

Social parasitism among ants: a review (Hymenoptera: Formicidae)

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Abstract

The latest review of social parasitism in ants was published in 1990. Since then, comparatively few new parasitic species have been discovered, but research has progressed our knowledge of the evolution of social parasitism and the mechanisms involved in the maintenance of parasitic relations between species. Temporary social parasitism, slave-making, inquilinism and xenobiosis are confirmed as the primary manifestations of ant social parasitism. So-called intraspecific social parasitism should be clearly set off against the obligatory interspecific relations of social parasite and host species.

A few evolutionary transitions from one of the interspecific forms to another do occur, mainly from slave-making to a derived, workerless state. Nevertheless there is no evidence for the evolution of all types of social parasitism towards inquilinism via multiple pathways as had been formerly suggested. Emery's rule *sensu lato* has been confirmed by molecular techniques. Host-parasite recognition is mediated by cuticular signatures and involves imprinting. Increasingly, social parasitic ants are considered interesting with respect to understanding conflict and cooperation among ants. Co-evolution of social parasites with the respective host species and influence of social parasites on host populations are intensively studied. There are still unanswered questions with respect to the unequal distribution of social parasites among the extant ant subfamilies and genera, as well as their geographic distribution including the lack of slave-makers in the tropics.

Key words: Social parasitism, slave-making, temporary parasitism, inquilinism, xenobiosis, evolution, Emery's rule, review.

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Introduction

Social parasitism, the parasitic dependence of a social insect species on one or several free-living social species, is an intriguing feature found in groups such as wasps, bees, and especially manifold in ants. Slave-makers, temporary parasites, inquilines and guest ants have been studied since Pierre HUBER (1810) and Charles DARWIN (1859). The latest comprehensive overview of social parasitism in ants was published in "The Ants" by HÖLDOBLER & WILSON (1990). D'ETTORRE & HEINZE (2001) provided a recent review of ant slavery. Ant social parasitism remains as fascinating as ever. Many additional details have been discovered and investigated during the past 20 years, and warrant another comprehensive review.

On the basis of general information this paper shall address preferably those instances of social parasitism that have either been discovered or intensively studied recently. In HÖLDOBLER & WILSON (1990) many then already known details and a list of parasitic species can be found. Nevertheless numerous genera and species have to be mentioned in the text. For their taxonomy and ranges see Appendix 1, as digital supplementary material to this article, at the journal's web pages.

In this review, "castes" are defined according to function, with "queen" meaning a mated, egg-laying individual, irrespectively of whether it is a dealate gyne, an intermorph or a morphologically worker-like specimen. Since all kinds of such female reproductives occur in ants, and often also in social parasitic ants, this statement is neces-

sary as had been suggested by BUSCHINGER & CROZIER (1987) (Appendix 2).

Terminology around social parasitism: intraspecific social parasitism, autoparasitism, non-social inquilines, guests, and parasites

What is social parasitism and what is not? The answer apparently depends a lot on personal preferences and experiences of individual authors. A plethora of terms have been in use to denote the various manifestations of social symbiosis and parasitism among social insects, particularly among ants. Often several synonyms have been proposed, and even modern authors sometimes create substitutes for well established terms, increasing confusion. Most recently, HERBERS (2006, 2007) suggested replacing the terms "slavery", "slave-making ants" and "dulosis" by "piracy" and "pirate ants". These terms have been adopted by some, e.g., by BONO & al. (2007) and TSUNEOKA (2007). Parasitism usually denotes the dependence of one species, the parasite, on one or more other species, the host(s). In obligatory parasitic relationships, parasites cannot survive without the host. This holds true for social parasites among the social insects as well.

However, the term "parasitism" sometimes is used also for intraspecific phenomena such as nest usurpation in bumblebees or in birds, and some ant researchers have coined terms like "intraspecific social parasitism" and "intraspecific slavery" (HÖLDOBLER 1976, POLLOCK & RISSING 1989,

HÖLDOBLER & WILSON 1990, FOITZIK & HEINZE 1998, 2000, 2001). With focus on social bees, BEEKMAN & OLDROYD (2008) provided an overview of such intraspecific parasitism with a particularly valuable list of references. The term "intraspecific social parasitism", however, may cause confusion and may blur the very particular character of the obligatory social parasitism among different ant species (e.g., SAVOLAINEN & VEPSÄLÄINEN 2003). Like in some non-parasitic ants, "intraspecific slave raids" have been observed occasionally also in slave-making species (TOPOFF & al. 1984, SCHUMANN 1992, LE MOLI & al. 1993).

BOLTON (1986a, b) has coined the term "autoparasitism" for the behaviour of young queens seeking adoption in conspecific colonies, which later reproduce by budding or fission. In polygynous species this is a reciprocal behaviour in that the "autoparasitic" generation may become host for the next generation. Therefore it should not be considered as "parasitic".

Social parasitism or inquilineism often has been stated also for non-social organisms, so-called "guests" in nests of social insects, such as mites, beetles and other arthropods (e.g., AKINO & al. 1999). The parasitism among two social species, however, is something particular. It should not be confounded with ordinary kinds of parasitism like that of mites or nematodes that may plague both social and non-social hosts alike. Another instance of confusing use of the term inquiline is for ants nesting in termite mounds (e.g., WOOD & SANDS 1978, LEPONCE & al. 1999): as far as is known they don't have social relations to each other. At best the ants prey upon their compulsory hosts.

Finally, "social symbiosis" (e.g., HÖLDOBLER & WILSON 1990) is an inaccurate, although widely used, description of a social parasite's relationship with its host as "symbiosis" in other instances often refers to a relationship that is mutually beneficial. Following myrmecological tradition the term will not be used in this paper. This review will only consider the interspecific forms of social parasitism, the obligatory parasitism between ant species.

Various types of obligatory ant social parasitism

Social parasitism is expressed in many forms, particularly in ants. The various heterospecific associations among ants have been classified in different ways. HÖLDOBLER & WILSON (1990), following a suggestion of WASMANN (1891), distinguished between "compound nests" and "mixed colonies". The latter would comprise the temporary parasites, the slave-makers and the inquilines, where the host species workers at least temporarily care for the parasite brood. "Compound nests" covers all types of casual or regular nesting in close vicinity (plesio-biosis), stealing food from other species (cleptobiosis), stealing brood (lestobiosis) and sharing nests and trails but keeping the two species' broods separate (parabiosis). Xenobiosis in this classification is listed among the "compound nests". Here, the obligatory parasitic ants shall be arranged in four basic types, including xenobiosis (e.g., BUSCHINGER 1986), which still appears justified and helpful, though a few exceptional instances cannot unambiguously be attributed to one or the other.

Guest ant relations, xenobiosis. Xenobiotic ants in general are distantly related to their respective hosts at best. Parasite and host may even belong to different subfamilies. The association, however, is obligatory for the guest

ants which cannot survive for longer time without the hosts. Different from the other three types of social parasitism where parasite brood rearing is accomplished by the host species, guest ants care for their own brood. Xenobiosis has been included in this survey also because it had been discussed as a possible precursor of inquilineism (e.g., WILSON 1971, HÖLDOBLER & WILSON 1990).

Guest ant relations have been stated in three genera of ants, *Formicoxenus*, *Polyrhachis* and (possibly) *Megalomyrmex*. The guest ants of the myrmicine tribe Formicoxenini now all are attributed to one apparently monophyletic genus, *Formicoxenus* (see FRANCOEUR & al. 1985) (Appendix 1). They have small colonies with up to about a hundred individuals. The colonies dwell the nest material or the nest walls of their hosts, which are much bigger species of the genera *Formica*, *Manica* or *Myrmica* with large, populous nests. These guest ants build their own little nests well separated from the brood chambers of the hosts, and they themselves care for their brood. They are dependent upon the hosts with respect to nutrition and perhaps shelter. *Formicoxenus* may solicit regurgitated food directly from a host worker or participate in food exchange (trophallaxis) between two host specimens. Some *Formicoxenus* species exhibit queen and male polymorphism (FRANCOEUR & al. 1985) and the colonies may be functionally monogynous (BUSCHINGER & WINTER 1976, BUSCHINGER 1979). LENOIR & al. (1997) have demonstrated a chemical mimicry between parasites and hosts in two species pairs, *Formicoxenus provancheri* / *Myrmica incompleta* and *F. quebecensis* / *M. alaskensis*. The guest ants acquire the cuticular hydrocarbons from their hosts during the first days of their adult life.

Another, recently investigated instance of xenobiotic exploitation of host species is represented by a couple of formicines living in association with certain Ponerinae. *Polyrhachis lama* (Formicinae) in Java has been found living in nests of a common *Diacamma* species (Ponerinae). Only very few among the parasitized nests contained a *Polyrhachis* queen, whereas in most nests only workers of this species could be found together with a brood of both species (MASCHWITZ & al. 2000). Similarly, *Polyrhachis loweryi* (Formicinae) in Queensland, Australia, was found in colonies of a large *Rhytidoponera* species (Ponerinae) (MASCHWITZ & al. 2003). Again, a couple of mixed colonies contained workers and a brood of host and parasite, whereas a queen of the parasitic *Polyrhachis* was found in only one mixed colony. The *Polyrhachis* workers were not inseminated, though some of them laid male-destined eggs. Evidently, in both *Polyrhachis* species the workers from queenright (i.e., containing a *Polyrhachis* queen) mixed colonies invade neighbouring host species nests, carry young brood stages with them and rear this brood with food that is furnished by the host workers (MASCHWITZ & al. 2004).

There are more records of *Polyrhachis* species found in association with distantly related formicine (*Camponotus* spp.), myrmicine (*Myrmicaria* sp.) and ponerine species. Closer examination may reveal some more instances of xenobiosis in this group (KOHOUT 1990, MASCHWITZ & al. 2000). All the species that are suggested to coexist with ponerine hosts belong to one species group, *P. viehmeiyeri* group of subgenus *Myrmhopla* (see KOHOUT 1990, DOROW 1995). For the *P. lamellidens* group in *Polyrhachis* subgenus *Polyrhachis*, a couple of records exist in which a kind

of temporary parasitism in nests of *Camponotus* spp. has been suggested (for details see MASCHWITZ & al. 2000) (Appendix 1).

Finally, species belonging to the genus *Megalomyrmex* sometimes have been mentioned as guest ants (BRANDÃO 1990, HÖLLDOBLER & WILSON 1990). Whether or not they belong to this group is somehow questionable, however (see "Evolutionary modifications of life cycles in parasitic ants").

Temporary parasitism. In temporary parasitism, the parasitic species depends on a host species only during the founding phase of new colonies by young queens. Usually after her nuptial flight and insemination, the parasitic queen attempts to penetrate a host colony where she replaces the original queen and manages to be tolerated by the workers. A non-parasite worker force develops from the parasite's eggs, with the aid of the host colony workers, which eventually disappear due to natural aging and losses. The colony becomes a pure society of the parasitic species. Mature colonies of temporary social parasites grow as large as the host species colonies; they may live for many years and rear numerous sexuals.

Some peculiar behaviours of queens have been observed during colony foundation. Queens of *Lasius umbratus* and related species in the subgenus *Chthonolasius* (subfamily Formicinae), grasp and chew a worker of the host species (*L. niger*) and then enter the host nest. There the parasite queen is said to become more attractive than the original queen (GÖSSWALD 1938), which finally dies of starvation or is expelled from the colony. A closely related species, *L. reginae*, after invading a nest of *L. alienus* attacks the much bigger host queen and throttles her to death (FABER 1967). Queens of *Bothriomyrmex decapitans* and other species of this genus during colony take-overs cut off the head of the host species queen (of genus *Tapinoma*, both subfamily Dolichoderinae) (SANTSCHI 1906).

Lasius fuliginosus (Formicinae) exhibits a social hyperparasitism in that the queen founds her colony in a nest of *L. umbratus* which is itself a temporary parasite of *L. niger* and a few related species (SEIFERT 2007). In certain instances the parasitic foundation of new colonies of *Lasius* (*Chthonolasius*) species may be pleometrotic, with several parasite queens simultaneously invading a host colony (SEIFERT & BUSCHINGER 2002). MATTHEIS (2003) provided evidence for pleometrotic foundation also of *Lasius* (*Dendrolasius*) *fuliginosus* colonies. He suggests that colony foundation occurs only in orphaned colonies of *Lasius umbratus*.

Temporary parasitism occurs in several (perhaps all) species of wood ants of the *Formica rufa* group and of *Formica* (*Coptoformica*) species. In some species the queens may alternatively either penetrate a *Formica* (*Serviformica*) sp. nest, or join a polygynous colony of their own species. Such colonies then reproduce by budding, often forming huge multi-nest supercolonies (HÖLLDOBLER & WILSON 1990).

Myrmica vandeli might be a temporary social parasite of *M. scabrinodis* in marginal parts of its range, but is free living in stronger populations (RADCHENKO & ELMES 2003). SEIFERT (2007) discussed such a facultative temporary parasitism of *M. vandeli* as being very probable. FRANCOEUR (2007) suggested a temporary parasitic life history in the newly described *Myrmica semiparasitica*. Nevertheless temporary parasitism in this genus as yet has

not been firmly demonstrated, and its existence in the genus still needs proof.

A possible temporary parasitism also has been suggested for *Solenopsis enigmatica* from the West Indies, with parasite workers in the mixed nests, though the authors, DEYRUP & RUSAK (2008), have described the species as a new "inquiline". A further problem in this instance arises from the fact that the host species belongs to another genus, *Pheidole*. Such instances should be very carefully studied since temporary parasitism between members of different genera would represent a novelty.

Permanent parasitism with slavery, dulosis. The permanently parasitic species depend upon the hosts throughout their lives. In the case of the slave-making or dulotic ants, the young queen has to penetrate a host species nest, eliminate the host colony queen and take over her workers and the brood. In some genera (*Chalepoxenus*, *Harpagoxenus*) all adult host workers are killed or evicted. The conquered brood comprises worker pupae from which new slaves will soon emerge, and with their aid a number of slave-maker workers are subsequently reared.

The slave-maker workers are usually unable to forage, to feed their larvae, or even to eat by themselves. On the other hand, they are often predisposed for effective fighting. Slave-maker workers may be equipped with specialized piercing mandibles as in *Polyergus* (Formicinae) and *Strongylognathus* (Myrmicinae), or with toothless, pincers-like mandibles for cutting off the appendages of their opponents as in *Harpagoxenus sublaevis* (Myrmicinae) (see BUSCHINGER & al. 1980, HÖLLDOBLER & WILSON 1990). Others have strong stings (the myrmicine genus *Chalepoxenus*, see BUSCHINGER & al. 1980, EHRHARDT 1982), or produce aggressive glandular secretions or "propaganda" substances (*Raptiformica*, see REGNIER & WILSON 1971). They attack independent, neighbouring colonies of the slave, i.e., host, species, fight against the defenders, and finally carry back the brood to the slave-maker's nest. Thus, the slave stock may be replenished several times a year (BUSCHINGER & al. 1980). Propaganda substances also are used by slave-raiding *Harpagoxenus sublaevis* and by the inquiline ant, *Leptothorax kutteri* (see ALLIES & al. 1986). In quite a number of presumed slave-making species slave raids as yet have not been observed. This is the case in *Strongylognathus*, where raiding actually has been observed in only two or three among the 24 described species; e.g., SANETRA & GÜSTEN (2001) reported on slave raids of *Strongylognathus afer* in laboratory conditions. For a recent review of the sociobiology of slave-making ants see D'ETTORRE & HEINZE (2001).

Formica (*Raptiformica*) *sanguinea* (Formicinae) is one example that mediates between temporary parasitism and dulosis in that large colonies often exist without having slaves. A sizeable fraction of the conquered pupae usually is eaten in these slave-maker's nests.

Rossomyrmex (Formicinae) with four species from Spain, southwestern Russia and Kazakhstan, Turkey, and China is characterized by its peculiar recruitment of nest mates for slave raids: these ants carry each other to the target nests of their slaves of genus *Proformica* (see MARIKOVSKY 1974, BUSCHINGER & al. 1980, HÖLLDOBLER & WILSON 1990).

The Amazon ants, genus *Polyergus*, are the most intensively studied group at present. The genus has a Holarctic

range with *P. breviceps* and *P. lucidus* in North America and *P. rufescens*, *P. nigerrimus* and *P. samurai* in temperate and Mediterranean Eurasia (Appendix 1). For colony founding, the young queen penetrates a nest of the host species, eventually kills the host queen, and uses the host workers to rear her brood. A colony of *Polyergus* will conduct slave raids on nests of species of *Formica* (subgenus *Serviformica*), and worker pupae of the hosts are taken. The workers hatching from these pupae are necessary for foraging and for feeding and rearing the slave-maker's brood in the mixed society, and for nest building. *Polyergus* workers are incapable of surviving without slaves, even when plentiful food is available. North American *Polyergus lucidus* has at least three host species though single colonies always contain only one of them. Raids target only at nests of the host species already present in the nest (GOODLOE & al. 1987). The authors suggested imprinting of the slave-makers on the respective host species.

Recent progress has been made in studies on colony foundation of *Formica sanguinea* (see MORI & LE MOLI 1998). After mating the females may return to a *F. sanguinea* colony, then join a slave raid of this colony and establish a colony in an invaded host nest. *Polyergus* species colony foundation also was studied in more detail recently (MORI & al. 2000, JOHNSON & al. 2001, 2002). The large Dufour's gland is responsible for a kind of chemical disguise (ERRARD & D'ETTORRE 1998). Only mated and egg-laying host queens are attacked by a *Polyergus* foundress queen, probably due to a kairomonal effect signalling queen and colony suitability (JOHNSON & al. 2002). After killing the host queen the cuticular hydrocarbon profile of the *Polyergus breviceps* queen changes into that of the attacked host queen. Cuticular compounds from the host queen apparently are transferred to the parasite queen during the aggressive interaction.

Slave-makers belonging to the tribe Formicoxenini, with genera *Chalepoxenus*, *Harpagoxenus*, *Myrmoxenus*, *Protomognathus* and certain species of genus *Temnothorax*, are another focal point of recent interest. Their particular advantage is small colony size which is favourable for laboratory observations of slave-raiding and colony foundation (BUSCHINGER & al. 1980). Dense populations in the field with often several host species colonies on one square meter enable studies on effects of the slave-makers on their hosts. For more details see "Evolutionary aspects of social parasitism".

Remarkably, since HÖLLDOBLER & WILSON (1990) only few other slave-making ant species have been described, a *Rossomyrmex* species each from Turkey (TINAUT 2007) and China (XIA & ZHENG 1995), and four species of *Strongylognathus*, i.e., *S. minutus* and *S. pisarskii* from Europe, and *S. potanini* and *S. tylonum* from China (see Appendix 1). In none of these instances information on life history was provided.

Permanent parasitism without slavery, inquilinism.

Permanent parasites that do not enslave their host species often do not produce a worker caste. Termed inquilinism, this syndrome is adaptive in that the host workers take over all husbandries and the parasite queen can invest all energy into the production of sexuals. Nonetheless, in a few instances inquiline workers have been observed to exist (SUMNER & al. 2003). The reproductive females usually coexist with the queens of the host species in their nests, and the

parasite brood is reared by the host workers simultaneously with their own larvae. In a few instances, e.g., *Anergates atratulus*, the parasite apparently invades only orphaned host species colonies, whereas the so-called "ultimate parasite" *Teleutomyrmex schneideri* sometimes rides on the back or clings to the thorax of the host colony queen similar to an ectoparasite (KUTTER 1968).

Occasionally a distinction is made between queen-tolerant and queen-intolerant inquilines according to their coexistence with the host queens in the host nest, although inquilines typically are queen-tolerant. The few queen-intolerant inquilines either invade queenless colonies (*Anergates atratulus*) or actively eliminate the host queens such as *Leptothorax goesswaldi* (see BUSCHINGER & KLUMP 1988) and a couple of species in the genera *Myrmoxenus* and *Chalepoxenus* which presumably are degenerate slave-makers (Appendix 1).

Another distinction can be made with respect to morphology. Some species like *Teleutomyrmex* and *Anergates* appear highly specialized and are perhaps "old". For these parasites a long evolutionary history has been assumed, perhaps including descent from slave-makers (KUTTER 1968, WILSON 1971, HÖLLDOBLER & WILSON 1990). Their particular morphological characters, which in part occur also in other inquilines, were termed "the anatomical parasitic syndrome" by WILSON (1984).

Other inquilines, e.g., the parasites of the formicine genus *Plagiolepis* are anatomically less aberrant but may also have a long parasitic history. The parasitic group (formerly genus *Paraplagiolepis*) comprises the two species, *P. xene* and *P. grassei*, and at least five undescribed ones (STUEWER 1992, CAGNIANT 2006, A. Buschinger, unpubl.), as well as the former genus *Aporomyrmex* with *Plagiolepis ampeloni* and *P. regis* (Appendix 1). The most prominent features of this group are reduction in size (ARON & al. 1999) and a marked polymorphism of both queens and males. Only *P. grassei* has a few own workers. All the species are living within highly polygynous and polydomous colonies of the host species.

Numerous other inquiline species resemble closely their host species, and are often systematically attributed to their host genera, such as *Leptothorax kutteri*, *L. goesswaldi*, and *L. pacis* (all formerly genus *Doronomyrmex*); all three are difficult to tell apart from the host species *L. acervorum*. Curiously enough, sometimes two of these species may occur in sympatry, all living with the one common host species, and sometimes two of the parasitic species even share one host colony (BUSCHINGER 1986, 1990). Finally, some inquiline gynes appear as merely smaller specimens of the host species, e.g., *Temnothorax minutissimus*, though their status as separate species is unquestionable (BUSCHINGER & LINKSVAYER 2004).

Inquilinism is the most frequent type of social parasitism, and several new inquiline ant species have been discovered since HÖLLDOBLER & WILSON (1990). HORA & al. (2005) and FEITOSA & al. (2008) recently described miniature queens of *Ectatomma parasiticum* (Ectatomminae) as an inquiline species. This is the first case of social parasitism in the poneroid complex of ant subfamilies. HEINZE (1989) and HEINZE & ALLOWAY (1991) described two new inquilines of *Leptothorax* spp. from North America, *L. wilsoni* and *L. paraxenus*. The latter is perhaps queen-intolerant, eliminating the host colony queen(s), though this has

not been firmly established (cf. ALLOWAY 2009). JOHNSON (1994) provided additional information on the life history of the inquiline ant, *Pogonomyrmex anergismus*, a very rare parasite of *Pogonomyrmex rugosus* and *P. barbatus*. JOHNSON & al. (1996) studied *P. colei*, an extremely rare inquiline of *P. rugosus* and supposedly its closest relative. *Myrmica schenckioides* has been described as a new supposedly parasitic species from the Netherlands (BOER & NOORDIJK 2005), though only one specimen had been found in a pitfall trap. KINOMURA & YAMAUCHI (1992) found a new workerless socially parasitic *Vollenhovia*, *V. nipponica*, in Japan. For its life history see SATOH & OHKAWARA (2008). HÖLLDOBLER & WILSON (1990) did not yet refer to any social parasites among the leaf-cutter ants (Attini). It is remarkable therefore that five inquiline taxa in this tribe now have been described (SCHULTZ & al. 1998, SUMNER & al. 2004, SOUZA & al. 2007). AGOSTI (1994) described the first inquiline, and social parasite, in the formicine genus *Cataglyphis*. WARD (1996) reported a new workerless parasite in the ant genus *Pseudomyrmex*, *P. inquilinus*, the second one in the genus, and the third one in the subfamily Pseudomyrmecinae. Only one temporary social parasite of this subfamily, genus *Tetraponera*, had been known prior to HÖLLDOBLER & WILSON's listing (1990) (Appendix 1).

Frequency and systematic distribution of parasitic ants

Among the ca. 12,500 described ant species (AGOSTI & JOHNSON 2009), the ca. 230 known parasitic species represent but a small fraction. For the very well known fauna of Switzerland, the census of KUTTER (1968) remarkably showed about one third of the ca. 110 ant species then known to be parasitic. Most parasitic ant species are rare and not easily found in populations and colonies of their hosts. The actual global number of parasitic species thus might be considerably higher. As had been predicted (WILSON 1984), new species continue to be detected, particularly in the tropics.

The distribution of social parasite species among the 22 extant ant subfamilies (BOLTON 2003, plus Martialinae, RABELING & al. 2008) is surprisingly unequal. Although the subfamilies apparently do not differ fundamentally in their form of social organization, social parasites are known mainly among the Myrmicinae and the Formicinae (about 33 out of 139 and 9 out of 25 genera, respectively). Some genera consist of parasitic species only (e.g., *Anergates*, *Bothriomyrmex*, *Chalepoxenus*, *Formicoxenus*, *Harpagoxenus*, *Myrmoxenus*, *Polyergus*, *Protomognathus*, *Strongylognathus*, *Teleutomyrmex*). Other genera comprise numerous independent and a few parasitic species each (e.g., *Formica*, *Lasius*, *Leptothorax*, *Myrmica*, *Plagiolepis*, *Temnothorax*), sometimes due to recent synonymization of formerly separate parasitic genera with their host genera (Appendix 1). Remarkably, the temporary parasitic genus *Bothriomyrmex* (Dolichoderinae) represents the most diverse taxon among the social parasites with ca. 38 valid species and numerous subspecies (JOHNSON 2007).

Although several ant subfamilies comprise few species in total, it is difficult to understand why parasites are (nearly) missing, for instance, from the large group of "poneromorph subfamilies" (BOLTON 2003), where a microgynic social parasite of *Ectatomma tuberculatum* (Ectatomminae) only recently has been described as the first instance (HORA

& al. 2005). Moreover, among the huge subfamilies of Myrmicinae and the Formicinae the numerous parasitic species are concentrated in only a few genera (BUSCHINGER 1986, 1990). For example, the genus *Camponotus* with an estimated 1,500 species comprises but one known social parasite, the inquiline *Camponotus universitatis* (see TINAUT & al. 1992).

A survey of the parasites in different subfamilies reveals that all four basic types of parasitic life habits (xenobiosis, temporary parasitism, dulosis and inquilinism) evolved within both the Formicinae and the Myrmicinae, temporary parasitism in addition among the Dolichoderinae (one genus, *Bothriomyrmex*) and Pseudomyrmecinae, and inquilinism in the Myrmeciinae (BUSCHINGER 1986). Within the myrmicine tribe Formicoxenini slave-making has evolved apparently six times independently (BEIBL & al. 2005). Inquilinism in this tribe originated at least twice (BUSCHINGER 1981), and xenobiosis once (FRANCOEUR & al. 1985). Among the Formicinae the slave-maker genera *Polyergus* and *Rossomyrmex* have evolved independently from one another (HASEGAWA & al. 2002). WILSON (1984) assumed an independent, convergent evolution of nine parasitic species from the large myrmicine genus *Pheidole*. Such polyphyletic origins of very similar parasitic life cycles indicate that there are certain widespread, though perhaps not universal features of normal social behaviour which often become the starting point for parasitic evolution (BUSCHINGER 1970, 1990).

Evolutionary aspects of social parasitism

The most important and also the most controversial aspect of the evolution of social parasitism is how and why some ants have switched over from independent life to social parasitism. The problem may be split into several questions. How to explain the generally close systematic relationship between hosts and parasites? Which selective forces and which ecological conditions might be responsible for or might favour the development of parasitic life habits? Which behaviours in normal social species give rise to the particular parasitic behaviours, i.e., dependent colony foundation and slave raiding? Recent molecular genetic studies have brought a lot of new insights, and often also support previously published assumptions. Nevertheless, the questions remain under scrutiny.

On the first question, concerning the close systematic relationship between hosts and parasites, most authors are in accord. EMERY (1909) pointed out that all the inquilines, slave-makers and temporary parasites are close relatives of their respective host species ("Emery's rule", LE MASNE 1956). The validity of Emery's rule has been intensively discussed, particularly since genetic methods could be applied. A major debate has dealt with this rule in a "strict" and in a "loose" form.

In fact, EMERY (1909) had formulated his statement a bit thoughtlessly. At his time it had been known quite well that slave-maker species each can parasitize two or more slave species at once. Hence, Emery's rule in the strict sense, saying that every parasitic species derives directly from its host species was obsolete from the beginning (BUSCHINGER 1970, 1990). Multiple host species may also occur among inquilines (HEINZE & al. 1995). Molecular studies have confirmed that Emery's rule usually applies but in the loose sense: the parasites derive from the species group

or, more frequently, the genus to which their hosts belong (e.g., BAUR & al. 1995, PARKER & RISSING 2002, SUMNER & al. 2004).

SMITH & al. (2007), studying social parasites and their hosts in allodapine bees, stated that "recent molecular phylogenetic studies have revealed a mixture of the two forms [loose and strict Emery's rule] in various ant and wasp groups". They found both pairs of sister species where one species parasitizes the other and parasites less closely related to their respective hosts. Extinctions and host switches have to be taken into consideration when evaluating host-parasite relationships (cf. BUSCHINGER 1970).

Either way, the close relationship of host and parasite may be due to a common ancestor, or to parasites' ability to coexist only with very closely related host species (BUSCHINGER 1986). In order to live in a mixed society the two species must have compatible communication systems and similar pheromones for nestmate recognition, and the parasite's larvae must be adapted to, among others, the glandular food secretions and feeding habits of the host species workers. When closely related species are involved, these conditions are most easily fulfilled.

Sympatric or allopatric origin of social parasites? The question thus focuses on the sympatric or allopatric origin of parasite and host: whether the parasite has directly evolved within and from an independent species, or whether speciation first occurred, perhaps due to a geographical barrier, and subsequently one species went over to parasitize its sister species.

To date most authors lean towards the hypothesis of a sympatric origin of parasitic species, in the nests and populations of the independent ancestor, which then became the host species (KUTTER 1968, BUSCHINGER 1970, BUSCHINGER 1990, FRANKS & BOURKE 1990, BOURKE & FRANKS 1991, WARD 1996, SAVOLAINEN & VEPSÄLÄINEN 2003). After a parasite and a host have established as different species both the parasite and the host may go through further evolution, adaptation and speciation. This may explain the apparent host shift of some parasites and the use of several hosts by one parasite species (BUSCHINGER 1990). Allopatric speciation of parasite and host, on the other hand, had been favoured by, among others, WILSON (1971, 1975) and by HÖLLDOBLER & WILSON (1990), probably influenced by the widespread belief that speciation can only occur when populations of a species are geographically separated.

Direct evidence in favour of the allopatry scenario is lacking: not a single instance is known of two closely related or sister species with partially overlapping ranges, where one species would parasitize the other in the contact zone, and live independently in the remainder of its range. In contrast, there is potential support of the sympatry scenario: there are a few cases particularly in the genus *Myrmica*, where small females, "microgynes", occur together with "macrogynes" in the same polygynous nest. In some instances the microgynes are believed to still belong to the same species as the queens of ordinary size (*M. ruginodis*, see ELMES 1976, 1978, PEARSON 1981; *Temnothorax rugatulus*, see RÜPPELL & al. 2001). PEARSON (1981) speculated that the interactions of the macrogyne and microgyne forms of *Myrmica ruginodis* "may provide information about the early or pre-parasitic condition". In other instances microgynes (*M. microrubra*, *M. hirsuta*) have been

described as separate, parasitic species. SAVOLAINEN & VEPSÄLÄINEN (2003) confirmed the species status of *M. microrubra* and *M. hirsuta* with molecular methods but *M. microrubra* was synonymized later with *M. rubra* (see STEINER & al. 2006). For queen polymorphism and queen size polymorphism see also BUSCHINGER & HEINZE (1992) and HEINZE (2008).

Polygyny: origin of dependent colony foundation?

BUSCHINGER (1990) hypothesized that all forms of true social parasitism originate from the adoption of conspecific young queens in colonies of polygynous species. The social organization of the ancestral, and eventual host species (group), and the host's variation in space and time, may be responsible for the development of an emerging parasite to become an inquiline, a temporary parasite, or a slave-maker.

Roughly one half of all ant species investigated for numbers of queens per colony are polygynous or at least facultatively polygynous. In many species monogynous and polygynous colonies occur within a single population, whereas other species are always polygynous (BUSCHINGER 1974, KELLER 1993, HEINZE 2008). Primary polygyny may be a rare consequence of pleometrosis. More frequently, however, young queens are later accepted in already existing polygynous or perhaps also monogynous colonies (secondary polygyny). Polygyny often results in polydomy, where a single colony inhabits several neighbouring nest sites. Sometimes daughter colonies with one or several queens branch off and eventually may interrupt the contacts to the mother colony (ROSENGREN & PAMILO 1983).

The adoption of newly inseminated queens in existing conspecific colonies resembles the events when a young queen of a social parasite penetrates an allospecific, i.e., its host species', colony. Therefore, several authors, including WHEELER (1910), KUTTER (1968), ALLOWAY & al. (1982), ELMES (1973, 1978), BOLTON (1986b), and BUSCHINGER (1970, 1986, 1990) have speculated that polygyny might be the precursor of social parasitism. After all, this hypothesis is the only one that would provide an explanation for the dependent colony foundation of all true social parasites (except the xenobionts).

BUSCHINGER (1990) suggested an intraspecific preparasitic stage of incipient social parasites. Because the assumption of a sympatric speciation and, even more so, the isolation of a preparasitic genotype within a deme and even within the nests of a given non-parasitic species appear quite unusual and unrealistic at the first glance, this suggestion needs some explanation.

There are many reports on ants, e.g., of the genus *Formica*, where sexual offspring from one and the same nest may exhibit alternative behaviours, some mating on top of the nest, others flying off to swarm (ROSENGREN & PAMILO 1983). Such intranidal variation leads to assortative mating (e.g., WEST-EBERHARD 1986, 2005). The process is similar to sympatric speciation by host shift (MUNDAY & al. 2004). If a tendency to produce fewer workers in favour of sexual production (the "deficient genes" of BUSCHINGER 1990) somehow is linked with the tendency to mate near the nest, and for the females to remain there, the genetic condition of an incipient parasite, a "preparasite", has been achieved. In polygynous species this linkage evidently can happen (BUSCHINGER 1990). Intranidal mating provides an at least partial sexual isolation be-

tween the swarming phenotypes and those remaining in place. Nest-mating increases inbreeding, and thus the accumulation of "deficient genes", and it can be expected to gradually increase the genetic differences between nest-mating and swarming genotypes.

Other mechanisms may then enhance the speciation process. For example, a conceivable means to produce a higher number of sexuals would be to reduce them in size. Smaller sexuals have less energy for a long mating flight and for independent colony foundation but tend to remain in the mother colony and indeed, inquiline and temporary parasitic ant queens often are considerably smaller than the related host species queens (e.g., ARON & al. 1999).

In essence, there apparently are some traits in the social organization of ants which are involved in the frequent and convergent formation of inquilines, slave-makers and temporary parasites. These traits probably are polygyny, polydomy, inbreeding, and perhaps territorial behaviour (see below), which in various combinations may give rise to the major types of social parasitism. In most groups of (potential) host species apparently only one option, inquilinism or temporary parasitism, is available. In other groups, e.g., the genera *Leptothorax* and *Temnothorax*, queen-tolerant and queen-intolerant inquilines and slave-makers perhaps evolved in a radiative manner from a common, pre-parasitic stage.

Territorial behaviour as origin of slave-making?

Much of the relevant literature on the origin of parasitic behavioural patterns from ordinary social ones refers to the conspicuous behaviour of slave raiding. Territoriality is often observed among neighbouring conspecific ant colonies (HÖLLDOBLER 1976, 1979). A dominant colony may invade a weaker one, kill the adults and rob its broods. From such brood items workers may develop which join the workforce of the dominant colony. HÖLLDOBLER (1976) described such "intraspecific slavery" in *Myrmecocystus*. WILSON (1975), ALLOWAY (1979, 1980), POLLOCK & RISSING (1989), and STUART & ALLOWAY (1982, 1983) put forward the hypothesis that interspecific dulosis originated from such intraspecific slavery. Intraspecific slavery, however, does not address the parasitic mode of colony formation. ALLOWAY (1980), STUART & ALLOWAY (1983) and TOPOFF (1990) have tried to combine both territorial competition and the adoption of young queens as a pre-adaptation for parasitic colony foundation.

Predation on foreign ant brood as origin of slave-making? Another hypothesis on the origin of slavery had been put forward already by DARWIN (1859). With reference to the then known slavery of *Polyergus* and *Formica* (*Raptiformica*) he suggested that slave-making originated from predation on brood of other species. Pupae which by chance were not consumed could hatch and become an additional workforce. Selection would have favoured colonies gaining ever more slaves by this means. 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.

This "predation hypothesis", however, like the "territorial hypothesis", does not address the parasitic foundation of colonies in all known slave-making species. Another major counterargument is the fact that slavery did not evolve among those groups of ants which are particularly speci-

alized predators of other ants, such as some *Myrmecia*, *Gnamptogenys*, and several army ant species (HÖLLDOBLER & WILSON 1990). *Cerapachys* (see HÖLLDOBLER 1982) and *Sphinctomyrmex* (see BUSCHINGER & al. 1990) store captured ant brood over days or weeks in their nests, but then consume them all.

Selective forces involved in the evolution of social parasitism. No really convincing answers exist to the question on the selective forces involved in the evolution of social parasitism. Several authors (e.g., KUTTER 1968) have stressed that independent colony foundation by single young queens is a hazardous period, and that this risk could be reduced either by joining a colony of their own species (leading to polygyny), or by invading a foreign colony and becoming an inquiline or temporary parasite. However, penetrating a foreign colony is also a risky venture. It could be selected for only when it is more successful than independent colony founding. KUTTER (1968), HÖLLDOBLER & WILSON (1990) and HEINZE (1993) also discussed the difficulties of solitary founding in cold climates as a possible reason for the high frequency of parasitic ants in higher latitudes.

Evolutionary modifications of life cycles in parasitic ants

Apart from the fundamental questions on the evolutionary origin of social parasitism a large body of information has accumulated referring to evolutionary modifications of life cycles and behaviour within parasitic species groups. Considerable advances in this field have been achieved in recent times.

WILSON (1971) and HÖLLDOBLER & WILSON (1990) had suggested several evolutionary pathways, all of which end up in an ultimate state of permanent parasitism or inquilinism. Therefore it should be of interest to look for such pathways particularly in groups or genera where several of the types of social parasitism are represented. However, the theory of there being gradual pathways to inquilinism has been questioned (BUSCHINGER 1986, 1990, BOURKE & FRANKS 1991) because there is practically no evidence for transitions from xenobiosis, temporary parasitism or slavery to a typical inquilinism, as will be shown below. In addition, a major argument against these pathways is the fact that inquilines are found in a comparatively high number of genera in which the other kinds of social parasitism, hence potential precursors, are unknown (BUSCHINGER 1990).

A route from xenobiosis to inquilinism? The frequent coexistence of nests of different ant species in close proximity has, surprisingly, not often led to the evolution of xenobiotic relations in ants in general. Within the apparently monophyletic (FRANCOEUR & al. 1985) guest ant genus *Formicoxenus*, or in the tribe Formicoxenini, there is no workerless inquiline that could be postulated to have evolved from the guest ants (e.g., HEINZE 1995). In the other group that contains guest ants, *Polyrhachis*, again nothing points in the direction of an evolutionary transition from one of the observed instances towards inquilinism.

In the myrmicine genus *Megalomyrmex*, *M. symmetochus* is suggested as being a guest ant of the fungus-growing *Sericomyrmex amabilis* (see BRANDÃO 1990, HÖLLDOBLER & WILSON 1990). However, this conclusion may be questioned since ADAMS & al. (2000) claimed that at least one *Megalomyrmex* species conducts raids on the fungus of its attine host, a behaviour that has been termed agro-

predation. Most *Megalomyrmex* species apparently are free-living or at most pillagers of brood and fungus for food from certain attine species. *Megalomyrmex mondabora* is always associated with nests of several attine species and was, therefore, referred to as a social parasite (ADAMS & LONGINO 2007), although these "parasite" ants just consume fungus and larvae of the "host". The *Megalomyrmex* life histories are reminiscent of "thief ants", such as the lestopibiotic *Solenopsis fugax* (cf. HÖLLDOBLER & WILSON 1990). Again, there is no reason to assume the evolution of inquilines from the (perhaps even non-existing) xenobiosis in this group of about 31 species (BRANDÃO 2003) (Appendix 1).

A route from slave-making or temporary parasitism to inquilinism? Any discussion involving the evolution of dulosis or temporary parasitism must take into consideration that both life histories comprise the feature of parasitic colony foundation. Nevertheless, many suggestions for the origin of slavery exclusively refer to the slave-making process itself.

DARWIN (1859) proposed an evolutionary scenario for the wood ants (*Formica* and allied genera), that began with brood predation for food and led via the facultative slavery of the subgenus *Raptiformica* to the obligatory dulosis of the Amazon ants, genus *Polyergus*. Later, two workerless inquilines, *Formica talbotae* and *F. dirksi*, were detected in this group (WING 1949, TALBOT 1977). Whether the latter two species are descendants of temporary parasite ancestors, or derive directly from independent polygynous forms, is open to question.

Within the myrmicine tribe Formicoxenini (Appendix 1), an evolution from slave-making species to workerless, permanently parasitic forms has been documented in the genus *Myrmoxenus* (= *Epimyrmex*). The life history of this genus, which was supposedly a "remarkably clear evolutionary progression leading from temporary social parasitism to full inquilinism" (WILSON 1975), had to be rewritten completely (BUSCHINGER 1989a, HÖLLDOBLER & WILSON 1990). In this genus neither a temporary parasite nor a typical full inquiline has been found as yet. Instead, five species conduct slave raids with group recruitment and sting-fighting. During colony foundation the young queen throttles the host colony queen over weeks or even months until she finally dies. In *Myrmoxenus krausseii* the number of workers is drastically reduced to only about 3 - 5 (one population is workerless; BUSCHINGER 1989b), and slave-raiding is, thus, ineffective, even though under laboratory conditions the workers are still capable of performing all raiding activities.

Finally, three *Myrmoxenus* species have been found with only queens and no workers (*M. adlerzi*, *M. corsicus*, *M. birgatae*). Nevertheless, the young queens throttle the host queens to death as do their slave-making relatives. Thus, they differ from true inquilines which coexist with the host species queens or invade orphaned host colonies (WINTER 1979, BUSCHINGER & al. 1983, BUSCHINGER & WINTER 1985, DOUWES & al. 1988). Also, in this genus an evolution from normal swarming behaviour of the alate sexuals to mating in the mother colony, and thus inbreeding, has been found. Three of the slave-raiding species have mating flights; two slave-raiding species (*M. algerianus*, *M. bernardi*) and all the "degenerate slave-makers" and workerless species of the genus mate inside the nest (Appendix 1).

In this context note that experimental crossbreeding of several *Myrmoxenus* species with very different life habits has clearly demonstrated that they belong to one genus and that they are very closely interrelated (JESSEN & KLIN-KICHT 1990, BUSCHINGER 2001).

An evolution obviously paralleling that of *Myrmoxenus* has been observed in the genus *Chalepoxenus*, which also belongs to the Formicoxenini, and which also comprises both actively dulotic species (*C. muellerianus*, *C. kutteri*) and at least one apparently degenerate slave-maker (*C. brunneus*) (CAGNIANT 1985, EHRHARDT 1987, BUSCHINGER & al. 1988, 1989, SCHUMANN 1992) (Appendix 1). During slave-raids the *Chalepoxenus* workers sting their opponents to death. Surprisingly, this genus, like *Myrmoxenus*, parasitizes a couple of *Temnothorax* species, and even more surprising, several *Temnothorax* species may be hosts of both a *Chalepoxenus* and a *Myrmoxenus* species. Both genera are distributed around the Mediterranean. As in the workerless *Myrmoxenus* species, the workerless *Chalepoxenus brunneus* also has preserved the host-killing behaviour of its dulotic congeners. One major difference between the dulotic *Chalepoxenus* species and *C. brunneus* is that the dulotic *Chalepoxenus* queens kill or drive off all adult workers, and take over only the host species brood, whereas the *C. brunneus* queen stings only few of the host workers, and somehow is accepted by the others.

In a third group of social parasites of the tribe Formicoxenini no evolutionary trend, such as one from slavery to inquilinism, is discernible. *Harpagoxenus sublaevis*, *Leptothorax* (= *Doronomyrmex*) *kutteri*, *L. (= D.) goesswaldi* and *L. (= D.) pacis*, the four European parasites of a common host species, *Leptothorax acervorum*, all exhibit different strategies of host exploitation. Nevertheless all four, according to Emery's rule, should be closely related to the host species, and thus also to each other. Morphological, karyological and ethological evidence support this assumption (BUSCHINGER 1990): *Harpagoxenus sublaevis* is an actively dulotic species with a life history similar to that of *Chalepoxenus*. The one dissimilarity is that *H. sublaevis* has a different fighting technique when raiding for slaves or taking over a host colony. With secateur-like mandibles it cuts off the appendages of the host species workers. Apart from *L. acervorum* which is the most frequent host of *H. sublaevis*, *L. muscorum* and *L. gredleri* are also enslaved. *Leptothorax kutteri* is a typical inquiline. It is workerless, and usually several reproductive queens coexist with the *L. acervorum* queens in a nest. Morphologically, *L. kutteri* has few peculiarities, and closely resembles the host species (BUSCHINGER 1966, ALLIES & al. 1986). *Leptothorax goesswaldi* was long believed to represent another workerless inquiline. However, the *L. goesswaldi* queen, soon after mating in August, penetrates a host colony and waits there until the next spring. She then develops fertility and slowly kills the colony's *L. acervorum* queens by cutting off their antennae (BUSCHINGER & KLUMP 1988). *Leptothorax goesswaldi* therefore may be termed a "murder-parasite" in the sense of FABER (1967), or a queen-intolerant inquiline. *Leptothorax pacis*, finally, is apparently a third inquiline of *L. acervorum*, which lives with functional host queens. Host species sexuals are often produced alongside the parasites' offspring (BUSCHINGER 1971, BUSCHINGER & al. 1981). More recent observations, however, revealed that the *L. acervorum* queens in nests infested by

L. pacis, albeit not showing signs of being physically damaged, have reduced fertility (BUSCHINGER 1990). Host species sexuals are reared for one or two years after the invasion of a colony by *L. pacis*, from larvae which are still present. In this group of Formicoxenini the larvae usually hibernate once, and often twice, before pupation. It is not conceivable that the three workerless species, *L. kutteri*, *L. goesswaldi* and *L. pacis*, which are morphologically very similar to their common host *L. acervorum* (former genus *Doronomyrmex*) have originated from the morphologically much more specialized slave-maker genus *Harpagoxenus*.

The inquiline status of the North American species *Leptothorax* (= *Doronomyrmex*) *pocahontas* is questionable, and its life history remains enigmatic (BUSCHINGER & HEINZE 1993). As in Europe, the tribe Formicoxenini in North America comprises several slave-making and inquiline genera and species (BUSCHINGER 1981, BEIBL & al. 2005) (Appendix 1) with a couple of slave-making ants (*Temnothorax duloticus*, *Temnothorax* sp., *Protomognathus americanus*, *Harpagoxenus canadensis*) and a few inquilines (*Temnothorax minutissimus*, *Leptothorax paraxenus*, *L. wilsoni*). *Harpagoxenus canadensis* has a number of ill-defined slave species that belong to the *L. muscorum* complex (BUSCHINGER & al. 1980, STUART & ALLOWAY 1983). Again, nothing suggests that inquilines in this group originate from dulotic relatives.

The social parasites in the tribe Tetramoriini, from the genera *Strongylognathus*, *Anergates* and *Teleutomyrmex*, require a special consideration. *Strongylognathus* is a Palearctic genus of ca. 25 species, all characterized by saber-shaped piercing mandibles. They live as parasites together with *Tetramorium* species, and probably most of them are active slave-makers. Two species, *S. testaceus* and *S. karawajewi*, apparently are queen-tolerant inquilines though they have retained a comparatively high number of own workers (SANETRA & BUSCHINGER 2000). *Anergates atratulus* is a long-known workerless inquiline of *Tetramorium* species that probably invades already orphaned host colonies. The males are wingless, "pupoid". Mating thus occurs inside the mother colony whereas mated gynes disperse on the wing. The sex ratio is considerably female-biased (0.67 - 0.98 female sexuals / total sexuals), and males are able to mate with at least three, but supposedly many more gynes (HEINZE & al. 2007). Several *Anergates* queens (up to four observed) may coexist in one host colony. Inbreeding, thus, occurs regularly but is not obligatory. *Teleutomyrmex schneideri*, finally, is the famous "ultimate social parasite" (HÖLLDOBLER & WILSON 1990), extremely rarely found in colonies of European *Tetramorium* spp. and probably sharing the host species with *Anergates atratulus*. *Teleutomyrmex schneideri* has been found in the Swiss and French Alps, in the Pyrenees, in Spain (ESPADALER & CUESTA 2006), and once in Turkmenistan (BUSCHINGER 1995). A second species, *T. kutteri*, was described from the Spanish Sierra Nevada (TINAUT 1990) (Appendix 1).

In this tribe Tetramoriini, the parasitic genera *Strongylognathus*, *Anergates* and *Teleutomyrmex* apparently have separate phylogenetic origins in the host genus *Tetramorium* (see SANETRA & BUSCHINGER 2000). The host species among the Tetramoriini traditionally were named *Tetramorium caespitum* and / or *Tetramorium impurum*. However, recent investigations of SCHLICK-STEINER & al. (2006) have demonstrated that the *Tetramorium caespitum* / *impurum*

complex in Europe comprises at least seven species. Since it is very difficult *a posteriori* to attribute the records of *Tetramorium* hosts in the literature to one or the other taxon among those newly detected it is preferable at present to name the host species "*Tetramorium* sp." In any case, also in the tribe Tetramoriini nothing points to an evolution of the inquiline genera from slave-making ancestors.

In summary, little evidence supports the hypothesis of different evolutionary pathways leading from xenobiosis, temporary parasitism or slavery to inquilinism as had been suggested (e.g., HÖLLDOBLER & WILSON 1990). Instead, as pointed out under "Evolutionary aspects of social parasitism", a separate origin of inquilines directly from independent, i.e., non-social-parasite, ancestors appears more probable.

Mechanisms involved in the coexistence of two or more species in one nest

The first problem a parasite queen has to cope with is to be accepted in a host species colony. Many papers have addressed this subject. LENOIR & al. (2001) discussed a "chemical insignificance" of young social parasites when penetrating a colony, just like callow ants that quite easily can integrate into a foreign colony. In addition, host and parasite probably are similar in their semiochemistry and the two factors together may facilitate the "necessary mimicry to bypassing the colony odor barrier". The authors also reviewed the various chemical weapons applied by social parasites such as propaganda, appeasement or repellent substances mainly during the usurpation period.

More generally, the coexistence of two or, in slave-maker colonies, even more species within a colony implies a number of mechanisms ensuring mutual tolerance and more or less perfect cooperation. On the other hand, this coexistence also gives rise to conflicts, more than in mono-specific colonies, that have been addressed in numerous recent publications.

Host specificity and host-parasite recognition, imprinting. Some progress has been achieved mainly with respect to imprinting and host specificity. Slave-makers (*Chalepoxenus muellerianus*) are known to imprint on their specific slave species. The slave-maker workers search for, and attack, preferably neighbouring colonies belonging to the same species that is already present as slaves in their colony (SCHUMANN & BUSCHINGER 1995). Young queens of *C. muellerianus* also tend to attempt to penetrate colonies of the host species present in their colony of birth, for parasitic colony foundation (SCHUMANN & BUSCHINGER 1994). Imprinting mainly occurs in young slave-maker workers and queens after hatching from pupae. However, the results also suggested a pre-imaginal learning already during the larval and / or pupal instars (SCHUMANN & BUSCHINGER 1994). Host choice apparently is due to a blend of predisposition and early learning. That host specificity thus is a matter of host choice in *Myrmoxenus* and *Chalepoxenus* is further supported by experiments showing that several species could be reared with non-natural hosts, i.e., that the properties of the host species may be comparatively irrelevant (SCHUMANN & BUSCHINGER 1995, BUSCHINGER 2001). Even mate recognition during sexual behaviour of a parasite species may be influenced by the host species that had reared the parasites (BEIBL & al. 2007).

The other way round, also the host species may imprint on their slave-makers. BLATRIX & SERMAGE (2005) have

studied this phenomenon in the slave-makers *Chalepoxenus muellerianus* and *Myrmoxenus ravouxi*. The principal host species of both, *Temnothorax unifasciatus*, imprints better on the parasites than *Temnothorax parvulus*, a species that in nature is never parasitized by any slave-maker or inquiline.

The mentioned findings in myrmicine slave-makers match the observations of GOODLOE & al. (1987) in North American *Polyergus lucidus* (Formicinae): in any single nest of this species only one out of three possible slave species has been found. The slave-makers raid only colonies of that particular species. The *Polyergus* scouts must be responsible for this selective raiding. BONO & al. (2007) also observed in an area with two sympatric hosts present (*Formica occulta* and *Formica* cf. *argentea*) that individual colonies of the slave-maker *Polyergus breviceps* differed in host preference during raiding and specialized on only one of the two available host species. In line with this, for European *Polyergus rufescens*, LE MOLLI & MORI (1987) stated "we can assume that social experience immediately following eclosion of *F. cunicularia* workers can fully explain their enslavement in nature and, therefore, the inter-specific altruism of this host species towards the parasite."

Cooperation within a slave-maker colony. The necessary cooperation within a slave-maker nest requires mutual tolerance of the slaves which may have been captured as pupae from several host colonies and which may even belong to two or three host species. Interestingly, the pattern of acceptance among slaves can differ from the acceptance of slave brood by the slave-makers themselves, as in a topical example from SCHUMANN & BUSCHINGER (1991): *Harpagoxenus sublaevis* enslaves up to three host species, *Leptothorax acervorum*, *L. muscorum* and *L. gredleri*. The slave-makers raid on colonies of all host species indiscriminately and on a few occasions all three host species have been found within one and the same *Harpagoxenus* colony. However, *L. acervorum* slaves refuse pupae of *L. muscorum* brought in by the *Harpagoxenus*, whereas *L. muscorum* slaves accept *L. acervorum* pupae. As a consequence, *Harpagoxenus* colonies with only *L. acervorum* slaves, and with a mixed stock of *L. acervorum* and *L. muscorum* slaves are frequent, whereas colonies with *L. muscorum* alone are rare, although *H. sublaevis* queens invade colonies of *L. acervorum* and *L. muscorum* for colony foundation at about equal rates.

Slave species differ also in their inherent tendency to cooperate with slave-makers, as follows from experiments by MORI & al. (1996). These authors tested the acceptance of slave-maker cocoons (*Polyergus rufescens*) by free-living workers of two slave species, *Formica cunicularia* and *F. rufibarbis*. Workers of both species cared for the foreign brood and for conspecific brood at comparable rates. This was different, however, with cocoons of the facultative slave-maker, *Formica (Raptiformica) sanguinea*: They were not accepted by the two slave species although both can serve as slaves in colonies of *F. sanguinea*. An interspecifically recognisable brood pheromone and brood mimicry by *Polyergus* but lack of those in *Raptiformica* and, more generally, a closer phylogenetic relationship between *Polyergus* and the slave species may be responsible for the observed differences.

Chemical recognition signals. Since D'ETTORRE & HEINZE (2001) provided a detailed account of chemical re-

cognition in slave-making ants and their slaves the subject shall be only briefly addressed here. Chemical analyses of *Polyergus rufescens* and its slave species revealed that newly hatched slave-makers develop or acquire a cuticular hydrocarbon profile matching that of the slave species present (D'ETTORRE & al. 2002). Social integration of *P. rufescens* workers into host colonies thus appears to be due to the ability to modify their cuticular hydrocarbon profile accordingly. In analogy, the slave-maker queen of *Polyergus breviceps* kills a host colony queen and during this process she changes her cuticular hydrocarbon profile (JOHNSON & al. 2001).

Eggs, as other brood instars, of slave-making *Polyergus breviceps* must elicit rearing behaviour from several host species. According to JOHNSON & al. (2005), two host species nevertheless discriminated against and rejected slave-maker eggs, despite hydrocarbon analyses that revealed an adaptation to local host species. The authors suggested that host rearing of *P. breviceps* eggs might reflect an evolutionary equilibrium that is maintained by probability and cost of recognition errors.

Dominance behaviour. Among social parasites, particularly among slave-maker workers, dominance behaviours are frequently observed, mainly in orphaned colonies (i.e., where the parasite queen was lost). Slave-maker workers usually have well-developed ovaries but at least better developed ones than their slaves (BUSCHINGER 1990), and thus have a considerable reproductive potential (HEINZE 1996). FRANKS & SCOVELL (1983) considered this in context with dominance hierarchies detected among slave-maker workers. In their experiments, the queen solicited food preferentially from dominant workers. The authors suggested that the queen thus might limit their production of eggs, and that the hierarchies, on the other hand, may be explained as competition for the production of males.

BLATRIX & HERBERS (2004) studied dominance hierarchies in colonies of the slave-maker ant *Protomognathus americanus*. Both in queenright and queenless colonies near-linear dominance hierarchies were found that were correlated with reproductive activity. The queen, when present, dominates the workers and monopolizes reproduction. In queenless nests only one of the *Protomognathus* workers lays eggs that develop into males. In contrast, in *Polyergus rufescens*, the slave-maker workers produce up to 100% of the males reared by a queenright colony (BRUNNER & al. 2005). The authors suggested that slave-maker workers are more strongly selected to increase direct fitness by producing sons than workers of independent species.

Coevolution of social parasites and their hosts

In this section, further aspects of interactions between host and parasite species shall be addressed, namely those revolving around the important question of whether and how the antagonistic actions of the parasites, especially slave-makers, elicit measurable evolutionary reactions in the host species or their populations. Whereas an "evolutionary arms race" is clearly demonstrable on the side of the parasites with their sometimes conspicuous adaptations such as strong mechanical armament, chemical secretions and changes in life cycles, sex ratios and sexual behaviour, it is more difficult to detect reactions of the host forms (DAVIES & al. 1989).

In this context, we have to consider the following. Though published data are rare, it is evident that social parasites, particularly the inquilines and the slave-makers, never occur throughout the range of the respective host species. In fact, they often occupy only small parts of this range (e.g., WILSON 1971, ZAMORA-MUÑOZ & al. 2003). Usually the parasites are found in more or less isolated patches within the host range, and often these patches are characterized by particularly high densities of the host species (A. Buschinger, unpubl.). Consequently, population sizes of the parasites also are much smaller than those of the host species. Between three and ten parasitized colonies per 100 host colonies is often a realistic estimate, within a patch where the parasite is present at all. Inquilines may be even rarer: only 10 of 776 (1.3%) nests of *Pogonomyrmex rugosus* were parasitized by the inquiline, *P. colei* in a survey by JOHNSON & al. (1996), while at two other sites none out of 1499 potential host colonies contained the parasite. Taking a conservation point of view, TRONTTI & al. (2006) concluded that populations of the rare Mediterranean *Plagiolepis xene*, an inquiline of *P. pygmaea*, are genetically highly vulnerable, as a consequence of their rarity.

Of course a slave-maker colony can attack and decimate several host colonies in the vicinity of its nest, but there will always remain numerous host colonies that never experience any impact by slave-makers. Interestingly, different slave-maker species may harm their respective hosts differently. According to HARE & ALLOWAY (2001) the slave-maker *Protomognathus americanus* in enclosure experiments did not significantly damage one of its hosts, *Temnothorax longispinosus*, whereas another host, *Temnothorax curvispinosus*, experienced marked reductions in productivity when the slave-maker *Temnothorax duloticus* was present.

Given the restricted ranges of social parasites and the very low densities as compared to their hosts it is altogether hard to imagine how social parasitism should exert sufficient selection pressure to stimulate the evolution of particular defensive mechanisms in a host species as a whole. Nevertheless, coevolution and the subject of coevolutionary arms race among hosts and parasites have been addressed in recent times, frequently at the population level, e.g., by BRANDT & FOITZIK (2004), BRANDT & al. (2005, 2007), DAVIES & al. (1989), D'ETTORRE & HEINZE (2001), FISCHER-BLASS & al. (2006), FOITZIK & al. (2003), JOHNSON & HERBERS (2006).

Little has been known on host-parasite coevolution with respect to inquilines or temporary parasites. Of relevance in this context, though, is that experimental introduction of parasitic queens into host colonies often fails (ALLIES & al. 1986). Colony-founding dulotic *Harpagoxenus* queens frequently are killed or driven off when they try to invade a (too) large host colony. In laboratory experiments with small colonies of the host species *Leptothorax acervorum*, only about one half of the *Harpagoxenus* queens were successful (WINTER & BUSCHINGER 1986). These and similar observations have led to the question whether enslaved ants may become rebellious and perhaps abscond from their nest or even fight against the slave-makers, once they have been enslaved.

A priori, such rebellions appear improbable given the fact that the slaves integrate into the slave-maker colony when hatching from pupae, imprinting on their masters and

on the slaves already present. A couple of papers have nevertheless addressed the topic. One line of argument was that of GLADSTONE (1981) who argued that ant slaves have no alternative to staying in the slave-maker nest because no other behaviour would increase their fitness. In this, the author did not consider the possibility that slaves that have absconded might reproduce by laying eggs and rearing male offspring which would spread genes for such rebellious behaviour. Several other authors have made opposing observations. ALLOWAY & DEL RIO PESADO (1983) described some kinds of slave aggression against the slave-makers, though in experiments under semi-natural conditions. CZECHOWSKI (1994) also observed some slave emancipation in *Formica sanguinea* colonies that had been enriched with many pupae of the non-natural host species, *Formica polyctena*. Finally, ACHENBACH & FOITZIK (2009) found that slaves of the North American slave-maker, *Protomognathus americanus*, destroy and eat considerable proportions of the slave-maker's brood, particularly queen and worker pupae. In this way they reduce the numbers of slave raids on neighbouring host species colonies, and the numbers of parasite colony foundations. Since the host colonies in the population are quite closely related among each other, the rebellious slaves thus would gain indirect fitness by helping their non-enslaved relatives.

BRANDT & al. (2007) compared two slave-makers from Europe and North America using mitochondrial DNA and microsatellite markers. They found "limited gene flow between individual populations of both host and parasite species, allowing for a geographic mosaic of coevolution". So the host species *in toto* does not evolve any conspicuous adaptations in response to parasite pressure. However, the authors were able to measure local reactions of the host populations to the presence of the parasites, as well as adaptations of the slave-maker *Protomognathus americanus* to local host populations.

With an emphasis on coevolutionary dynamics, BRANDT & al. (2005) discussed the different interactions of host and parasite in slave-makers, queen-tolerant and queen-intolerant inquilines, focusing on the myrmecine tribe Formicoxenini. According to these authors, slave-making ants act as parasites during colony foundation, while their frequent slave raids follow a predator-prey dynamic; "... theory predicts that their associations are best described in terms of a highly antagonistic coevolutionary arms race". In contrast, BRANDT & al. (2005) further argued, queen-tolerant inquilines act as "true parasites", because of their rarity exerting a low selection pressure on their hosts, and queen-intolerant inquilines are better classified as parasitoids.

Students of host-parasite systems other than ones in the Formicoxenini also found evidence of local coevolution, partly differing from the conclusions by BRANDT & al. (2005). Thus, ZAMORA-MUÑOZ & al. (2003), investigating the very rare and local slave-maker *Rossomyrmex minuchae* in Spain, observed that the host species *Proformica longiseta* is less aggressive towards the slave-maker in areas where the parasite is present, as compared to *Proformica* from unparasitized populations. They found evidence suggesting that the "low level of aggression might be an apomorphic trait, evolved by the parasite selection pressure. For the first time in slave-maker ants, we demonstrate that the decreasing of a trait (aggressiveness) could be considered a counter-defense consequence of an arms race, a co-

evolutionary process in progress that matches with a Mafia system" (ZAMORA-MUÑOZ & al. 2003).

In contrast to this counterintuitive experience, D'ETTORRE & al. (2004) reported that colonies of the slave species *Formica rufibarbis* may recognize the presence of slave-maker nests (*Polyergus rufescens*) in their vicinity, and become more aggressive towards the parasites than in areas where the slave-maker is lacking. The aggressiveness was particularly enhanced in the summer, when slave-makers are conducting their raids.

All in all, at present it is difficult to figure out a clear, general tendency in the issue of host-parasite coevolution for any of the known types of social parasitism that would hold across all major taxonomic ant groups with social parasites.

Conclusion

As HEINZE (2008) has put it for ants in general, we are far from understanding the evolution also of social parasites, and the appeal of TSCHINKEL (1991) to collect much more data on ant life histories applies to social parasitic ants as well. Somehow it is disappointing to see that during the past 20 years fewer new parasitic species have been described than over comparable earlier time stretches, although it is likely that the discovery curve has not yet been saturated. Also, often no or very few life history details have been provided for new species.

It is recommendable to search for unknown parasite species, particularly in regions where only few have been found as yet. Many known parasitic species remain to be studied both in the field and in the laboratory in order to find out details of their life histories. The life history, temporary parasitism, of *Bothriomyrmex* has been studied in only one out of the ca. 38 species! Sometimes surprising differences may be found when even very closely related parasite species are carefully studied. An impressive example is the group of three presumed "inquilines" of *Leptothorax acervorum*, one of which, *L. goesswaldi*, turned out to kill the host colony queens by the unique (and derived?) method of slowly biting off the host queen's antennae. As was shown in the section on coevolution, even considerable intraspecific variation may occur in the relations of parasites and their hosts when different populations are compared.

In essence, many interesting questions remain. Why is social parasitism, and particularly dulosis, much more frequent in temperate zones than in tropical countries? What is the reason for the unequal distribution of the different types of social parasitism among the ant genera? Why are certain ant genera or tribes particularly rich in social parasites? Why are certain species particularly preferred hosts for social parasites? What are the genetic implications of inbreeding which is so frequent in parasitic ants? – Myrmecology, and particularly the study of social parasites, remains exciting!

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Zusammenfassung

Die letzte Übersicht über den Sozialparasitismus bei Ameisen wurde 1990 publiziert. Vergleichsweise wenige neue

parasitische Arten wurden seither entdeckt, doch wurden Fortschritte erzielt im Hinblick auf die Evolution des Sozialparasitismus und die an der Aufrechterhaltung der parasitischen Beziehungen zwischen den Arten beteiligten Mechanismen. Temporärer Sozialparasitismus, Dulosis, Inquilinismus und Xenobiose werden als die Hauptformen des Sozialparasitismus bei Ameisen bestätigt. Der so genannte intraspezifische Sozialparasitismus sollte gegen die obligatorischen, interspezifischen Beziehungen zwischen Parasiten- und Wirtsarten klar abgegrenzt werden.

Es gibt einige wenige evolutive Übergänge zwischen diesen Formen, hauptsächlich von der Dulosis zu einem abgeleiteten Zustand ohne Arbeiterinnen. Dennoch ist kein Hinweis auf eine Entwicklung aller Formen des Sozialparasitismus auf unterschiedlichen Wegen hin zum Inquilinismus zu finden, wie das früher vorgeschlagen worden war. Die Regel von Emery im weiteren Sinn wurde mittels molekularer Untersuchungen bestätigt. Die Wirts-Parasit-Erkennung beruht auf chemischen Cuticula-Merkmalen, wobei Prägung beteiligt ist. Sozialparasitische Ameisen finden zunehmend Interesse mit Blick auf das Verständnis von Konflikt und Kooperation zwischen Ameisen. Koevolution von Sozialparasiten und deren jeweiligen Wirtsarten sowie der Einfluss der Sozialparasiten auf die Wirtspopulationen werden intensiv untersucht. Offene Fragen betreffen die ungleichmäßige Verteilung von Sozialparasiten innerhalb der lebenden Unterfamilien und Gattungen von Ameisen, sowie ihre geografische Verbreitung einschließlich des Fehlens von Sklavenhaltern in den Tropen.

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