit this character, at least facultatively. In many species monogynous (one reproductive queen) and polygynous colonies (more, perhaps many fully functional queens) occur within one and the same population, other species are always polygynous (BUSCHINGER 1974a). Polygyny may be a consequence of pleometrosis, the founding of a new colony through more than one queen. More frequently, however, young queens are later accepted in already existing polygynous or perhaps also monogynous colonies. Often a polydomy results, the colony inhabits several neighboring nest sites, and sometimes daughter colonies with some queens branch off and may interrupt the contacts to the mother colony (ROSENGREN and PAMILO 1983).

The adoption of newly inseminated queens in existing conspecific colonies resembles the events when young queens of social parasites,inquilines, temporary parasites or slavemakers, invade their host species colonies. Several authors, including WASMANN (1908, 1909), WHEELER (1910), KUTTER (1969), ALLOWAY et al. (1982), ELMES (1973, 1978), BOLTON (1986a) and BUSCHINGER (1970, 1986) therefore speculated that polygyny might

be the precursor of social parasitism. After all, this hypothesis is the only one providing an explanation for the non-independent colony foundation of all true social parasites.

For the evolution of slavery, BUSCHINGER (1970) suggested a hypothesis based on behaviors observed in polydomous colonies, where brood and adults often are carried from one nest to the other. I shall return to this idea in detail later on.

A more or less separate problem is the question of how the speciation event occurred, whereby the parasite species was differentiated from the ancestral, and later host species. In principle, all the three evolutionary pathways as discussed above, need not violate the rule of allopatric speciation. 1. Predation a priori occurs between already distinct species, and the most closely related species are particularly preadapted to coexist as slave-maker and slave, respectively, once this behavior is established. 2. Intraspecific territorial behavior may be extended to raiding of related sympatric species. And 3. gathering brood stages from neighboring conspecific nests, belonging to the same supercolony, also might be extended to "raiding" on conspecific, but less familiar nests of a neighboring supercolony, or on nests of a closely related, distinct species. It is even conceivable that young queens of a polygynous species sometimes, and occasionally even successfully, may penetrate a nest of a related species.

There are, however, some serious arguments against these possibilities, and much of the observations on parasitic ants are easier explained with the assumption of a sympatric origin of parasitic species directly from the later host species.

Thus, we do not know of any instance where the ranges of two most closely related species partially overlap, the species being in parasitic relations in the contact zone, and free-living in the remainder of their ranges. On the other hand, there are a few cases in the genus *Myrmica*, where small females, "microgynes", occur together with "macrogynes" in the same polygynous nest. Some such microgynes (*M. microgyna*, PEARSON 1981; *M. hirsuta*, ELMES 1978) have been described already as separate, parasitic species. In other instances the microgynes are still believed to belong to the same species as the queens of ordinary size (*M. ruginodis*, ELMES 1976, 1987; PEARSON 1981; *Leptothorax longispinosus*, HERBERS 1984). PEARSON (1981) speculates that the interactions of the macrogyne and microgyne forms of *Myrmica ruginodis* "may provide information about the early or pre-parasitic condition".

Before going into details, however, let us first consider some quite recently investigated examples, where we are able in fact to trace evolutionary processes in groups of socially parasitic ants.

Apparent evolutionary pathways within parasitic ant groups

The first example refers to the genera *Epimyrma* and *Myrmoxenus* where we can identify an evolutionary progression from one of the traditional types of parasitism, dulosis, to a derived type which may or may not be termed "inquilinism".

The myrmicine genus *Epimyrma* presently comprises about 10 species. All of them are parasites of *Leptothorax* (subgenus *Myrafant* SMITH 1950 sensu BOLTON 1982). *Myrmoxenus gordiagini* is a species sharing many characters with *Epimyrma* and it should presumably be included in the latter. We have studied the life history, morphology and social organization of most of these species (BUSCHINGER et al. 1983, 1986; DOUWES et al. 1988; JESSEN 1987; WINTER and BUSCHINGER 1983). They all share an identical karyotype which was not found in 39 *Myrafant* species investigated, including the respective host species (FISCHER 1987). The colony foundation of the young queens involves a conspicuously derived behavior also shared by all 8 species investigated including *M. gordiagini*: The parasitic queen, after having penetrated a host species colony, throttles the host queen with her mandibles around the neck or throat over a prolonged period, until she is dead. In all species the parasite queen, if she succeeds, is accepted by the adult host workers.

Table 1. Evolution from slavemakers to workerless "murder-parasites" in the probably monophyletic group *Epimyrma* and *Myrmoxenus*

Species	Mating flight (MF) or adelphogamy (A)	Colony foundation with throttling	Slave raids	Number of parasite workers
1. <i>E. ravouxi</i> (= <i>goesswaldi</i>)	MF	+	+	high
2. <i>E. stumperi</i>	MF	+	+	high
3. <i>Myrmoxenus</i> (= <i>Epimyrma</i> ?) <i>gordiagini</i>	MF	+	+	high
4. <i>E. algeriana</i>	A	+	+	high
5. <i>E. bernardi</i>	A	+	+	moderate (?)
6. <i>E. kraussei</i> (= <i>foreli</i> , = <i>vandeli</i>)	A	+	(+)	low or none
7. <i>E. corsica</i>	A	+	-	none
8. <i>E. adlerzi</i>	A	+	-	none

Among the *Epimyrma* species we observed two evolutionary trends: One is a reduction of the number of *Epimyrma* workers, and a transition from active dulosis to a workerless permanent parasitism. The other concerns sexual behavior, with mating flights predominating in the slave-making species (*E. algeriana* and *E. bernardi* are exceptions), and adelphogamy within the mother nest in the "degenerate slave-makers" and workerless parasites (Tab. 1) (for more details see BUSCHINGER 1989).

This example clearly demonstrates an evolution from one of the classic types of social parasitism, dulosis, to another type, within one most probably monophyletic group. The ultimate condition, however, is different from most known examples of inquilinism in that *E. corsica* and *E. adlerzi*, both workerless, do not coexist with the host species queens, but assassinate them like their dulotic relatives do.

The second example, also from the myrmicine tribe Leptothoracini, is the genus *Chalepoxenus* (BUSCHINGER et al. 1988, 1989; CAGNIANT 1985; EHRHARDT 1987). In this genus which mainly comprises active slavemakers parasitizing *Leptothorax* species, we recently found evidence that one species, *C. brunneus*, has evolved towards a workerless parasitism (Tab. 2). As in *Epimyrma*, the colony foundation behavior remains fairly unaffected, the *C. brunneus* queen eliminates the host queen, as her dulotic congeners do. One major difference is that the dulotic *Chalepoxenus* queens kill or drive off all adult workers, too, whereas the *C. brunneus* queen stings only few of her host workers, and somehow is accepted by the others.

A third example, again represented by members of the tribe Leptothoracini, is different in that a clearly demonstrable evolutionary trend cannot be found. The four parasites of a common host species, *Leptothorax acervorum*, all exhibit different strategies. Nevertheless

Table 2. Evolution from slavemakers to a workerless "murder-parasite" in the genus *Chalepoxenus*

Species	Mating flight (MF) or adelphogamy (A)	Colony foundation with elimination of host ♀	Slave raiding	Number of parasite workers
1. <i>C. muellerianus</i> (= <i>gribodoi</i>)	MF	+	+	high
2. <i>C. insubricus</i> (? = <i>muellerianus</i>)	MF	+	+	high
3. <i>C. siciliensis</i> (? = <i>muellerianus</i>)	MF	+	+	high
4. <i>C. kutteri</i>	MF	+	+	high
5. <i>C. brunneus</i>	MF + A	+	-	none

Table 3. The four social parasites of *Leptothorax acervorum*
A linear evolutionary order cannot be established

	<i>L. acervorum</i>	<i>D. kutteri</i>	<i>D. goesswaldi</i>	<i>D. pacis</i>	<i>H. sublaevis</i>
Life habits	Independent, facultatively polygynous	Inquiline, facultatively polygynous	Parasitic, kills host queens, monogynous	Parasitic, sterilizes (?) host queens, monogynous	Dulotic monogynous
Morphological similarity	1	2	3	4	5
Karyotypes	n=13 (1)	n=23 or 25 (3)	n=ca. 28 (5)	n=26 (4)	n=20 (2)
Interspecifically effective ♀ sex-pheromone		x	x	x	x
Hybridization possible		x	x	x	x
<i>L. acervorum</i> : Host species (for <i>H. sublaevis</i> also <i>L. muscorum</i> and <i>L. gredleri</i>), <i>Doronomyrmex goesswaldi</i> , <i>D. kutteri</i> , <i>D. pacis</i> : Workerless parasites, <i>Harpagoxenus sublaevis</i> : Slave-maker.					

they all, according to EMERY's rule, should be closely related to the host species, and thus also among each other. Morphological, karyological and ethological evidence support this assumption (Tab. 3).

1. *Harpagoxenus sublaevis* is an actively dulotic species with a life history similar to that of *Chalepoxenus*, except for a different fighting technique: With secateur-like mandibles it cuts off the appendages of the host species workers when invading a colony for slave-raiding, or colony foundation. Apart from *L. acervorum* which is the most frequent host species, also *L. muscorum* and *L. gredleri* are enslaved.

A closely related North American species, *H. canadensis*, has a number of ill-defined slave species belonging to the *L. muscorum*-complex (BUSCHINGER 1966, 1968; BUSCHINGER et al. 1980; STUART and ALLOWAY 1983).

2. *Doronomyrmex kutteri* is a typical inquiline; it is workerless, and usually several reproductive queens coexist with the *L. acervorum* queens in a nest. Morphologically, *D. kutteri* has few particularities, it closely resembles the host species (BUSCHINGER 1965; ALLIES et al. 1986).

3. *Doronomyrmex goesswaldi* for a long time was believed also to represent a workerless inquiline living together with the host queens in polygynous *L. acervorum* colonies (BUSCHINGER 1974b). Recent field and laboratory results, however, revealed that the *D. goesswaldi* queen, soon after mating in August, penetrates a host colony, and during the next spring, while developing fertility, she slowly kills the colonies *L. acervorum* queens by cutting off their appendages. *D. goesswaldi*, thus, follows a similar strategy as *Epimyrma* which throttles the host queens to death. No *goesswaldi* workers, however, are produced, and the species therefore is not a slave-maker (BUSCHINGER and KLUMP 1988). It may be termed a "murder-parasite" in the sense of FABER (1969).

4. *Doronomyrmex pacis* apparently represented a third inquiline of *L. acervorum*. It is usually found coexisting with host species females which, when dissected, prove to be inseminated, and corpora lutea in their ovaries show that they are, or at least were, functional queens. Often also host species sexuals are produced alongside of the parasites' offspring (BUSCHINGER 1971; BUSCHINGER et al. 1981). Recent observations of two colonies, however, revealed that the *acervorum* queens in nests infested by *D. pacis* apparently have a quite reduced fertility, without being physically damaged (BUSCHINGER unpubl.). Host species sexuals are reared for one or two years after the invasion of a colony by

D. pacis, from larvae which are still present. In this group of Leptothoracini the larvae usually hibernate once, and often twice, before pupation.

In Table 3 these species are arranged according to decreasing overall morphological similarity with the host species, *L. acervorum*. *D. kutteri* and *D. goesswaldi* could be interchanged, being about equally similar to the host species. *D. pacis* with a glossy cuticle and a longer postpetiolar spine is clearly more different, and *H. sublaevis* is very distinct because of its large head, antennal scrobes, toothless secateur-like mandibles and very marked petiolar and postpetiolar appendages.

With reference to karyotypes a parallel sequence cannot be found. *H. sublaevis* has the lowest chromosome number ($n = 20$) among the parasites. *D. kutteri* may have a haploid number of 23 or 25, depending upon the population (FISCHER 1987). *D. pacis* has $n = 26$, and for *D. goesswaldi* the exact number could not yet be ascertained, but is close to $n = 28$. I do not intend to suggest a linear evolutionary increase or decrease of chromosome numbers in this group, however, the parasites in general have higher numbers than the species of the host group, subgenus *Leptothorax* s. str.: *Harpagoxenus canadensis* with $n = 18$ has the same number as one of its host-species of the *L. muscorum*-group, others of this group have $n = 17$ and $n = 15$. Among the slaves of *H. sublaevis*, *L. muscorum* has $n = 17$ and *L. gredleri* $n = 11$, less than *L. acervorum* with $n = 13$ (FISCHER 1987).

The available evidence thus does not speak well for a descent of the workerless *Doronomyrmex* parasites from the slavemaker *Harpagoxenus*, this being different from the *Epimyrma*/*Chalepoxenus* case. The opposite way, an evolution of the slave-maker from an already workerless parasite, also appears improbable.

Table 4. The four known ant groups comprising "clusters" of social parasites which represent different types of parasitism

Host-species group	Inquilines	Temporary parasites	Slave-makers	"Degenerate" forms
<i>Formica</i> sensu lato (incl. <i>Serviformica</i>)	<i>F. talbotae</i> <i>F. dirksi</i>	<i>F. rufa</i> (obligatory) <i>F. lugubris</i> , <i>aquilonia</i> and others (facultative) <i>Coptoformica</i> spp.	<i>Polyergus</i> spp. (obligatory) <i>Rossomyrmex</i> (obligatory) <i>Raptiformica</i> spp. (facultative)	
<i>Tetramorium</i>	<i>T. microgyna</i> <i>T. parasiticum</i> <i>Teleutomyrmex schneideri</i>	-----?	<i>Strongylognathus</i> spp.	<i>S. testaceus</i> <i>Anergates atratulus</i>
<i>Leptothorax</i> (<i>Myrafant</i>)	<i>L. minutissimus</i>		<i>L. duloticus</i> <i>Protomognathus americanus</i> <i>Epimyrma</i> spp. <i>Myrmoxenus gordiagini</i> <i>Chalepoxenus</i> spp.	<i>E. kraussei</i> , <i>E. corsica</i> <i>E. adlerzi</i> <i>C. brunneus</i>
<i>Leptothorax</i> (<i>Leptothorax</i>)	<i>Doronomyrmex kutteri</i> <i>L. faberi</i> <i>Doronomyrmex goesswaldi</i> ¹ <i>D. pacis</i> ¹ <i>D. pocahontas</i> ¹		<i>Harpagoxenus sublaevis</i> , <i>H. canadensis</i> (<i>H. zaisanicus</i> presumably = <i>sublaevis</i>)	

¹ *Doronomyrmex goesswaldi* and *D. pacis* are no typical inquilines, see text. – *D. pocahontas* in laboratory culture produced numerous workers, its state is unsettled as yet.

Nevertheless, the four parasites are closely related among each other, more closely than with their common host, *L. acervorum*, and they probably form a monophyletic group (which includes *H. canadensis*, too). This is indicated, in addition to the high chromosome numbers, by a number of common characters, each of them alone not being conclusive, but in their totality they are quite suggestive. Thus, all the four parasites possess a ventral postpetiolar spine, an enlarged DUFOUR's gland, and grey wing buds in the pupal instar as compared to white ones in *L. acervorum*. The females of all four exhibit a stationary sexual calling behavior, whereas *L. acervorum*, at least in Europe, makes mating flights. Finally, they are linked by a partial interspecific effectivity of the female sexual pheromones, and I obtained hybrid females from crossbreeding *D. kutteri* with *D. goesswaldi* and *D. pacis*, respectively (BUSCHINGER 1972, 1975, 1981).

The "clusters" of social parasites each belonging to one group of host species (genus or subgenus) and representing different types of parasitic relations are listed in Table 4. Apart from the abovementioned two groups parasitizing the two *Leptothorax* subgenera we find such a situation with *Tetramorium*, having slave-making (*Strongylognathus*) and inquiline (*Teleutomyrmex*, *Tetramorium*, *Anergates*) parasites, and very markedly with *Formica*. In the latter group, three types are represented, namely inquilinism, temporary parasitism, and dulosis.

In three of these four groups a linear phylogenetic order is not perceptible, apart from a few "degenerate" forms which are easily derived from one of the main types, such as the "degenerate slave-makers" in *Epimyrma* and *Chalepoxenus* or *Strongylognathus testaceus*, and perhaps *Anergates* which might represent an inquiline having secondarily specialized on the exploitation of already orphaned *Tetramorium* colonies. In the *Formica* group one might speculate that the temporary parasites represent the ancestors of the dulotic species (WASMANN 1909), however, there is as yet little empirical evidence for this assumption. And whether or not the two inquilinous *Formica* species are descendants of dulotic or temporary parasitic ancestors also cannot yet be decided.

Evidence for the independent origin of inquilines, temporary parasites, and slave-makers in various ant groups

Going through the list of socially parasitic ants in WILSON (1971) or HÖLLDOBLER and WILSON (1990), it becomes evident that the clusters shown above are in fact exceptional. If WILSON's scheme (Fig. 1A) was right, we should expect to find inquilines predominantly in groups where one or more of the other types of parasitism, the presumed predecessors of inquilines, occur. This, however, is by no means realized. Table 5 reveals that no less than 15 systematically scattered genera of ants are parasitized exclusively by inquilines. In five other genera only temporary parasites but no inquilines or slave-makers are met with, and but one questionable case of an isolated slave-maker (*Nothidris*) is recorded (HÖLLDOBLER and WILSON 1990).

Xenobiosis is restricted to three genera, namely *Monomorium* with one questionable instance, *Megalomyrmex* (Solenopsidini) with two species living together with species of the genera *Sericomyrmex* and *Cyphomyrmex* (Attini), and *Formicoxenus*. The latter is closest related to *Leptothorax* s. str. (Myrmicinae), but coexists exclusively with non-related ants of the genera *Myrmica*, *Manica* (Myrmicinae) and *Formica* (Formicinae) (FRANCOEUR et al. 1985). It is hard to derive any inquiline of the host species groups from one of the xenobiotic taxa.

The predominance of "isolated" inquilines (i. e. with no related parasites of any other type) becomes even more significant when we take into account that in some of the host genera listed in Table 5 inquilinism very probably has evolved several times convergently. Thus, WILSON 1984 suggests an independent origin of nine parasites of tropical *Pheidole*

Table 5. Host ant genera parasitized by one type of social parasites exclusively¹
In several genera, e. g. *Pheidole* and *Myrmica*, inquilinism has evolved several times independently (see text)

Only inquilines		Only temporary parasites	
1. <i>Myrmecia</i>	9. <i>Pogonomyrmex</i>	1. <i>Tetraponera</i>	4. <i>Conomyrma</i> ³
2. <i>Pseudomyrmex</i>	10. <i>Acromyrmex</i>	2. <i>Aphaenogaster</i>	5. <i>Lasius</i>
3. <i>Crematogaster</i>	11. <i>Serrastruma</i>	3. <i>Tapinoma</i>	
4. <i>Strumigenys</i>	12. <i>Solenopsis</i>		
5. <i>Manica</i>	13. <i>Anoplolepis</i>		
6. <i>Monomorium</i> ²	14. <i>Camponotus</i>		
7. <i>Myrmica</i>	15. <i>Plagiolepis</i>		
8. <i>Pheidole</i>			

¹ After HÖLLDOBLER and WILSON (1990). – ² One questionable instance of a xenobiotic *Monomorium noualhier* living with *M. subnitidum*, is recorded (only one worker of the "guest-ant" has been found, WHEELER 1910). – ³ TRAGER (1988) reports on a kind of temporary slave-making in *Conomyrma medeis* which invades nests of and forms mixed colonies with *C. bureni*; the latter, however, disappear after a while.

species. Similar convergent evolution of several inquiline species or species groups may have occurred in *Monomorium*, *Myrmica* (BOLTON 1988), and *Plagiolepis*. This assumption is not improbable, taking into consideration that within the Leptothoracini, slavery has evolved at least four, perhaps five times independently (*Harpagoxenus* from subgenus *Leptothorax*; *Epimyrma*, *Chalepoxenus*, *Protomognathus* and *L. duloticus* from subgenus *Myrmica*) (BUSCHINGER et al. 1980; STUART and ALLOWAY 1983).

What are the conclusion thus far?

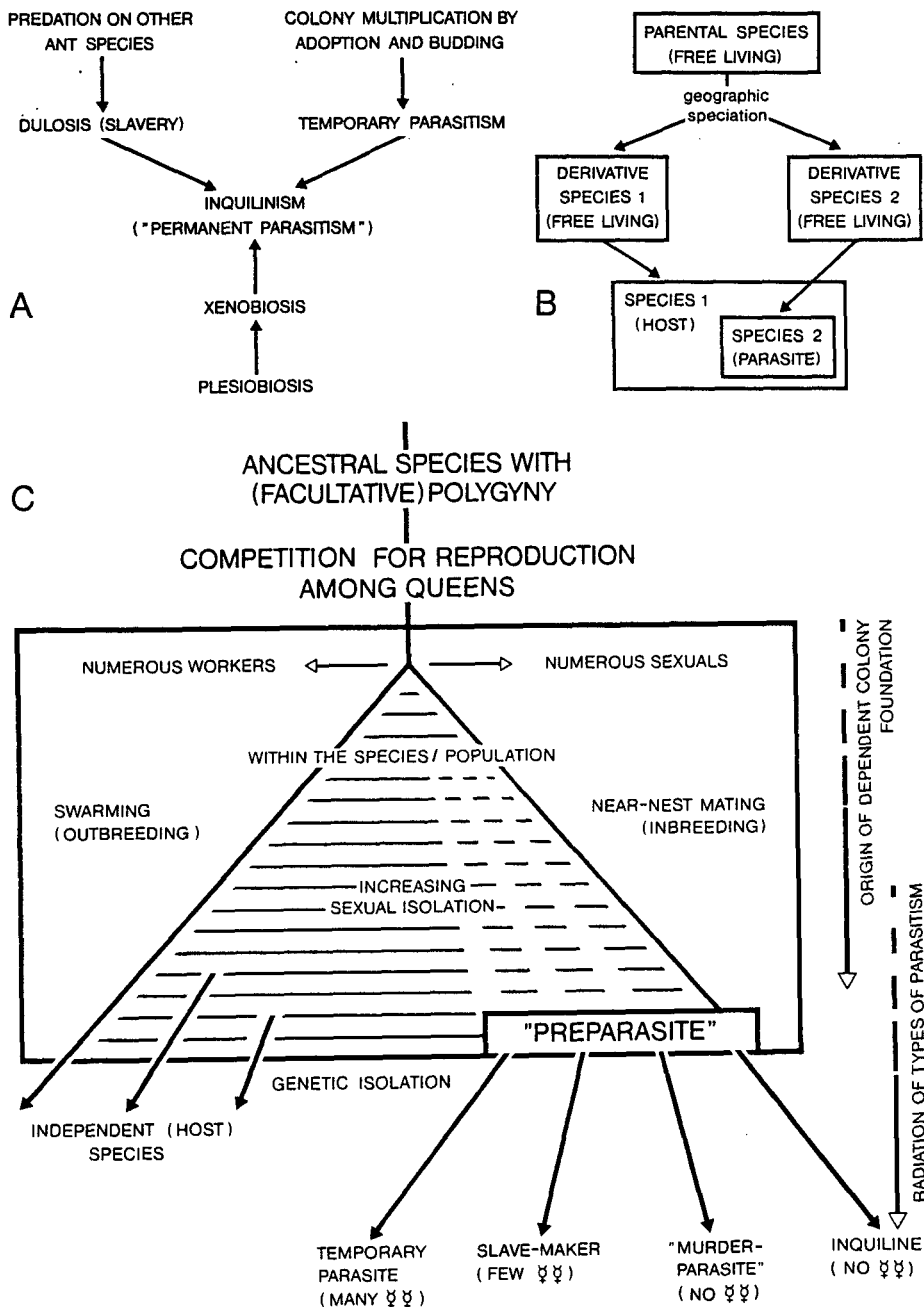
1. Wherever interspecific true social parasitism (except xenobiosis) arose, the various forms of slavery, temporary parasitism and inquilinism very probably evolved independently from each other, inquilinism being the most frequent form.
2. In a few host genera (or subgenera) two or three types of parasitism occur; however, even then there is no conclusive evidence of an evolutionary sequence between the members of different types (the "degenerate slave-makers", Tab. 2 and 3, do not represent true inquilines).
3. All types of true social parasitism are linked by the common feature of parasitic colony foundation of the young queens who penetrate host species nests.

The new hypothesis: Sympatric speciation and radiative evolution of social parasites

With these facts and arguments in mind I hypothesize that all forms of true social parasitism originate from the adoption of conspecific young queens in colonies of (facultatively) polygynous species. The social organization of the ancestral, and later host species group, its variations in space and time, model the emerging parasite to become an inquiline, temporary parasite, or slave-maker.

In most groups of host species apparently but one option, inquilinism, or temporary parasitism, is open. In other groups, e. g. the subgenus *Leptothorax* (Tab. 3), inquilines, "murder"-parasites, and slave-makers evolved in a radiative manner from a common, pre-parasitic stage. Figure 1C presents a scheme of the factors and processes involved according to this hypothesis.

Since the assumption of a sympatric speciation, moreover, the isolation of a preparasitic genotype within a deme and even within the nests of a given non-parasitic species appears quite unusual and unrealistic I have to explain in more detail why I believe in such a possibility.



A: Hypothetical evolutionary pathways of social parasitism in ants (according to WILSON 1971, p. 361); B: Allopatric speciation due to geographic isolation and subsequent transition of one derivative species to parasitism of the other (according to WILSON 1971, p. 360); C: The hypothesis of sympatric speciation and "radiative" evolution of social parasites among ants. Within a polygynous species, or a population of such a species, a subpopulation of reproductives emerges which mate close to, or within the nests. Due to an increasing sexual isolation between the "preparasite" and the original form the genetic differences between the two are growing, until genetic isolation is achieved. Depending upon certain features of the "host" population, and of the "preparasite" the latter has several options to develop into one or the other type of a social parasite. Only rarely more than one type is found in one and the same group (genus or subgenus) of host species

Certainly, the allopatric speciation model (e. g. MAYR 1963; FUTUYMA and MAYER 1980) is the most convincing; parsimonious and well-documented mechanism of species multiplication when solitary forms are considered, or social insects having monogynous colonies.

In polygynous species, on the contrary, where several or even numerous functional queens may coexist in a nest, and where young queens may be recruited into existing colonies every year, a single atypical, "deficient", specimen is well able to survive, and even a certain fraction of "deficient" queens need to immediately lead to a serious handicap or even to the extinction of the colony. Certain hereditary "deficiencies" may well be able to propagate in such conditions. In the sense of WEST-EBERHARD (1986) they may not be "deficiencies", but intraspecific alternative reproductive strategies adapted to varying environmental conditions.

For a better understanding of the following I will recall that numerous ant species or genera, among them those most seriously affected by social parasitism, are forming enormous populations over huge areas, and that locally, again often over considerable areas, very high population densities are found. Thus, *Leptothorax acervorum*, host species of at least four social parasites (see above), has a holarctic distribution with highest population densities (up to four nests per m^2) in arctic and alpine coniferous forests. Also the genera *Formica* and *Lasius* have holarctic ranges with many species found from W-Europe through E-Asia. At present, numerous subpopulations of these species are isolated, e. g. in mountainous areas, or islands, and very probably the degrees of such isolations have changed many times throughout the Pleistocene and in earlier epochs.

A genetic "deficiency" of the kind taken into conservation here may be a disturbance in the caste-determination system, for example causing a higher production of young queens at the cost of worker formation. In a monogynous species such genes for an ill-balanced queen-worker ratio would not spread but quickly be eliminated. In a polygynous species forming polydomous supercolonies such genes should naturally occur, and even quite frequently.

We may expect a general competition for sexual reproduction if there is any genetical variation among conspecific queens coexisting in a colony (WEST-EBERHARD 1981). ROSENGREN and PAMILO 1983 discuss the possibility that some queens might become "cheaters", producing only sexuals at the expense of queens producing supporting workers as well.

Genes for an unbalanced, queen-biased caste ratio in such conditions need not emerge as new mutations, they might just represent atavistic states (cf. ELMES 1976). In primitive ant societies the numbers of workers are lower than in the higher evolved ones, and the workers are usually more queen-like in their morphology. Perhaps the often intermorphous condition of workers in many slave-maker species is due to this fact: In *Harpagoxenus sublaevis*, *Protomognathus americanus*, and *Epimyrma* spp. the ovaries of workers often have as many ovarioles as those of the queens, and in *Chalepoxenus* the workers even possess receptacula. *Epimyrma* and *Myrmoxenus* workers are exceptional among the Myrmicinae in having at least rudimentary ocelli, which usually are present only in queens of this subfamily. And the worker numbers of slave-maker species are generally lower than in related, comparable non-parasitic species.

Let us now assume that a given supercolony of a polygynous, independent ant contains too many "deficient", predominantly queen-producing queens. Its workforce will decrease, and perhaps a neighboring, "sound" population will invade its area. But many young queens bearing the deficient genes can infest this "sound" population. There is no mechanism perceptible which would really eliminate these genes, except for the extinction of the whole species. In nature, it is better conceivable that the frequencies of "normal" and "deficient" genes or genotypes will fluctuate interdependently like predator and prey or host and parasite populations (cf. POOLE 1974).

In general, social parasites very frequently have certain relations to polygyny, either in being (facultatively) polygynous themselves like their host species (manyinquilines, some temporary parasites, e. g. of the genus *Formica*), or in parasitizing polygynous host species (most slave-makers, which themselves are usually monogynous) (BUSCHINGER 1970). This supports the hypothesis of polygyny being favorable for the evolution of dependent nest foundation and parasitism. In fact, BOLTON (1986a, b) terms "autoparasitism" the behavior of young queens seeking adoption in conspecific polygynous colonies, which later reproduce by budding or fission, and WHEELER (1910, p. 439) suggested the idea of a "transition from parasitism of the queen on the same to parasitism on an alien species".

The "deficient" genes causing a queen bias might even be advantageous under certain conditions, for example when colonies with only "normal" queens due to bad nutrition etc. are not able to produce young queens at all. Colonies with queens being heterozygous for (codominant) "deficient" genes may reproduce under these suboptimal conditions, and the "normal" genes are carried on as well. The "deficiency", too high queen production, might also become manifest only as a polygenic effect, whenever "latent deficiency genes" by chance are combined somewhere in the range of a species.

It appears plausible, then, that there are manifold possibilities for certain "deficient" genes to survive and to spread in populations of polygynous species.

The other, more important question is how such deficient genotypes could achieve a partial, and later absolute, isolation within and from the original gene pool. A second phenomenon which is also widespread among polygynous ants, intranidal mating and inbreeding, is apparently involved. In many polygynous species mating occurs within, on top of, or in close vicinity of the mother nest. This may be adaptive in certain ecological conditions. HEINZE and BUSCHINGER (1987) speculate that in some non-parasitic ant species the evolution of flightless, intermorphic queens is due to a selective advantage of mating and remaining within a suitable habitat as compared to swarming and getting lost in the less favorable surrounding area. BOLTON (1986b) similarly discusses the evolution of apterous females in the *Monomorium salomonis*-group.

There are also many reports on ants, e. g. of the genus *Formica*, where sexual offspring from one nest may exhibit diverse behaviors, some mating on top of the nest, others flying off (ROSENGREN and PAMILO 1983). If the tendency to produce fewer workers in favor of sexual production (the "deficient" genes) somehow is linked with the tendency to mate in or on the nest, and for the females to remain there, the genetic condition of an incipient parasite, a "preparasite", is already achieved. This linkage evidently occurs automatically in polygynous species.

Nest-mating provides an at least partial sexual isolation between the swarming phenotypes and those remaining in place. Nest-mating increases inbreeding, and thus the accumulation of "deficient" genes, and it will gradually increase the genetic differences between nest-mating and swarming genotypes.

Other mechanisms may enhance the speciation process. Thus, a conceivable means to produce more sexuals would be to reduce them in size. Smaller sexuals have less reserves for a long mating flight, and the females would be less adapted to independent colony foundation. Both features are not disadvantageous, however, when mating occurs without swarming, and the young queens join existing colonies. And often the inquiline and temporary parasitic ant queens are considerably smaller than the related host species queens.

The "preparasite" may also disperse into distant, and thus genetically somewhat different populations of the "host" species (the huge ranges of host species have been mentioned above; for a general consideration of differences between parapatric subspecies see HEWITT 1988). Or, if we assume a deleterious effect of the "preparasite" on its original "host" population, a less familiar genotype may invade the infested area. Under both conditions the sexual isolation of the "preparasite" increases, finally ending up in a genetic

isolation. The differences between the original population (including the "preparasite") and the "new" host population may refer to sexual pheromones, to preferred mating times and sites, or to size of sexuals, all varying within species with sufficiently large ranges.

The geographic shift of the "host" population, or the spreading of the "preparasite" into other host populations, according to my hypothesis, provides the third important contribution to the formation of a social parasite, together with polygyny and an alternative mating strategy. This step may be responsible particularly for the type of parasitism which originates from the preparasitic condition.

Thus, the "preparasite" may be already completely workerless, or produce only very few workers, the host species remains polygynous, and queens of the new parasite and the (now) host species coexist. A typical inquiline has been formed, which subsequently may more or less diverge morphologically from the host species. Apparently this is the most "easy" and thus most frequent way of origin of a parasite.

As BUSCHINGER (1970) has already suggested, the incipient parasite may still be able to produce a certain, low number of workers. The nests with many "preparasites" in a supercolony will not produce sufficient workers, but may depend upon a net intake of worker brood (pupae) from neighboring nests with more "normal" queens. Brood exchange is not uncommon in polydomous ant species (ROSENGREN and PAMILO 1983). Due to the increasing genetic distance between the "preparasite" and its "host" the colonies with "normal" workers will increasingly resist the pillaging of their brood, and thus may select the "preparasite" workers for becoming more aggressive. When genetic isolation is finally completed, similar as in inquilines, the parasite has become a slave-maker, which will be further selected for higher fighting and raiding effectivity. Of course, the parasitic queens also have to get into host colonies by force, and it is not surprising that they usually fight with the same species-specific techniques as their workers during slave-raids.

When a "preparasite" producing no workers is confronted with a "host" population which is only facultatively polygynous or where a transition to monogyny occurs, the host population may select for more aggressive "preparasite" queens who have to overcome the resistance of host colonies against the adoption of young queens. The parasite does best when eliminating the host colony queen(s), as is observed in the "murder-parasite" *D. goesswaldi* (BUSCHINGER and KLUMP 1988). The fact that the latter species is parasitizing the facultatively polygynous *L. acervorum*, and may eliminate several host species queens in one nest, is not a serious discrepancy in this hypothesis. It may have attained the "murder" behaviour while parasitizing predominantly monogynous populations of *L. acervorum*. In the genus *Epimyrma* we observe a similar phenomenon: Most species coexist with monogynous host species, and throttle their queens to death, but *E. stumperi* is living with a (secondarily?) polygynous host species, and eliminates all host queens met with in a nest (KUTTER 1951).

Finally, the "preparasite" may have lost the capacity to found new colonies independently, but has retained the capacity to produce some workers. The "host" form slowly went over to strict monogyny and monodomy, thus preventing the preparasite to develop slave-making behavior. Like in the case of a "murder" parasite, the "preparasite" still has to invade "host" nests, and it will also be selected for aggressivity resp. for developing a behavior to replace the host queens. Different from a "murder" parasite, however, selection then could favor a higher worker production again, thus forming a temporary parasite.

The origin of temporary parasites is most difficult to understand, and admittedly represents the least conclusive part of this hypothesis. In addition to a switch from polygyny towards monogyny other factors may be involved. Thus, it is striking that temporary parasites usually have high worker numbers, and attack host species with large colonies (*Lasius fuliginosus*, host *L. umbratus*; *Bothriomyrmex* spp., hosts *Tapinoma* spp.), as compared to most slave-makers. Large colonies are difficult to overwhelm for slave-raiding, and they

are usually more dispersed, particularly when monogynous, which would require high numbers of slave-maker workers and imply high costs of search for and exploitation of suitable slave species nests.

The original condition, thus may be identical for incipient slave-makers and temporary parasites, but in the latter case the evolutionary increase of colony size in the hosts may have rendered slave-making more and more difficult. So temporary parasitism and building up an own, functional workforce remained as the only option.

A further problem arises from the existence of the polygynous, facultative temporary parasites in the genus *Formica*. They may either reproduce by budding, or (rarely) found new colonies through single queens who invade colonies of the subgenus *Serviformica*. Most probably the temporary parasitic behavior here represents a relic condition, the typical, monogynous. *F. rufa* exhibiting the original, obligatorily temporary parasitic behavior, and the other species having switched over to polygyny again. In another temporary parasite, *Lasius fuliginosus*, also polygynous and polydomous colonies are known (STITZ 1939), whereas *L. umbratus*, host species of *L. fuliginosus*, and temporary parasite itself (host *L. niger*), is apparently monogynous.

Conclusion

The hypothesis presented here describes an evolutionary scenario which accounts for all known forms of social parasitism among ants, and which interpretes the complete life cycles of the taxa involved. It is quite evident that polygyny plays a crucial role in the evolution of parasitic colony foundation. A sympatric origin of more or less deleterious genotypes dependent upon their ancestral, and erstwhile conspecific, host forms appears conceivable and could well account for the frequent, convergent evolution of parasitic species in various ant subfamilies and genera.

Very little evidence, however, was found supporting the idea that inquilinism be the final step of several evolutionary pathways, via dulosis, temporary parasitism, or xenobiosis. The known facts instead speak in favor of inquilinism being one of four options open to a "preparasite", a subpopulation of reproductives living in dependence upon a polygynous ancestral form, and slightly developing sexual and eventually genetic isolation. During this process various features of the "preparasite" (production of few, or no workers) and of the "host" (colony sizes, nest distances, transition to monogyny, etc.) may shape the developing parasite to become a workerless inquiline, a "murder"-parasite, a slave-maker, or a temporary parasite. From these conditions, as was shown, only rarely an evolution to a derived type of parasitism has occurred. The main types of parasitism, thus should have evolved in a radiative manner out of a common primary stage, the intra-specific "preparasite".

Appendix

Systematic survey of the ant taxa mentioned in the text

Fam. Formicidae	Subfam. Pseudomyrmecinae
	<i>Pseudomyrmex</i> Smith, 1858
	<i>Tetraponera</i> Smith, 1852
Subfam. Myrmeciinae	Subfam. Myrmicinae
<i>Myrmecia</i> Fabricius, 1804	Tribus Myrmicini
Subfam. Ponerinae	<i>Manica</i> Jurine, 1807
Tribus Cerapachyini	<i>Myrmica</i> Latreille, 1802
<i>Cerapachys</i> Smith, 1857	<i>M. hirsuta</i> Elmes, 1978
<i>Sphinctomyrmex</i> Mayr, 1866	<i>M. microgyna</i> Pearson, 1981
Tribus Ectatommini	<i>M. ruginodis</i> Nylander, 1846
<i>Gnamptogenys</i> Roger, 1863	<i>Pogonomyrmex</i> Mayr, 1868

- Tribus Pheidolini
Aphaenogaster Mayr, 1853
Nothidris Ettershank, 1966
Pheidole Westwood, 1841
- Tribus Crematogastrini
Crematogaster Lund, 1831
- Tribus Solenopsidini
Monomorium Mayr, 1855
M. noualhier (Emery, 1895)
M. salomonis (Linnaeus, 1758)
M. subnitidum Emery, 1895
Megalomyrmex Forel, 1884
Solenopsis Westwood, 1841
- Tribus Leptothoracini
Leptothorax Mayr, 1855
 Subgenus *Leptothorax* Mayr, 1855
 (BINGHAM 1903; SMITH 1950)
L. acervorum (Fabricius, 1793)
L. faberi Buschinger, 1982
L. gredleri Mayr, 1855
L. muscorum (Nylander, 1846)
L. muscorum auct. (1)
 Subgenus *Myrafant* Smith, 1950
L. duloticus Wesson, 1937
L. longispinosus Roger, 1863
L. minutissimus Smith, 1942
Doronomyrmex Kutter, 1945
D. goesswaldi (Kutter, 1967)
D. kutteri (Buschinger, 1965)
D. pacis Kutter, 1945
D. pocahontas Buschinger, 1979 (2)
Formicoxenus Mayr, 1855
Harpagoxenus Forel, 1893
H. canadensis Smith, 1939
H. sublaevis (Nylander, 1848)
H. zaisanicus Pisarski, 1963
Chalepoxenus Menozzi, 1922
C. brunneus Cagniant, 1985
C. insubricus Kutter, 1950
C. kutteri Cagniant, 1973
C. muellerianus (Finzi, 1921)
C. siciliensis Kutter, 1973
Epimyrmex Emery, 1915
E. adlerzi Douwes et al., 1988
E. algeriana Cagniant, 1968
E. bernardi Espadaler, 1982
E. corsica (Emery, 1895)
E. kraussei Emery, 1915
E. ravonxi (André, 1896)
E. stumperi Kutter, 1950
Myrmoxenus Ruzsky, 1902
M. gordiagini Ruzsky, 1902
- Protomognathus* Wheeler, 1905 (3)
P. americanus (Emery, 1895)
- Tribus Tetramoriini
Anergates Forel, 1874
A. atratulus (Schenck, 1852)
Rhoptromyrmex Mayr, 1901
R. mayri Forel, 1912
R. schmitzi (Forel, 1910)
Strongylognathus Mayr, 1853
S. testaceus (Schenck, 1852)
Teleutomyrmex Kutter, 1950
T. schneideri Kutter, 1950
Tetramorium Mayr, 1855
T. microgyna Santschi, 1918
T. parasiticum Bolton, 1980
- Tribus Dacetini
Serrastruma Brown, 1948
Strumigenys Smith, 1860
- Tribus Attini
Acromyrmex Mayr, 1865
Cyphomyrmex Mayr, 1862
Sericomyrmex Mayr, 1865
- Subfam. Dolichoderinae
Bothriomyrmex Emery, 1869
Conomyrma Forel, 1913
C. bureni Trager, 1988
C. medeis Trager, 1988
Tapinoma Foerster, 1850
- Subfam. Formicinae
Anoplolepis Santschi, 1917
Camponotus Mayr, 1861
Formica Linnaeus, 1758
 Subgenus *Formica* Linnaeus, 1758
 (Forel, 1913)
F. aquilonia Yarrow, 1955
F. dirksi Wing, 1949
F. lugubris Zetterstedt, 1840
F. rufa Linnaeus, 1758
F. talbotae Wilson, 1977
 Subgenus *Serviformica* Forel, 1913
 Subgenus *Raptiformica* Forel, 1913
 Subgenus *Coptoformica* Müller, 1923
Lasius Fabricius, 1804
L. fuliginosus (Latreille, 1798)
L. niger (Linnaeus, 1758)
L. umbratus (Nylander, 1846)
Myrmecocystus Wesmael, 1838
Plagiolepis Mayr, 1861
Polyergus Latreille, 1805
Rossomyrmex Arnoldi, 1928

The taxonomy of many ant groups is presently under revision. In particular the position of the parasitic genera and species with respect to their more or less closely related host groups is seriously debated. In the tribe Leptothoracini to which I refer much in this paper, clearly a number of paraphyletic taxa exist. There is substantial evidence that the subgenera *Leptothorax* s. str. (with its parasitic genera *Doronomyrmex*, *Harpagoxenus*, and with *Formicoxenus*) and *Myrafant* (with its parasite genera *Epimyrmex*, *Myrmoxenus*, *Chalepoxenus*, *Protomognathus*) constitute two separate evolutionary entities. A formal reorganization of the group, however, is as yet problematical because the position of several other subgenera of *Leptothorax* remains unclear.

1. "*L. muscorum* (Nylander)" is mentioned for North America by numerous authors. It is still doubtful whether this species exists there. Recent investigations reveal a complex of related species, of which *L. retracts* Francoeur, 1986 and *L. sphagnicolus* Francoeur, 1986 have been formally described. *L. spec. A.* (HEINZE and BUSCHINGER 1987) with a queen polymorphism, and several others still have to be described.
2. The status of *D. poahontas* both as a member of this genus and as an inquiline is questionable. No host species queen has ever been found in its colonies, and in laboratory culture numerous workers of the species have been produced (BUSCHINGER, unpubl.).
3. *P. americanus* is presently included in *Harpagoxenus* but evidently belongs to the *Myrafant* group. In HÖLDOBLER and WILSON (1990) it is therefore listed as *Protomognathus* already.

Acknowledgements

Much of the author's field and laboratory studies of socially parasitic ants have been supported by a series of grants of the Deutsche Forschungsgemeinschaft. I am grateful to E. O. WILSON for providing access to the chapter "Symbioses among ant species" of the forthcoming book of HÖLDOBLER and WILSON (1990) "The Ants". The referees and N. P. KRISTENSEN have helped to improve the manuscript considerably with comments and linguistic correction.

Zusammenfassung

Sympatrische Speziation und radiative Evolution sozialparasitischer Ameisen: Häretische Hypothesen und zugrundeliegende Fakten

Entsprechend den derzeit diskutierten Hypothesen entstanden die Hauptformen des Sozialparasitismus bei Ameisen, Sklavenhaltung, temporärer Parasitismus und Inquilinismus, aus bestimmten Verhaltensmustern unabhängiger Ameisen, so der Erbeutung anderer Ameisen zu Nahrungszwecken oder dem Territorialverhalten, die beide als Vorläufer von Sklavenhaltung gelten, und der Polygynie, aus der temporärer Parasitismus und Inquilinismus entstanden sein könnten. Für letzteren wurde auch angenommen, daß er das Endstadium in einer Anzahl getrennter Evolutionsreihen darstelle, die von Sklaverei, temporärem Parasitismus bzw. Xenobiose ausgehend zu diesem permanent parasitischen, arbeiterrlosen Zustand führen. Man nahm an, daß die Speziation, die Entstehung parasitischer Arten aus den ihnen nahe verwandten Wirtsarten, aufgrund vorübergehender geographischer Isolation erfolgte, und daß anschließend eine der neu entstandenen Tochterarten zur Parasitierung der anderen überging.

Es wird gezeigt, daß die Haupttypen des sozialen Parasitismus wahrscheinlich unabhängig voneinander entstanden. 15 Ameisengattungen werden ausschließlich von Inquilinen parasitiert, fünf andere Gattungen ausschließlich von temporären Parasiten. Nur in vier Gruppen selbständiger Ameisen (*Formica*, *Tetramorium* und die *Leptothorax*-Untergattungen *Leptothorax* und *Myrafant*) kommen jeweils mehrere Typen von Sozialparasiten vor. Innerhalb dieser Gruppen gibt es jedoch kaum Hinweise auf phylogenetische Übergänge von einem Typ zum anderen. Die wenigen Ausnahmen, hauptsächlich arbeiterrlose Arten der Gattungen *Epimyrma* und *Chalepoxenus*, sind Parasiten, die sich eindeutig von sklavenhaltenden Verwandten ihrer Gattung ableiten lassen. Sie unterscheiden sich von normalen Inquilinen darin, daß sie die Königinnen der Wirtsvölker eliminieren, so wie die aktiv dulotischen Vertreter ihrer Gattungen.

Entsprechend der neuen Hypothese entstanden dagegen alle Formen des interspezifischen, echten Sozialparasitismus (außer der Xenobiose) aus einem gemeinsamen „präparasitischen“ Stadium, einer Teilpopulation von Geschlechtstieren in polygynen Kolonien und Arten, mit abweichendem Sexualverhalten (Kopula in Nestnähe statt Hochzeitsflug) und unterschiedlichen Produktionsraten von Geschlechtstieren und Arbeiterinnen. Argumente für eine sympatrische Speziation werden dargelegt. Verschiedene Eigenschaften der Ausgangs- und späteren Wirtsarten (Koloniegröße, Populationsdichte und -struktur, Übergang von Polygynie zu Monogynie etc.) ebenso wie des „Präparasiten“ (Produktion von wenigen bzw. keinen Arbeiterinnen etc.) könnten den entstehenden Parasiten so beeinflussen, daß er sich in Richtung Sklavenhalter, Inquilinie oder temporärer Parasit entwickelt. Diese Eigenschaften lassen gewöhnlich nur eine, oder in wenigen Gattungen einige, Möglichkeiten offen. Innerhalb einer Wirtsartengruppe haben sich die verschiedenen Typen von Sozialparasitismus somit in radiativer Weise aus dem gemeinsamen „präparasitischen“ Stadium entwickelt. Dies erklärt, weshalb die abhängige Koloniegründung ein gemeinsames Merkmal aller echten Sozialparasiten unter den Ameisen ist.

Literature

- ALLIES, A. B.; BOURKE, A. F. G.; FRANKS, N. R., 1986: Propaganda substances in the cuckoo ant *Leptothorax kutteri* and the slave-maker *Harpagoxenus sublaevis*. J. Chem. Ecol. 12, 1285–1293.
- ALLOWAY, T. M., 1979: Raiding behaviour of two species of slave-making ants, *Harpagoxenus americanus* (Emery) and *Leptothorax duloticus* Wesson (Hymenoptera: Formicidae). Anim. Behav. 27, 202–210.
- 1980: The origins of slavery in leptothoracine ants (Hymenoptera: Formicidae). The American Naturalist 115, 247–261.
- ALLOWAY, T. M.; BUSCHINGER, A.; TALBOT, M.; STUART, R.; THOMAS, C., 1982: Polygyny and polydomy in three North American species of the ant genus *Leptothorax* Mayr (Hymenoptera: Formicidae). Psyche 89, 249–274.
- BOLTON, B., 1982: Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). Bull. Br. Mus. nat. Hist. (Ent.) 45, 307–370.
- 1986a: A taxonomic and biological review of the tetramoriine ant genus *Rhoptromyrmex* (Hymenoptera: Formicidae). Syst. Entomol. 11, 1–17.
- 1986b: Apterous females and shift of dispersal strategy in the *Monomorium salomonis*-group (Hymenoptera: Formicidae). J. Nat. Hist. 20, 267–272.
- 1988: A new socially parasitic *Myrmica*, with a reassessment of the genus (Hymenoptera: Formicidae). Syst. Entomol. 13, 1–11.
- BOURKE, A. F. G.; FRANKS, N. R., 1987: Evolution of social parasites in leptothoracine ants. In: Chemistry and Biology of Social Insects. Ed. by J. EDER and H. REMBOLD. München: Peperny. 37–38.
- 1990: Alternative adaptations, sympatric speciation, and the evolution of parasitic, inquiline ants. B. J. Linnean Soc. (in press).
- BUSCHINGER, A., 1965: *Leptothorax (Mychothorax) kutteri* n. sp., eine sozialparasitische Ameise (Hymenoptera, Formicidae). Ins. Soc. 12, 327–334.
- 1966: Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hym., Formicidae). I. Freilandbeobachtungen zu Verbreitung und Lebensweise. Ins. Soc. 13, 5–16.
- 1968: Untersuchungen an *Harpagoxenus sublaevis* Nyl. (Hymenoptera, Formicidae). III. Kopula, Koloniegründung, Raubzüge. Ins. Soc. 15, 89–104.
- 1970: Neue Vorstellungen zur Evolution des Sozialparasitismus und der Dulosis bei Ameisen (Hym., Formicidae). Biol. Zbl. 88, 273–299.
- 1971: Zur Verbreitung und Lebensweise sozialparasitischer Ameisen des Schweizer Wallis (Hym., Formicidae). Zool. Anz. 186, 57–59.
- 1972: Kreuzung zweier sozialparasitischer Ameisenarten, *Doronomyrmex pacis* Kutter und *Leptothorax kutteri* Buschinger (Hym., Formicidae). Zool. Anz. 189, 169–179.
- 1974a: Mono- und Polygynie in Insektensozietäten. In: Sozialpolymorphismus bei Insekten. Ed. by G. H. SCHMIDT. Stuttgart: Wiss. Verlags GmbH. 862–896.
- 1974b: Zur Biologie der sozialparasitischen Ameise *Leptothorax goesswaldi* Kutter (Hym., Formicidae). Ins. Soc. 21, 133–144.
- 1975: Sexual pheromones in ants. In: Pheromones and Defensive Secretions in Social Insects. Proc. Symp. IUSSI Dijon 1975, 225–233.
- 1981: Biological and systematic relationships of social parasitic leptothoracini from Europe and North America. In: Biosystematics of Social Insects. Ed. by P. E. HOWSE and J.-L. CLÉMENT. London, New York: Academic Press. 211–222.
- 1986: Evolution of social parasitism in ants. Trends Ecol. Evol. 1, 155–160.
- 1989: Evolution, speciation, and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae). J. evol. Biol. 2, 265–283.
- BUSCHINGER, A.; CAGNIANT, H.; ERHARDT, W.; HEINZE, J., 1989: *Chalepoxenus brunneus*, a workerless “degenerate slave-maker” ant (Hymenoptera, Formicidae). Psyche 95, 253–263.
- BUSCHINGER, A.; EHRHARD, W.; FISCHER, K., 1981: *Doronomyrmex pacis*, *Epimyrma stumperi* und *E. goesswaldi* (Hym., Formicidae) neu für Frankreich. Ins. Soc. 28, 67–70.
- BUSCHINGER, A.; EHRHARD, W.; FISCHER, K.; OFER, J., 1988: The slave-making ant genus *Chalepoxenus* (Hymenoptera, Formicidae). I. Review of literature, range, slave species. Zool. Jb. Syst. 115, 383–401.
- BUSCHINGER, A.; EHRHARD, W.; WINTER, U., 1980: The organization of slave raids in dulotic ants – a comparative study (Hymenoptera; Formicidae). Z. Tierpsychol. 53, 245–264.
- BUSCHINGER, A.; FISCHER, K.; GUTHY, H.-P.; JESSEN, K.; WINTER, U., 1986: Biosystematic revision of *Epimyrma krausseii*, *E. vandeli*, and *E. foreli* (Hymenoptera: Formicidae). Psyche 93, 253–276.
- BUSCHINGER, A.; KLUMP, B., 1988: Novel strategy of host-colony exploitation in a permanently parasitic ant, *Doronomyrmex goesswaldi*. Naturwissenschaften 75, 577–578.

- BUSCHINGER, A.; PEETERS, C.; CROZIER, R. H., 1990: Life pattern studies on an Australian *Sphinctomyrmex*: functional polygyny, brood periodicity and raiding behavior. *Psyche* 96, 287–300.
- BUSCHINGER, A.; WINTER, U.; FABER, W., 1983: The biology of *Myrmoxenus gordiagini* Ruzsky, a slave-making ant (Hymenoptera, Formicidae). *Psyche* 90, 335–342.
- CAGNIANT, H., 1985: Contribution à la connaissance des fourmis marocaines: *Chalepoxenus brunneus* n. sp. (Hymenoptera, Myrmicidae). *Nouv. Rev. Ent. (N.S.)* 2, 141–146.
- DARWIN, C. R., 1859: On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. 1st ed. London: J. Murray.
- DOUWES, P.; JESSEN, K.; BUSCHINGER, A., 1988: *Epimyrmica adlerzi* n. sp. (Hymenoptera: Formicidae) from Greece: Morphology and life history. *Entomol. scand.* 19, 239–249.
- EHRHARD, W., 1987: Biosystematics of the slavemaking ant genus *Chalepoxenus*. In: *Chemistry and Biology of Social Insects*. Ed. by J. EDER and H. REMBOLD. München: Peperny. 39–40.
- ELMES, G. W., 1973: Miniature queens of the ant *Myrmica rubra* L. (Hymenoptera, Formicidae). *The Entomologist* 106, 133–136.
- 1976: Some observations on the microgyne form of *Myrmica rubra* L. (Hymenoptera, Formicidae). *Ins. Soc.* 23, 3–22.
- 1978: A morphometric comparison of three closely related species of *Myrmica* (Formicidae), including a new species from England. *Syst. Entomol.* 3, 131–145.
- 1987: Temporal variation in colony populations of the ant *Myrmica sulcinodis*. *I. J. Anim. Ecol.* 56, 559–571.
- EMERY, C., 1909: Über den Ursprung der dulotischen, parasitischen und myrmekophilen Ameisen. *Biol. Centralbl.* 29, 352–362.
- FABER, W., 1969: Beiträge zur Kenntnis sozialparasitischer Ameisen. 2. *Aporomyrmex ampeloni* nov. gen., nov. spec. (Hym. Formicidae), ein neuer permanenter Sozialparasit bei *Plagiolepis vindobonensis* Lomnicki aus Österreich. *Pflanzenschutz Ber.* 39, 39–100.
- FISCHER, K., 1978: Karyotypuntersuchungen an selbständigen und sozialparasitischen Ameisen der Tribus Leptothoracini (Hymenoptera, Formicidae) im Hinblick auf ihre Verwandtschaftsbeziehungen. Darmstadt, PhD thesis.
- FRACOEUR, A.; LOISELLE, R.; BUSCHINGER, A., 1985: Biosystematique de la Tribu Leptothoracini (Formicidae, Hymenoptera). 1. Le Genre *Formicoxenus* dans la Région Holarctique. *Naturaliste can.* 112, 343–403.
- FUTUYMA, D.; MAYER, G., 1980: Non-allopatric speciation in animals. *Syst. Zool.* 29, 254–271.
- GAULD, I.; BOLTON, B., 1988: *The Hymenoptera*. Oxford: Oxford Univ. Press.
- HEINZE, J.; BUSCHINGER, A., 1987: Queen polymorphism in a non-parasitic *Leptothorax* species (Hymenoptera, Formicidae). *Ins. Soc.* 34, 28–43.
- HERBERS, J. M., 1984: Queen-worker conflict and eusocial evolution in a polygynous ant species. *Evolution* 38, 631–643.
- HEWITT, G. M., 1988: Hybrid zones – natural laboratories for evolutionary studies. *Trends Ecol. Evol.* 3, 158–167.
- HÖLDOBLER, B., 1976: Tournaments and slavery in a desert ant. *Science* 192, 912–914.
- 1979: Territoriality in ants. *Proc. Amer. Phil. Soc.* 123, 211–218.
- 1982: Communication, raiding behavior and prey storage in *Cerapachys* (Hymenoptera; Formicidae). *Psyche* 89, 3–23.
- HÖLDOBLER, B.; WILSON, E. O., 1990: *The Ants*. Cambridge, Mass.: The Belknap Press of Harvard University Press.
- JESSEN, K., 1987: Biosystematic revision of the parasitic ant genus *Epimyrmica*. In: *Chemistry and Biology of Social Insects*. Ed. by J. EDER and H. REMBOLD. München: Peperny. 41–42.
- KUTTER, H., 1951: *Epimyrmica stumperi* Kutter (Hym. Formicid.), 2. Mitteilung. *Mitt. Schweiz. Entomol. Ges.* 24, 153–174.
- 1969: Die sozialparasitischen Ameisen der Schweiz. *Neujahrsblatt d. Naturforsch. Gesellschaft Zürich*.
- LE MASNE, G., 1956: Recherches sur les fourmis parasites. *Plagiolepis grassei* et l'évolution des *Plagiolepis* parasites. *C. R. Acad. Sci. Paris* 243, 673–675.
- MAYR, E., 1963: *Animal species and evolution*. Cambridge, Mass.: The Belknap Press of Harvard University Press.
- PEARSON, B., 1981: The electrophoretic determination of *Myrmica rubra* microgynes as a social parasite: Possible significance in the evolution of ant social parasites. In: *Biosystematics of Social Insects*. Ed. by P. E. HOWSE and J.-L. CLEMENT. London, New York: Academic Press. 75–84.
- POOLE, R. W., 1974: *An introduction to quantitative ecology*. New York: McGraw-Hill Inc.
- ROSENGREN, R.; PAMILO, P., 1983: The evolution of polygyny and polydomy in mound-building *Formica* ants. *Acta Entomol. Fennica* 42, 65–77.
- STITZ, H., 1939: Ameisen oder Formicidae. In: *Die Tierwelt Deutschlands*. Teil 37. Ed. by DAHL. Jena: G. Fischer.

- STUART, R. J.; ALLOWAY, T. M., 1982: Territoriality and the origin of slave raiding in lepto-thoracine ants. *Science* 215, 1262–1263.
- 1983: The slave-making ant, *Harpagoxenus canadensis* M. R. Smith, and its host-species *Leptothorax muscorum* (Nylander): Slave raiding and territoriality. *Behaviour* 85, 58–90.
- TRAGER, J. C., 1988: A revision of *Conomyrma* (Hymenoptera: Formicidae) from the southeastern United States, especially Florida, with keys to the species. *The Florida Entomol.* 71, 11–29.
- WASMANN, E., 1908: Weitere Beiträge zum sozialen Parasitismus und der Sklaverei bei den Ameisen. *Biol. Zbl.* 28, 257–271, 289–306, 321–333, 353–382, 417–441.
- 1909: Über den Ursprung des sozialen Parasitismus, der Sklaverei und der Myrmecophilie bei den Ameisen. *Biol. Zbl.* 29, 587–604, 619–637, 651–663, 683–703.
- WEST-EBERHARD, M. J., 1981: Intragroup selection and the evolution of insect societies. In: *Natural Selection and Social Behavior: Recent Research and New Theory*. Ed. by R. D. ALEXANDER and D. W. TINKLE. New York: Chiron Press. 3–17.
- 1986: Alternative adaptations, speciation and phylogeny. *Proc. Nat. Acad. Sci. USA* 83, 1388–1392.
- 1987: The epigenetical origins of insect sociality. In: *Chemistry and Biology of Social Insects*. Ed. by J. EDER and H. REMBOLD. München: Peperny. 369–372.
- WHEELER, W. M., 1910: *Ants*. New York, London: Columbia Univ. Press.
- WILSON, E. O., 1971: *The insect societies*. Cambridge, Mass.: Belknap Press of Harvard University Press.
- 1975: *Leptothorax duloticus* and the beginnings of slavery in ants. *Evolution* 29, 108–119.
- 1984: Tropical social parasites in the ant genus *Pheidole*, with an analysis of the anatomical parasitic syndrome (Hymenoptera: Formicidae). *Ins. Soc.* 31, 316–334.
- WINTER, U.; BUSCHINGER, A., 1983: The reproductive biology of a slavemaker ant, *Epimyrma ravouxi*, and a degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). *Entomol. Gener.* 9, 1–15.

Author's address: Prof. Dr. A. BUSCHINGER, Institut für Zoologie, Fachbereich Biologie, der Technischen Hochschule Darmstadt, Schnittspahnstr. 3, W-6100 Darmstadt, FRG