

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

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

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

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

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

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

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

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