

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

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

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

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

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

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

The types of social parasitism among ants

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

Xenobiosis

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

Temporary parasitism

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