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The Worker Caste of the Parasitic Ant Monomorium metoecus Brown and Wilson, with Notes on Behavior

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In a recent issue of ENTOMOLOGICAL NEWS we described the remarkable parasitic ant *Monomorium metoecus* from a single ergatogyne found in a nest of *M. minimum* (Buckley) at Tuscaloosa, Alabama (Brown and Wilson, 1957). On June 17, 1957, the type locality was revisited with the hope of obtaining additional material. Fortunately, the original collection site had not been disturbed, and *M. metoecus* was successfully located for the second time. A most interesting discovery made at this time was that *metoecus*, unlike the great majority of other permanent ant parasites, possesses a functional worker caste.

The new mixed colony was found at almost the identical spot, in open pine woods on the University of Alabama campus, where the type ergatogyne had been discovered seven years before. It was nesting in a deep vertical crevice in a partially buried, dead root stump at the base of a large loblolly pine (*Pinus taeda*), a situation that unfortunately rendered excavation very difficult and incomplete. The total adult population of the colony was roughly estimated at between one and two thousand; *minimum* workers outnumbered those of the parasite by about forty to one. Two dealate queens of *minimum* were recovered, but no queens or extreme ergatogynes (see below) of the parasite; the latter, if they existed, were presumed lost during excavation. Host and parasite workers were completely intermingled, with no apparent tendency toward concentration of either species anywhere inside or outside the nest. Following is a brief characterization of the newly discovered *metoecus* worker caste.

Worker: The six specimens studied (now deposited in the Museum of Comparative Zoology, United States National Mu-

seum, and personal collection of A. C. Cole, Jr.) are a rather heterogeneous lot, and it may be that it would better approximate their status caste-wise to consider them low-grade ergatogynes. They differ from the holotype ergatogyne in their narrower petiolar node, as seen from the rear (width 0.24–0.28 mm. vs. 0.35 mm. for the holotype; three workers of *M. minimum* from the host nest measured 0.12–0.14 mm.). The postpetiole is also proportionately narrower than in the holotype, and the ventrolateral conules are not so well developed; in fact, in several specimens the conules are not developed appreciably at all. The conules do not vary allometrically in this series, for some of the smallest specimens have them well developed, while the largest specimen has, to all intents and purposes, no conules at all. Although overall size (total length and bulk of whole body) is slightly to considerably less in the workers than in the ergatogyne, the head width measures about the same (workers, HW without compound eyes, 0.53–0.55 mm. vs. 0.54 mm. for the holotype). The alitrunk of the workers is shorter, both absolutely and proportionately (0.76–0.80 mm. vs. 0.88 mm.), and the convexity of the promesonotal and propodeal dorsal outlines is less marked than in the holotype. We may sum up by saying that the workers, if they are workers, show some discordance in their difference from the holotype, but in general are intermediate between the holotype and the host workers, and much closer to the former. The head width of three host nest workers measured is 0.38–0.41 mm.; alitrunk length (WL) 0.52–0.61 mm. (See text-figure.)

Prior to excavation of the nest, parasite workers were found in the files of *minimum* workers moving up and down the trunk of the pine tree during the day. Careful examination of these individuals at this time failed to reveal any peculiarities in their foraging behavior. Despite the fact that they are twice the size of the *minimum* workers, they followed the vertical odor trails on the pine trunk at about the same pace and with the same frequency of exploratory "side-tracking." Moreover, approximately the same percentage were carrying small dead insects (including psocids and aphids) gathered higher up in the

pine. Behavior in the vicinity of the nest, both before and after the disturbing effect of excavation, did not appear to differ significantly.

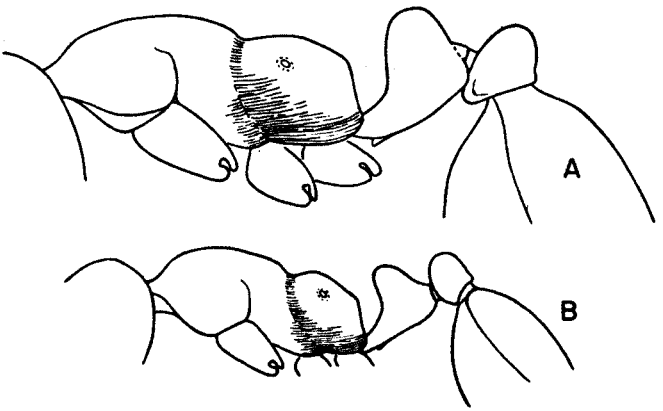

FIG. 1. A, *Monomorium metoecus* Brown and Wilson, worker alitrunk and nodes, side view. B, *Monomorium minimum* (Buckley), worker from host nest, alitrunk and nodes in side view. Both from same nest, described in text. Drawn to scale of Figure 1 in Brown and Wilson, 1957. Drawings by Nancy Buffler.

Following study in the field, most of the colony was removed and transported to Harvard University for further observation under laboratory conditions. Unfortunately, during the week-long automobile trip most of the *metoecus* workers died, only three individuals surviving to be transferred finally to an artificial nest. Once established in the nest, the *metoecus* workers continued to behave essentially like the *minimum* workers. A possible ethological difference that appeared at this time was the apparent proportionately longer periods of time spent by the three *metoecus* workers outside the nest. However, this phenomenon may have resulted in some way from the preceding heavy mortality of the parasite, e.g., the younger, nest-oriented workers may have been the first to die. Inside the nest, the *metoecus* workers were occasionally seen resting on or near the brood, but it could not be determined whether they were helping tend it. On several occasions they displayed aggressive be-

havior, in attacking alien worker ants placed near them, in defending against probing forceps tips, etc., that was apparently identical to the behavior of the host workers under similar conditions. *Metoecus* workers also fed directly on honey supplied the colony. On one occasion a parasite worker was observed exchanging food with a *minimum* worker by regurgitation, but it could not be determined whether this individual was donating or receiving. All in all, the total behavior of the parasite workers did not appear to differ in any significant way from that of the host workers within the existing limits of observation.

The question was now raised, whether the parasite worker is truly the worker caste of the previously described *M. metoecus,* as all of the morphological evidence seemed to indicate, or whether it represents instead merely another, aberrant worker caste of *M. minimum.* To test the latter hypothesis, the mixed colony, now presumed to be deprived of its parasitic reproductive form (or forms) and at first lacking brood of any sort, was maintained in the laboratory under optimum trophic conditions for a period of five months. During this time the *minimum* population more than doubled in size, but no new *metoecus* workers appeared. It was concluded that a *metoecus* reproductive form had indeed been present in the original mixed colony but had been lost during excavation and transfer to the laboratory. But of course it cannot be proved that the *metoecus* reproductive form was an ergatogyne similar to the holotype instead of a true queen or fertile worker.

The precise relationship of the parasite to its host was now considered. The large size of the *metoecus* worker suggested that the parasite might be dulotic, raiding other nests of *minimum* to increase the number of host workers. An experiment was conducted in which a small colony of *minimum* collected at Amissville, Rappahannock Co., Virginia, was placed in a common foraging arena 23 centimeters from the mixed colony. Within an hour both *minimum* and *metoecus* workers from the mixed colony began to penetrate the nest of the Amissville colony and remove brood. The invaders were actively resisted by the Amissville workers, and only after the latter had been over-

whelmed by numbers and mostly destroyed was all of the raided brood removed. The raided brood, consisting solely of large larvae and worker pupae, was completely eaten by the mixed colony within twenty-four hours after it had been transported to the mixed-colony nest. A control experiment was then conducted in which two colonies of *minimum* collected at Falmouth, Massachusetts, were placed together in a common foraging arena under conditions as similar as possible to those of the original experiment. At the time of writing these two colonies have been living together for a period of three months without a raid developing in either direction.

Despite the different outcomes of the original and control experiments, it is our opinion that *metoecus* is not a dulotic ant. There are several good reasons for arriving at this tentative conclusion. (1) The laboratory raid resulted in intense combat with complete destruction of the raided colony, and the captured brood was quickly eaten instead of being reared, conditions that suggest simple predation rather than dulosis. (2) Functional host queens were present in the mixed colony, not a normal condition associated with dulosis. (3) The *metoecus* workers show none of the modifications, either morphological or ethological, commonly associated with dulosis.

But whether the parasitism is dulotic in nature or not, it is clearly at a very primitive level. In fact, it is questionable whether on the basis of the present evidence the relationship can be properly called parasitism at all. There is at present no sure indication that the *metoecus* workers are ethologically degenerate in any way, i.e., that they do not perform their "fair share" of the work load. The relationship is reminiscent of non-parasitic parabiosis, except that in the known cases of parabiosis the participating colonies remain segregated in separate chambers within the nest and never mix their brood. It is perhaps much closer to the strange kind of symbiosis recently discovered as existing between the New Guinea dacetine ants *Strumigenys loriae* and *Kyidris yaleogyna* (Wilson and Brown, 1956). The two species live in completely mixed colonies, with *Kyidris* queens and workers forming a slight numerical minority of the adult population.

The *Kyidris* workers still perform normal tasks inside and outside the nest, but their behavior tends to be degenerate and ineffectual, and they do not carry a "fair share" of the work. For example, they hunt for insect prey along with the *Strumigenys* workers, but with very low efficiency, and they do not join in nest construction at all. Other cases of very primitive parasitism, or at least pre-parasitic symbiosis, may occur among species of the Nearctic *Formica obscuriventris* group, as described by King (1949, 1955) and King and Sallee (1951). Apparently various pairs of species of this group commonly form mixed colonies by the method of indiscriminate mutual adoption of newly-fertilized queens of one species by the established colony of another. Such mixed nests have been studied in Iowa by King and Sallee, and there is good evidence that they occur elsewhere (Brown, unpublished notes).

The cases of *Monomorium metoecus* and *Kyidris yaleogyna* suggest the possible first steps in one evolutionary pathway of permanent social parasitism. It is conceivable that parasitism of this sort starts when one species simply becomes resident with another, degenerating to the extent that it can no longer exist independently, but at first maintaining a normal, fully functional worker caste. Evolution proceeds as the worker caste ceases to function normally and is reduced in numbers, finally to be eliminated altogether.

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