Best regards, A. Buschinger

J. evol. Biol. 2: 265–283 (1989)

1010–061X/89/04265–19 $ 1.50 + 0.20/0

Evolution, speciation, and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae)

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Key words: Ants; evolution; inbreeding; social parasitism; speciation.

Abstract

The ant genus *Epimyrma* exhibits an evolutionary transition from fully developed slave-making to a completely workerless parasitic condition. Two of the actively dulotic species, like the closely-related *Myrmoxenus gordiagini*, engage in mating and dispersal flights as is usual in ants, whereas in the remaining five species intranidal mating of the sexuals and thus continuous inbreeding is observed; the females shed their wings in the nest and disperse on foot. The inbreeding species are very closely interrelated, as was recently demonstrated with hybridization experiments. The reduction of slave-making and the evolution of intranidal mating in this group can hardly be explained assuming ordinary models of speciation and spreading of species. I therefore suggest the scenario of an original, widespread, polytypic species with partially isolated, host-specific races and populations in which genetic dispositions for a reduction of worker numbers and slave-raiding, and for intranidal mating, were adaptive; the latter, however, encountered problems associated with inbreeding. Such a situation then selected for a sex-determination mechanism resistant to inbreeding which spread throughout the range of the species, completing the life-pattern. Due to intranidal mating and inbreeding, however, gene flow between populations is interrupted. The inbreeding system has evidently led to the conservation of a status quo in each population it has reached. The original host-specific races are morphologically and biologically discrete entities, which should be maintained as species, as they were described, even though they consist of reproductively isolated demes which themselves are built up of isolated, clone-like lineages.

1. Introduction

The myrmicine ant tribe Leptothoracini is extraordinarily rich in socially parasitic genera and species exhibiting various strategies of host species exploitation, such as

xenobiosis (guest-ants), dulosis (slave-makers), and inquilinism (permanent, usually workerless parasites) (Buschinger, 1981). Since Darwin's (1859) hypothesis on the origin of slavery among ants the evolution of social parasitism and the potential transitions from one type to the other have been the subject of numerous studies and discussions (Emery, 1909; Wilson, 1971; Buschinger, 1986). Most social parasites, however, are rare, or at least rarely found, and speculation thus often outweighs knowledge.

The leptothoracine genus *Epimyrma*, together with the closely related *Myrmoxenus gordiagini*, is exceptional, in that detailed studies have been carried out on eight out of about 11 valid species. Since Winter (1979) first detected the slave-raiding of one species, *E. ravouxi*, our studies have unraveled a variety of life cycles and parasitic strategies in as yet unparalleled diversity within a group of close relatives. Two evolutionary trends have been recognized in *Epimyrma*. One is a "degeneration" of active slavery, with a reduction of *E.*-worker numbers ending in complete workerlessness; the other is a change in sexual behavior, where a transition from swarming flights to intranidal mating and thus continuous inbreeding has occurred (Buschinger and Winter, 1982).

As will be shown, however, it is difficult to arrange the species involved in a traditional phylogenetic order with a stepwise reduction of slavery, a parallel transition to nest-mating, and the subsequent radiation of a species with these characters. I rather suggest an unconventional model of speciation assuming that the nest-mating species originated more or less simultaneously from a widely distributed superspecies with host-specific races, some of which had reduced slave-raiding and worker numbers to variable degrees. Reproductive isolation of the subspecies was completed through intranidal mating and inbreeding, which itself may have become possible through the spreading of a new, inbreeding-resistant mechanism of sex-determination.

2. The *Epimyrma* and *Myrmoxenus* species: Life cycles, ranges and relationships

Leptothoracine colonies, including those parasitized by *Epimyrma* and *Myrmoxenus*, are usually small, comprising 100–400 adult individuals, often fewer. Queens and workers are tiny, measuring 2.5–5 mm. Nests are easily accessible, often one-chambered cavities in wood or in rock crevices. Complete colonies can be collected, censused, and observed under laboratory conditions over years. Population densities of independent (host-) species can be high, with 3 or more nests/m^2, whereas the parasites occur in 1–10 %, often much less, of the host nests in a given locality (e. g. Buschinger, 1968; 1987; Buschinger and Winter, 1983).

Three *Epimyrma* species, *E. africana*, *tamarae*, and *zaleskyi*, are poorly known (Douwes et al., 1988), whereas detailed studies have been carried out on the following eight species: *Myrmoxenus gordiagini* (Buschinger et al., 1983); *Epimyrma ravouxi* (= *E. goesswaldi*) (Buschinger, 1982; Buschinger and Winter, 1983; Gößwald, 1933; Winter, 1979; Winter and Buschinger, 1983); *E. stumperi* (colony foundation: Kutter, 1951; slave-raids: Buschinger, unpubl.); *E. kraussei* (= *E.*

vandeli, = *E. foreli*) (Buschinger et al., 1986); *E. bernardi* (Buschinger and Winter, unpubl.); *E. corsica* (Buschinger and Winter, 1985); *E. adlerzi* (Douwes et al., 1988); *E. algeriana* (Buschinger et al., in prep.).

Table 1 presents an overview of the most important results of these studies, referring to colony foundation behavior, slave-raiding, parasite worker numbers, host species, sexual behavior, and ranges. A brief comparative description of life history traits will be given in the following.

Colony foundation

All the eight species mentioned above share a particular form of behavior of the young queens when they invade a host-species colony in order to found a society of their own there. They are accepted by most of the adult host-species workers, sting a few of them, which usually recover, but then eliminate the host colony queens slowly by throttling them with their mandibles. Colony foundation occurs in summer or fall, in the swarming species (see below) *M. gordiagini*, *E. ravouxi*, *E. stumperi*, and in winter (*E. algeriana*) or spring in the nest-mating species *E. kraussei*, *E. adlerzi*, *E. corsica*, and *E. bernardi*, where the inseminated young queens remain in their natal nest through fall and most or all of the winter.

Monogyny vs. polygyny

All species except *E. algeriana* are monogynous, and all host-species nests contain only one queen each, except for *Leptothorax tuberum*, which is facultatively polygynous. The *E. stumperi* queen thus has to throttle the host species queens one after the other when parasitizing a multiple-queened nest (Kutter, 1951). *E. algeriana* is polygynous in most populations studied. Colony foundation through single queens is apparently rare; many young queens remain in their mother colonies and develop fertility there (Buschinger et al., in prep.).

Monogamy of females

Queens are probably monogamous. This may be suspected at least for the nest-mating species (see below) with highly queen-biased numerical sex-ratios (*E. adlerzi*: 0.19 ♂/♀, Douwes et al, 1988; *E. algeriana*: 0.16–0.22 ♂/♀, Buschinger et al., in prep.; *E. corsica*: 0.08 ♂/♀, Buschinger and Winter, 1985; *E. kraussei*: 0.3 ♂/♀, Winter and Buschinger, 1983). In one of the swarming species, *E. ravouxi*, the sex ratio is 1.5 ♂/♀, and is thus male-biased, and polygamy cannot be excluded (Winter and Buschinger, 1983).

Parasite worker numbers

The species differ with respect to slave-maker workers found in their colonies. *M.gordiagini*, *E. ravouxi*, *E. stumperi* and *E. bernardi* (of which only few colonies have been collected; Espadaler, 1982) have considerable numbers of parasite-species

Table 1. Life history traits, ranges, and host species of *Epimyrma* spp. and *Myrmoxenus gordiagini*

Parasite species	Monogyny/ Polygyny	Col. foundation w. throttling	Mating behavior	Sexual brood[2]	Slave-raiding	Parasite worker number	Host species	Known range
M. gordiagini	M	+	swarming	slow	+	high	*Leptothorax lichtensteini*, *L. serviculus*	Dalmatia (Yu), Bulgaria, Kasachstan (USSR)
E. ravouxi	M	+	swarming	slow	+	high	*L. unifasciatus*, *L. nigriceps*, *L. affinis*, *L. interruptus*, and others	Central and southern Europe from Spain through Greece, presumably Georgia (USSR) ("*E. tamarae*")
E. stumperi	M	+	swarming	slow	+	high	*L. tuberum*	High Alps (CH,F)
E. bernardi	M	+	intranidal	slow	+	high(?)	*L. gredosi*	Sierra de Gredos (Spain)
E. algeriana	P[1]	+	intranidal	slow	+	high	*L. spinosus* (and 3 other spp.)	Atlas, Rif (Algeria, Morocco)
E. kraussei	M	+	intranidal	rapid	±	low	*L. recedens*	S-Europe, N-Africa from Spain through Turkey, Sardinia, Corsica, Crete
E. corsica	M	+	intranidal	rapid	–	none	*L. exilis*	Corsica (F), C-Italy, Dalmatia (Yu)
E. adlerzi	M	+	intranidal	rapid	–	none	*L. cf. exilis*	Greece

[1] Facultative polygyny. In most populations studied the colonies usually contain more than one functional *Epimyrma* queen.
[2] Slow brood: Female sexuals develop from hibernated larvae. Rapid brood: Females develop from eggs laid in the same year, without larval hibernation.

workers, up to about 70 in *E. ravouxi*. In the polygynous *E. algeriana* very high worker numbers, up to 200, have been recorded. In *E. kraussei* the worker number is reduced to a variable degree, dependent upon the local populations. Up to 20 workers were found in nests from southern Italy or northern Spain, in other populations, e. g. from northern Italy, there are 2–10 workers per nest and in a considerable fraction of colonies they are lacking. In one population from southern France, and in Crete, *E. kraussei* workers are nearly or totally absent. *E. corsica* and *E. adlerzi*, finally, are always workerless.

Slave-raiding

In the species with high worker numbers, *M. gordiagini*, *E. ravouxi*, *E. stumperi*, *E. bernardi*, and *E. algeriana*, slave-raids could be observed in laboratory experiments. These species employ a group-recruitment technique with a scout leading a file or a procession of up to 40 slave-maker workers towards a host-species nest, on a short-lived pheromone-trail (Winter, 1979; Buschinger et al., 1983). A large proportion of the workers of the attacked host colonies are stung to death, and their brood is carried over to the slave-maker nest. Part of the workers, with some of the brood, and the queen, often escape even in the restricted area of an experimental arena. We assume that in the field a good many of the host colonies survive a raid, as was observed in another leptothoracine slave-maker, *Harpagoxenus sublaevis* (Buschinger, 1983). *E. kraussei* colonies which have a sufficient number of *E.*-workers can also carry out raids on host-species nests, but population studies (Buschinger and Winter, 1983) revealed that raiding is rare or absent in the field. Workerless colonies of *E. kraussei*, and the workerless species *E. adlerzi* and *E. corsica* naturally cannot conduct slave-raids.

Host-specificity

M. gordiagini and the *Epimyrma* species are more or less host-specific. *E. ravouxi*, like other active slave-makers (Buschinger et al., 1980), enslaves a number of host species. Sometimes a single colony may contain two host species simultaneously (Gößwald, 1933; Buschinger and Winter, 1983). *E. bernardi* (with *L. gredosi*) and *E. stumperi* (with *L. tuberum*) were found with only one host species each, *E. stumperi* certainly because in its habitat no other potential host species occurs. *M. gordiagini* in Yugoslavia coexists with *L. lichtensteini*, whereas in its distant type area, near Koktschetaw, USSR, *L. serviculus* was reported as host species. Over most of its range *E. algeriana* parasitizes *L. spinosus*; only a few populations, which might represent a different subspecies of *algeriana* (Cagniant, 1968), have other host taxa. The degenerate slave-maker, *E. kraussei*, exclusively parasitizes *L. recedens*. The two workerless species, *E. corsica* and *E. adlerzi*, seem to have the same host species, *L. exilis*. The hosts of the two species, however, are morphologically somewhat different and might represent two separate species-level taxa (Douwes et al., 1988).

Colony life-span

Colonies of the actively dulotic species which replenish their slave stock repeatedly, over years, have a life expectancy of up to 10 years, as was shown with population studies in *E. ravouxi* (Buschinger and Winter, 1983), the single queen surviving this long. The *E. algeriana* societies, due to their polygyny, might have a considerably longer life-span because young queens remain in their natal nests and may replace old queens (Buschinger et al., in prep.). In contrast, colonies of the "degenerate slave-maker" *E. kraussei*, and of the two workerless species survive only 2–3 years, and then decline when the last host workers have died (Buschinger and Winter, 1983; 1985; Douwes et al., 1988).

Fast brood vs. slow brood

Myrmoxenus and the actively dulotic *Epimyrma* species produce only a few workers in the first year after colony foundation. Sexuals arise as "slow brood", as in *Myrmica* (Wilson, 1971), from hibernated larvae, and thus appear for the first time in the second year of a colony. In contrast, the "degenerate slave-makers" *E. kraussei* as well as *E. adlerzi* and *E. corsica* already rear their first sexual offspring as "fast" or "rapid" brood in the year of colony foundation, without a larval hibernation.

Mating behavior

As was mentioned above, the sexuals of some of the actively dulotic species, *M. gordiagini*, *E. ravouxi*, and *E. stumperi*, make mating flights, as is usual in most ant species. *E. algeriana*, *E. bernardi*, *E. kraussei*, *E. adlerzi*, and *E. corsica* mate inside the natal nests. The females shed their wings and remain there over the winter until they leave on foot, mostly in spring, in search of host colonies. The nest-mating species can thus be bred over generations in the laboratory. The swarming species, in contrast, usually do not mate under laboratory conditions. Their colony foundation behavior was therefore studied with newly-infested colonies found in the field (*E.r.*: Buschinger, 1982; Gößwald, 1933; *M.g.*: Buschinger et al., 1983); only Kutter (1951) was able to observe *E. stumperi* queens which had mated in a flight cage. Mates are full sublings in the monogynous, nest-mating species (*E. adlerzi*, *E. corsica*, *E. kraussei*, presumably *E. bernardi*).

Ranges of species

All members of the group are distributed around the Mediterranean; one species, *E. tamarae*, was reported from Georgia, USSR, and *Myrmoxenus* was originally described from east of the Urals.

The slave-making *E. ravouxi* has perhaps the largest known range, from northern Spain through Greece; *E. zaleskyi* from Czechoslovakia and *E. tamarae* might belong to this species, too (Buschinger and Winter, 1983).

The other swarming and slave-raiding species have comparatively much smaller ranges. Thus, *M. gordiagini* is known from its type area in the Soviet Union, from Bulgaria (Douwes, in litt., 1988), and from some populations along the Dalmatian coast of Yugoslavia (Buschinger et al., 1983). *E. stumperi* is restricted to a few localities at high elevations in the Alps (1800–2000 m; Buschinger, 1985a).

Among the nest-mating, slave-raiding species, *E. bernardi* has been found only in its type area, the Sierra de Gredos in central Spain (Espadaler and Restrepo, 1983), whereas *E. algeriana* has a wider range in the Atlas and Rif mountains of Algeria and Morocco (Cagniant, 1968; Buschinger et al., in prep.).

The degenerate slave-maker, *E. kraussei*, again has a very wide range, from North Africa through Spain, the South of France, Switzerland, Italy, Yugoslavia and Greece, to Turkey (Heinze, 1987). It has also been found in the Mediterranean islands of Sardinia, Corsica, Krk (Yug.) (Buschinger, 1985b), and Crete (unpubl.). *E. corsica* has been found in its type area, Corsica, in some places in Dalmatia (Buschinger, 1985b), and in one locality in central Italy (M. Mei, in litt.). *E. adlerzi* occurs in southern Greece (Douwes et al., 1988).

Evidence of close relationship

All the six *Epimyrma* species investigated, and *Myrmoxenus*, share an identical karyotype of n = 10 chromosomes, which is as yet unique among the 65 species of Leptothoracini studied (Douwes et al., 1988; Fischer, 1987). The throttling behavior of the young queens during colony foundation is also unique among the Leptothoracini. A similar behavior is only found in temporarily parasitic *Lasius* species (subfamily Formicinae) (Faber, 1967). The group-recruitment during slave-raids of *Myrmoxenus* and the *Epimyrma* species which have workers is only found in this group in Europe, not in the other slave-makers of the tribe (*Harpagoxenus*, *Chalepoxenus*). In two North American species, however, *Protomognathus* (= *Harpagoxenus*) *americanus* and *Leptothorax duloticus* (Buschinger et al., 1980), this behavior may have evolved convergently. These species differ markedly in their karyotypes (Fischer, 1987) from each other and from the *Epimyrma* group. Finally, the five nest-mating species have been successfully crossbred in nearly all possible combinations (Jessen, 1987; Jessen and Klinkicht, in prep.). With the exchange of sexual pupae between heterospecific nests, crossmated females were obtained after the sexuals had hatched. Hybrids were reared from the following species crosses: *E. adlerzi* × *E. corsica*, *E. adlerzi* × *E. kraussei* and *E. kr.* × *E. adl.*, *E. algeriana* × *E. adlerzi*, *E. algeriana* × *E. kraussei*, *E. bernardi* × *E. kraussei*, *E. kraussei* × *E. corsica* (always ♂ × ♀).

Conclusion

Myrmoxenus and *Epimyrma* represents a presumably monophyletic group of species which are certainly closely related, in which an evolutionary transition has

occurred from mating flights to intranidal mating, inbreeding, and dispersal of young queens on foot; a reduction of worker numbers and slave-raiding in some of these species, and the evolution of polygyny in at least one slave-making species.

3. Problems arising from a conventional phylogenetical arrangement of the *Epimyrma/Myrmoxenus* species

The actively dulotic species, in which the sexuals make mating and dispersal flights, probably represent the original condition in this group, and reduction of worker number and slave-raiding as well as intranidal mating are derived traits.

M. gordiagini has antennae with 12 (♀, ☿) or 13 (♂) segments like most of the host-species of subgenus *Myrafant*, whereas all *Epimyrma* species have 11/12-jointed antennae, except for *E. corsica* where a further reduction of antennal segments in females is frequent, and males usually have only 11 or 10, very rarely 12 antennomeres (Buschinger and Winter, 1985).

According to "Emery's rule" (Emery, 1909) socially parasitic ants very probably originated from their respective host-species groups. *M. gordiagini* might thus represent morphologically the state closest to the original, but has life habits identical to those of *Epimyrma ravouxi* and *E. stumperi*. After the reduction of the antennal segments to the condition found in this genus, a further speciation in a conventional manner, due to geographic isolation, may have occurred. Since active slave-makers often enslave several host species, a switch to a new host species, and adaptation to its pheromonal, seasonal, ecological, etc. peculiarities, and as a consequence, reproductive isolation from the original form, are easily conceivable.

What, however, was the next step?

The transition from swarming to nest-mating, inbreeding, and dispersal of young queens on foot, as well as the reduction of slave-raiding, imply a number of serious problems.

a) Obviously, the reduction of dispersal flights of the sexuals and colony foundresses strongly restricts the spreading capacities of a species. It is hard to imagine how a species like *E. corsica* would have reached the island of Corsica from the mainland, or vice versa, even if we assume a terrestrial connection during parts of the Pleistocene. Even more difficult to understand is how *E. kraussei* could have spread over all its present wide range on foot, in particular if we take into account that not only rivers, bays and high mountains are practically insurmountable barriers, but also all the areas in which the patchily-distributed host species is absent.

b) The obligatory inbreeding system in several of the *Epimyrma* species also affects the possibilities of a further speciation and evolution. Certainly the offspring of a local population with intranidal mating, living with one host species, may repeatedly try to penetrate nests of a second potential host species, and perhaps sometimes be successful.

For example in the Yugoslavian island or Krk we found one colony of *L. recedens* containing an *E. corsica* queen and her offspring. In this island, both *E. corsica* and *E. kraussei* occur, but always with their respective host species (*E.c.* with *L. exilis*, *E.k.* with *L. recedens*). This exceptional colony, however,

was the only one among a total of several hundred of the two *Epimyrma* species (collected all over their ranges), all others having the "normal" composition.

The parasites living with a second, new host species might be selected for better adaptation to it, and might develop morphological characters slightly different from those of the original form. However, due to intranidal mating, gene flow is interrupted not only between demes, but even between colonies belonging to the same population. Populations consist of clone-like groups of colonies (Buschinger et al., 1986). Lineages with adaptive characters may slowly outnumber the competing, less-adapted "clones", but, unlike in swarming species with outbreeding, such adaptive characters can hardly spread over a wider range.

Thus, if we assume transition to intranidal mating in one *Epimyrma* species alone, like *E. bernardi* or *E. algeriana*, it is hard to imagine how this trait could have spread over the range of this species, and how the other nest-mating species could have originated from the first one. A convergent and more or less simultaneous shift from swarming to nest-mating in at least five already-separate species is also difficult to understand. It would require a very strong selective pressure favoring intranidal mating, and again the spreading of this trait over the ranges of the species is not easy to imagine.

c) Seemingly the transition to intranidal mating is followed by a reduction of slave-raiding and worker numbers (Table 1). But, as demonstrated in the preceding section, it is hard to conceive that the reduction of worker numbers, or the complete loss of this caste, should have spread through all populations of the species, after they had already given up swarming flights and outbreeding.

An impressive fact demonstrating this difficulty is the presence of wings in the sexuals of all the nest-mating *Epimyrma* species. The evolution of workerlike (= ergatoid) or intermorphic queens, which is not uncommon in parasitic, and also in some independent ants (Heinze and Buschinger, 1987), would presumably be adaptive for these *Epimyrma* species, too, saving much energy which is wasted on building up the useless wings. Indeed, I found one *E. kraussei* colony in Spain which had an intermorphic queen. It had ordinary alate offspring, and I cannot say whether or not the wingless condition of the queen was genetically determined. However, if so, this trait could have spread only locally.

d) A problem also arises from the two biologically most derived species, the workerless *E. corsica* and *E. adlerzi*. Assuming a classical evolution, the two species should be the most closely related to each other. The neighboring ranges (Yugoslavia and Greece), and the common host species (*L. exilis*) seemingly corroborate this assumption, if the hosts are really conspecific. Morphologically, however, the two species differ considerably. *E. adlerzi* is most similar to the slave-raiding and swarming *E. ravouxi* (Douwes et al., 1988), whilst *E. corsica* represents morphologically the most distinct of all *Epimyrma* species.

e) An alternative hypothesis could be that a reduction of slave-raiding and worker number occurred first, followed by the transition to intranidal mating. However, the existence of *E. algeriana* and *E. bernardi*, both with workers, and actively slave-raiding, but with nest-mating sexuals, contradicts this assumption. It would also mean a convergent evolution of inbreeding in at least five separate species.

Conclusion

A conventional phylogenetical arrangement, particularly of the *Epimyrma* species exhibiting intranidal mating and reduction of slave-making, is problematic. It would require the convergent origin of these two features in at least five or three species, respectively, and their spreading over large areas despite the fact that intranidal mating drastically restricts the dispersal of young queens, and stops gene exchange within and between populations. The assumption of one species first having evolved these features, and of its subsequent radiation, would entail similar problems.

4. Conceivable adaptive value of intranidal mating and reduction of slave-raiding

Three of the species investigated, *M. gordiagini*, *E. ravouxi* and *E. stumperi*, have life cycles corresponding well to those observed in other dulotic ants in the tribe Leptothoracini (*Harpagoxenus*, *Chalepoxenus*, *L. duloticus*), and in other groups of ants (Buschinger et al., 1980). In this section, I will discuss which selective forces, and which factors, might be involved in the evolution of intranidal mating, and the reduction of slave-making, in the species *E. adlerzi*, *E. corsica*, and *E. kraussei*. *E. algeriana* and *E. bernardi*, which are nest-mating but have retained slave-raiding, require a separate consideration.

First of all, the nest-mating species with queens which dealate themselves in the mother nest, are extremely philopatric. Most young queens will remain in the immediate vicinity and try to establish their own colonies within a radius of a few meters. This might be adaptive for a social parasite which is certainly under strong selective pressure with regard to selecting its host species. A social parasite should be highly adapted to overcoming the resistance of host colonies against being parasitized, and to integrating well into the host population behaviorally, pheromonally, and ecologically (annual cycle, food requirements, brood care, etc.). Different host species, or populations of one host species, may vary considerably with respect to these features. Parasite queens dispersing on the wing might drift far out of their local host population; they might get lost, or be unsuccessful in a less suitable population. Young parasite queens may also learn, by an imprinting process (Goodloe and Sanwald, 1985; Le Moli and Mori, 1987), certain pheromonal labels of their local host populations, which are slightly different in other populations. A queen might then have difficulties in finding a suitable host nest.

The strength of this argument, however, should not be overestimated. Non-parasitic ants face the same dilemma with respect to suitable nesting sites, food, and other resources which are distributed unpredictably.

Therefore, the adaptive value of the modified reproductive behavior may more likely be found in the benefits of intranidal mating itself. As pointed out by Wilson (1963), nest-mating eliminates the loss of reproductives that occurs during dispersal, and it insures that queens are inseminated, even in rare species, as most social parasites are. An additional advantage may stem from the possibility that male

production can be reduced, as predicted by Hamilton's (1967) local mate competition theory. In fact, all intranidal-mating *Epimyrma* species have highly female-biased sex-ratios (see Section 2). Finally, intranidal mating and inbreeding will accumulate and preserve most effectively any genetical adaptations to a given host species and population. If we assume that the *Epimyrma* species originated from host-specific races (see Section 6), outbreeding would have involved the risk of loss of genetic adaptedness to the appropriate host species; in case of sympatry, of adaptedness to two or more host races. In fact, several instances of sympatric coexistence of 2 or 3 host-specific *Epimyrma* species are known: *E. kraussei*, *E. corsica*, and *E. ravouxi* in Corsica (Buschinger, 1985b); *E.k.* and *E.c.* in Krk (Yu.); and *E.k.* and *E. algeriana* in Algeria (Cagniant, 1968).

If intranidal mating and dispersal of young queens on foot evolve in a slave-making species, as in *E. algeriana* and *E. bernardi*, a competition between young queens and old colonies for host-species nests should occur. Colonies successfully raiding neighboring host nests for slaves leave fewer for their own offspring when they come to establish new colonies. A reduction of slave-raiding may therefore have a twofold advantage: Firstly, more female sexuals can be produced instead of slave-maker workers, and secondly, the host population can be used more effectively by the colony's own offspring because no host workers are killed during raids – the *Epimyrma* queens are accepted by the adult host workers and kill only few of them during colony foundation.

The reduction of slave-raiding, however, pays off only when the saved host colonies preferentially benefit the parasitic queen's own offspring, which requires that young queens remain near to the mother colony. Thus, it is directly linked to intranidal or near-nest mating and philopatry. The system also requires that the "clones" of parasites are comparatively rare, and separated from others by some distance, which reduces interference between such "clones". Field observations have revealed a patchy distribution of usually small demes of the species in question.

Compared to swarming and raiding species like *E. ravouxi*, the life-time sexual output of a "degenerate slave-maker" queen is lower, owing to the shorter life-expectancy of her colony, and to the lower number of host workers available for rearing her offspring (Winter and Buschinger, 1983). This apparent loss of fitness, however, may be compensated for by a reduction of the losses of sexuals during mating flights (Wilson, 1963), thus by a presumably higher fraction of daughters successfully founding colonies, and a higher production of grand- and great-granddaughters. Under the conditions of inbreeding the latter are as closely related to the mother queen as her direct daughters (coefficient of relationship equals or is close to 1). The strategy of a "degenerate slave-maker", therefore, increases its individual fitness rather than relying on a group selection mechanism.

The system of nest-mating and of locally-dispersing queens, with or without loss of the worker caste, obviously involves the problem of a detrimental concentration of parasites in a small fraction of the host population. In fact, in dense populations of *E. kraussei*, we found locations where parasitized nests were more frequent than free *Leptothorax* nests; *Epimyrma* colonies were sometimes as close together as

20–30 cm. However, this occurs only in few, small patches in large host-species populations. And, according to our experience with collecting numerous colonies of many parasitic ant species, the parasites practically always occur in the sites with the highest densities of their host species. This means that in these places the conditions for the host species are obviously very good; the host species is often only sparsely distributed in the remainder of its much larger area. The availability of suitable nesting sites in otherwise equally suitable habitats is one of the most important factors regulating the locally highly variable densities of *Leptothorax* populations (Herbers, 1986). I suspect that swarming females of the host species from peripheral, less dense and therefore less- or not-parasitized parts of a population will be attracted by such "optimal" sites, recolonize them and replenish the host population.

E. bernardi and *E. algeriana* exhibit intranidal mating, but have retained high worker numbers and slave-raiding activities. The data collected for *E. bernardi* is as yet insufficient, so that any interpretation would be very speculative. For *E. algeriana*, Buschinger et al. (in prep.) discuss the possibility of an alternative strategy to that observed in the "degenerate slave-makers". The latter reduce slave-making in favor of the rapid production of numerous, short-lived daughter colonies. *E. algeriana*, in contrast, has developed large colonies with numerous *E.*-workers, and polygyny, which makes colonies "potentially immortal". This unusual feature (most slave-makers are monogynous – Buschinger et al., 1980) has apparently quite recently evolved since functional monogyny, and sometimes agonistic behavior between queens in a colony occur, and one evidently monogynous population was found.

The monogynous fire ant, *Solenopsis invicta*, after its introduction to North America about 40 years ago, has apparently given rise to a polygynous form on several occasions (Ross and Fletcher, 1985). This may demonstrate that such a switch is also perhaps not too improbable in an *Epimyrma* species.

The polygynous colony structure of *E. algeriana* might be an adaptation to its main host species, *Leptothorax spinosus*, which forms exceptionally large colonies in parts of its range. A single *E. algeriana* queen might have problems in penetrating a large host colony, and when she has succeeded with a small one, her first, small worker force will have difficulties in raiding neighboring, large host colonies. A fraction of the young queens produced and inseminated in a colony thus remains there, and the combined, large worker force of the mother- and offspring-generations is able to conduct effective raids even on large host colonies. In this species, the transition to intranidal mating may have facilitated the development of polygyny in that it guarantees the presence of additional, inseminated queens, and the cooperation of only close relatives.

Conclusion

Intranidal mating, with or without reduction of slave-making, may be of some adaptive value. It implies, however, a high degree of inbreeding which causes a particular problem with respect to the sex-determination mechanism of the Hymenoptera.

5. The problem of sex-determination in an inbreeding ant species

In the Hymenoptera, normal males are haploid and arise from unfertilized eggs, whereas females are diploid and, except in secondarily thelytokous species, arise from fertilized eggs. According to current theory, sex-determination in outbreeding Hymenoptera is closely linked to heterozygosity (Whiting, 1943; Crozier, 1977). The theory predicts that females will be heterozygous for one or several sex-determining loci, of which many alleles occur in a population. In hemizygous, or in the rare homozygous conditions, these alleles determine male development.

Inbreeding reduces allelic diversity and increases homozygosity. Consequently, inbreeding yields diploid males, e. g., in honeybees and in the parasitoid *Bracon hebetor*, as has long been known. Diploid males have also been found in various ants, such as *Solenopsis invicta*, *Formica pressilabris*, and *Rhytidoponera* spp. (Ross and Fletcher, 1985; 1986).

Diploid and even triploid males were produced in an inbred strain of the ant *Harpagoxenus sublaevis* (Buschinger, unpubl.). In the fire ant, diploid male production represents a significant colony mortality factor, and generally these exceptional, usually bigger males are often sterile and less viable than normal ones (Ross and Fletcher, 1986).

In *Epimyrma stumperi* one diploid male pupa was found among 14 karyotyped, and 3 out of 4 prepupae of unknown sex had haploid, diploid, and a few tetraploid cells (Fischer, 1987). Presumably this was due to a certain degree of inbreeding even in this swarming species, because its populations are very small. The observation, however, indicates that in at least one species of the genus the usual sex-determination mechanism may be present.

In the nest-mating *Epimyrma* species, on the other hand, we did not find any extraordinary (e. g. bigger) males, even after several generations of laboratory inbreeding, and among a total of 28 males karyotyped (of *E. bernardi*, *E. corsica*, *E. kraussei*) none was diploid (Fischer, 1987).

Under inbreeding conditions, diploids must be highly homozygous, but nevertheless ordinary numbers of females, and, in the species in which they are found, workers are produced. Furthermore, the female-biased sex ratios did not change in laboratory cultures. Inbreeding without production of diploid males, however, is common in a number of mostly parasitoid Hymenoptera (Crozier, 1971; 1975; 1977; Hamilton, 1967). According to Crozier (in litt., 1988) the inbreeding *Epimyrma* species presumably "have evolved a different sex-determining mechanism not involving heterozygosity, following the same path as the inbreeding parasitoids".

Although such a mechanism of sex-determination would fit the observations, it is problematic to assume the convergent origin of this mechanism in several related but separate *Epimyrma* species independently, despite the fact that intranidal mating has evolved in various other parasitic ant genera (e. g., *Anergates*, *Teleutomyrmex*) (Wilson, 1971). There, several queens are sometimes found together in one nest (polygyny), which may thus reduce the degree of inbreeding; *Anergates* females are well known to leave their mother nests on the wing, after having mated. So females

of different origin may sometimes associate in one host nest, and hence their offspring can interbreed.

Conclusion

It is not improbable that an inbreeding-resistant sex-determination mechanism has evolved in *Epimyrma*. The occurrence of this mechanism in several separate species, however, requires an explanation of how it was established over all their ranges.

6. An unconventional hypothesis on speciation and the origin of inbreeding in Epimyrma

Taking all the facts together, and taking the various assumptions discussed above for granted, I suggest the following scenario for the origin of the inbreeding system in *Epimyrma*, and the speciation in this genus:

a) After a first *Epimyrma* species with the behavioral and eco-ethological traits of *E. ravouxi*, slave-making and outbreeding, had evolved, this species spread over a considerable range covering most of the presently known range of the genus. As *E. ravouxi* does, this species in various parts of its range enslaved different host species with variable preference, probably due to variable frequencies and suitabilities of the potential slave species.

Some *Epimyrma* populations may have specialized for certain host species in particular ecological conditions, or have been isolated geographically so much that they attained full reproductive isolation from the remaining original species. *E. stumperi* in the high Alps, and *E. ravouxi* which occurs mainly in mountainous areas, and also north of the Alps, may represent such instances. They retained the original life habits and were not affected by the following events.

b) Other populations of the original *Epimyrma* species, which were partially isolated from each other owing to the patchy distribution of suitable host-species populations, and perhaps also owing to their specialization for diverse host-species, may also have attained slight morphological differences. It is important to assume only a partial reproductive isolation with some, though restricted, gene flow, mediated by swarming males and females.

The populations were thus in the state of normal geographical and/or host races, without genetical isolation. The conclusiveness of this supposition is demonstrated by the fact that even today the species in question are not genetically isolated, as was shown by hybridization experiments (Jessen, 1987; Jessen and Klinkicht, in prep.).

c) Mating near to, or within the natal nests, was of selective advantage in that it reduced predation on swarming sexuals and disadvantages due to drifting out of the area with suitable host populations; it also guaranteed the insemination of nearly all queens (cf. Section 4). The tendency to intranidal mating, however, was counter-

selected because of deleterious inbreeding effects (unviable diploid males). A polyethism, with a fraction of sexuals remaining in place and others dispersing, may have developed in response to these two selective forces. Such mixed strategies are not unusual in polygynous independent or facultatively temporarily parasitic ants, e. g. of the genus *Formica* (Rosengren and Pamilo, 1983).

d) Simultaneously with the tendency for young queens to remain in the vicinity of the mother nest, a tendency to reduce slave-raiding could have developed, reducing the interference between colony foundation by own offspring and slave-raiding, as was discussed above. The disposition for degenerating dulosis and reduction of the worker caste had presumably already spread through much of the *Epimyrma* superspecies and, depending upon the structures and densities of local host and parasite populations, demes with more or less workers evolved. This disposition was either combined with, or even identical to, the disposition of larvae to develop into sexuals without a preceding hibernation ("rapid brood"). Philopatry of the young queens and reduction of slavery, however, like intranidal mating, imply the emergence of high degrees of inbreeding, that would interfere with the usual hymenopteran sex-determination mechanism.

e) In this situation, a modified sex-determination reducing the deleterious inbreeding effects should quickly become established in any of these populations. I suggest that this mechanism evolved somewhere in the range of the *Epimyrma* superspecies, and that it spread, e. g. via heterozygous, still swarming females, over all or most of its range. This mechanism was neutral, or of little advantage, for swarming genotypes. When combined, however, with the disposition to mate in or near to the nest, this inbreeding tendency would immediately be favored. The small amount of gene flow between populations and host races existed until the genes for swarming were replaced by those for nest-mating in each population affected.

According to this hypothesis, an inbreeding-resistant sex-determination mechanism overlaid the interactions of the adaptive traits; mating and remaining within the home area, and reduction of slavery in favor of founding more colonies, and eliminating the counteracting disadvantages of inbreeding. The result was the fixation of a *status quo* in many populations which went over to permanent intranidal mating and inbreeding, thus accumulating most effectively their host-specific adaptations, but cutting off any gene flow and preventing further evolution through spreading of adaptive genes. Speciation, the formation of reproductively isolated units out of former subspecies, was thus eventually achieved through the transition to inbreeding.

7. Final discussion

The hypothesis presented here provides a conceivable interpretation of what is observed in the genus *Epimyrma*. In particular, it explains how a series of evidently closely-interrelated taxa exists which are reproductively, but not genetically isolated, and which exhibit various degrees of reduction of slavery. The suggested sequence of evolutionary events could well account for the fact that *E. corsica* and *E. adlerzi*,

the two completely workerless and biologically thus most similar species, are morphologically so dissimilar. Both had, as "subspecies" of the original *Epimyrma*, already developed the state of workerlessness independently, before they were affected by the hypothetical new sex-determination mechanism. *E. kraussei* populations vary considerably with respect to worker numbers (Buschinger et al., 1986). The inbreeding resistance enabled the populations to switch over to permanent nest-mating, but the genes for reduction of workers could no longer reach the populations "still" producing useless workers. And in *E. algeriana*, which has retained high worker numbers and slave-raiding, the intranidal mating has at least facilitated the development of polygyny with a cooperation of close relatives, the formation of even larger worker forces, and thus a more effective exploitation of a host species with large colonies.

The high degree of isolation of the local, inbreeding populations, and their inability to colonize distant host populations may also explain why several *Epimyrma* species are found in a few sites distant from each other, but are absent between them even in some dense host-species populations well-suited to bearing a parasite population. If an *Epimyrma* deme by chance becomes extinct, it can only be replaced when a sufficiently dense host-species population, at least temporarily, bridges the gap to a neighboring *Epimyrma* deme. The patchy distribution of *E. corsica*, which was found in one small site in Corsica, in another one in the Abruzzi in central Italy, and in a few sites along the Dalmatian coast of Yugoslavia, could well be a result of the extinction of linking populations.

The rich variety of social structures in *Myrmoxenus/Epimyrma* as described in Section 2 is as yet unparalleled in other genera of parasitic, let alone independent, social insects. The evolutionary scenario suggested here may therefore not be applicable to other instances. Single traits found in *Epimyrma*, like intranidal mating or dispersal of young queens on foot, occur elsewhere in socially parasitic as well as in independent ants (Wilson, 1963). In contrast to *Epimyrma* in all the applicable examples[1] mentioned by Wilson the species are polygynous, which reduces the degree of inbreeding, and most of the species disperse, at least facultatively, on the wing.

In other parasitic (*Harpagoxenus sublaevis* – Buschinger, 1979) or independent (e. g. some *Monomorium species* – Bolton, 1986) species with apterous females which mate near the nests, the males are alate and ensure outbreeding.

Transitions from one type of social parasitism to another have been repeatedly suggested (cf. the scheme fig. 19-3 in Wilson, 1971), but evidence is scarce (Buschinger, 1986). The transition from slavery to the workerless condition as found in *Epimyrma* does not follow this scheme: *E. adlerzi* and *E. corsica* do not represent true inquilines in that they eliminate the host colony queens rather than coexisting with them.

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[1] *Epimyrma stumperi*, listed in Wilson (1963), is neither a temporary parasite, nor "polygynous by virtue of adding fertile queen-worker intercastes"; *Leptothorax muscorum* is not a bog "endemic" (cf. Heinze and Buschinger, 1987; Buschinger, 1968); *Formicoxenus* is functionally monogynous (Francoeur et al., 1985).

It is the as yet unique blend of features and evolutionary trends observed in *Epimyrma* which has provoked me to suggest this hypothesis, which is complicated but nevertheless most parsimonious.

I cannot exclude the remote possibility of an episodic occurrence of swarming in the normally nest-mating species, perhaps under the influence of very unusual weather conditions; however, I should then expect a higher uniformity, e. g. of *E. kraussei* populations with respect to coloration and worker numbers. The very low number of males produced in the inbreeding species is another argument against such a possibility.

A testable hypothesis is the assumption that the inbreeding-resistant sex-determination mechanism is lacking in the swarming species *E. ravouxi*, *E. stumperi* and *M. gordiagini*. The rarely-found diploid males (Section 5) support this hypothesis. If conditions can be produced under which the sexuals of these species mate in the laboratory, experimental inbreeding should yield more diploid males.

A final problem to be discussed here is that of the systematic rank of the taxa involved. It is somewhat similar to that of uniparental species among lizards or Rotifera. The various inbreeding "species", as was shown, are not genetically isolated. Due to host-species specificity, and to intranidal mating, they are certainly reproductively isolated. Moreover, owing to the continuous inbreeding between full siblings in monogynous nests, the populations are subdivided into clone-like lineages which again are reproductively isolated from each other.

The *Epimyrma* species presently recognized by taxonomists, on the other hand, represent entities which differ among each other morphologically and biologically (host species, worker number, slave-making or its absence). Each of them presumably is a monophyletic unit which probably was a more or less isolated "subspecies" before the transition to intranidal mating and inbreeding. I therefore suggest, as a practical solution, that the species rank should be retained for *E. algeriana*, *bernardi*, *kraussei*, *corsica* and *adlerzi*.

Acknowledgements

I am grateful to R. H. Crozier, B. Bolton, and five anonymous referees whose suggestions have helped to improve the manuscript considerably. I am especially obliged to "referee C" for his highly encouraging remarks. The Deutsche Forschungsgemeinschaft has supported the underlying experimental work and field research by a series of grants.

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Received 31 March 1988;
accepted 6 January 1989.
Corresponding Editor: P. Schmid-Hempel