Male Polymorphism and Gynandromorphs in the Ant *Cardiocondyla emeryi*

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The ant genus *Cardiocondyla* is characterized by a peculiar male polymorphism: in some species, males have all morphological characters of typical ant males, such as enlarged eyes, long and slender antennae, well-developed wings, and a bulky thorax. In others, the males are wingless and superficially resemble workers ("ergatoid males"), and in a third group of species, both male morphs occur [1]. Male morphology is associated with strikingly different reproductive behavior: winged males are thought to emigrate from the nest and to mate with virgin queens from other colonies, whereas wingless males stay in the nest where they attempt to monopolize all young queens eclosing in their own colony by killing rival ergatoid males [2–4]. Furthermore, whereas in winged males, as in the males of all other ants, bees, and wasps studied in this respect, spermatogenesis has stopped and the testes have started to degenerate by the time males reach sexual maturity, spermatogenesis continues throughout the whole adult life of ergatoid males [5]. The proximate causes of this fascinating male polymorphism are unknown. Here we present preliminary data on the behavior of both male morphs and report on the occurrence of gynandromorphs in *C. emeryi*, genotypic mosaics which combine morphological features of males and females. The latter finding indicates that male morphology in polymorphic *Cardiocondyla* is probably affected by the same factors that control caste differentiation in the female sex.

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Cardiocondyla are tiny myrmicine ants which live in colonies consisting of several dozen workers and numerous queens in cavities in sandy soil, hollow twigs, or under stones throughout the tropics and subtropics. Ten colonies of *C. emeryi* were collected between January 1 and 10, 1995 about five kilometers north of Bridgetown, Barbados, West Indies. The colonies nested under casuarina (*Casuarina equisetifolia*), manchineel (*Hippomane mancinella*), and palms approximately five cm deep in the sand, less than thirty meters from the sea. In the laboratory, the colonies were housed in 10 cm×10 cm×3 cm Plexiglas boxes with a layer of plaster. They were provided with purified sea sand which they used to construct small nests. The colonies were kept at a constant temperature of 25°C and fed twice a week with diluted honey and pieces of insects.

C. emeryi is a widely distributed cosmotropical tramp species. Its presence on Barbados has previously been noted by Wheeler [6]. It appears that ergatoid males of *C. emeryi* were hitherto known only from a single specimen from St. Thomas, Virgin Islands, which was erroneously considered the queen of a new, workerless parasitic ant species, *Xenometra monilicornis* [7], and recognized as an ergatoid male of *C. emeryi* only more than 50 years later [8]. Despite superficial similarities, ergatoid males clearly differ from workers in various characters, such as the more robust antennal scape, smaller eyes, and lighter coloration, and thus can be easily recognized by closer inspection. The colonies from Barbados produced several dozen winged and wingless males during one year of laboratory culture. Up to five or more winged males were regularly found occurring together, especially in larger colonies, but typically only one wingless male was present per nest, often in addition to several winged males. As in other *Cardiocondyla* [2, 3], wingless males appeared to be intolerant of each other – in three instances we observed fighting between two adult wingless males in large colonies, and in several other cases we found the severed bodies of freshly eclosed wingless males, presumably killed by an adult wingless male, or apterous males with mutilated antennae or legs. The wingless males apparently ignored winged males and vice versa, and no aggression was observed among winged males. Fighting among wingless males has been thought to be related to mating in the nest [3, 5], however, in *C. emeryi* both male morphs successfully copulated with freshly eclosing virgin queens in the nest, though winged males later emigrated from the nest.

In addition to winged and wingless males, we found seven individuals with approximately half of their heads and alitrunks being male and the other half queen, or with male morphology on one side and worker characteristics on the other. Two additional specimens showed a less balanced mosaic of male and queen characters, such as, e.g., a male body with the left half of the head clearly being female, with a shorter antenna, a smaller eye and a smaller lateral ocellus (Figs. 1, 2). A complex terminology has been proposed to describe the different varieties of such individuals [9]. For simplicity we refer to individuals half male, half queen as "gynandromorph" and to those half male, half worker as "ergatandromorph". In contrast to other ant species, where males have conspicuous genital appendages at the tip of the gaster, the genitalia are concealed in *C. emeryi* males [1] and cannot be seen without a closer inspection or dissection of the gaster. Dissection of two gynandromorphs and two ergatandromorphs showed that their gasters were invariably male on both sides. One gynandromorph combined an ovary consisting of three ovarioles on one side of the gaster and male genitalia on the
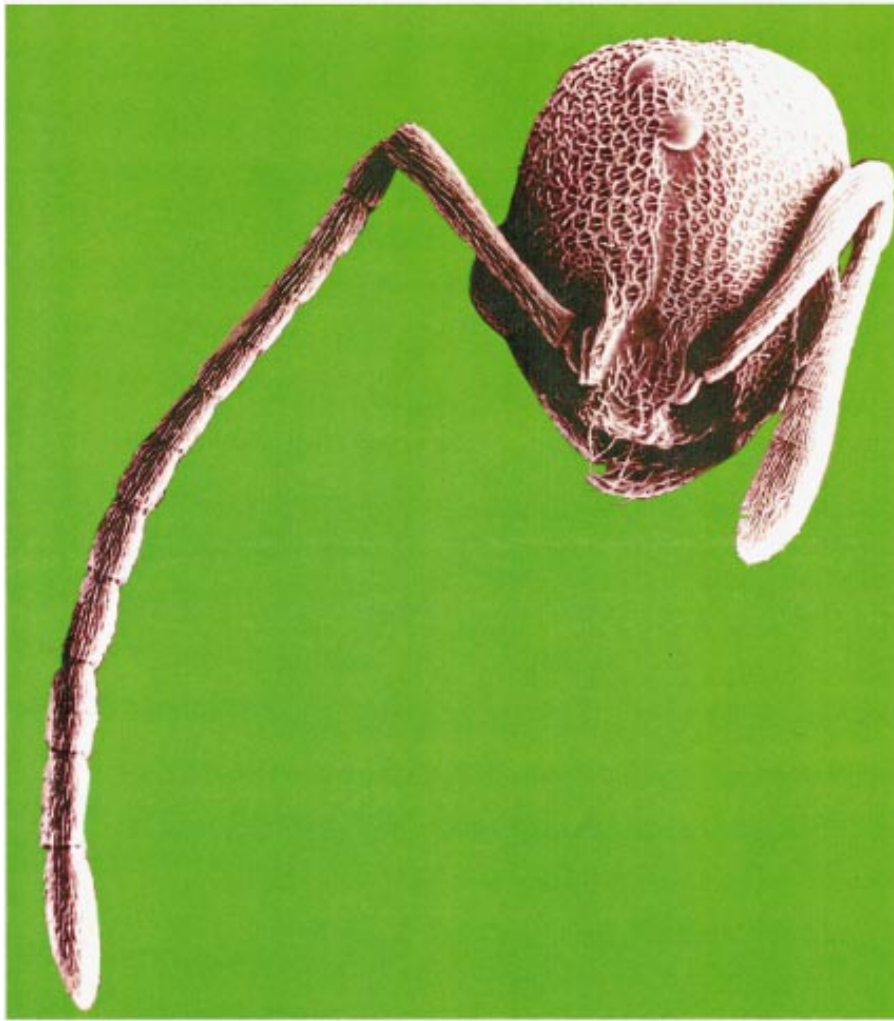
Fig. 1. SEM photograph of the head of a gynandromorph of the ant *Cardiocondyla emeryi* in frontal view. Half of the head is male (long antenna consisting of 13 segments, large lateral and median ocelli, large eye), half female (short antenna consisting of 12 segments, rudimentary lateral ocellus, small eye). At higher magnification, differences in the sculpture of the cuticula between the male and female halfs of the individual become visible. The photograph was colored using the computer program PhotoShop

Fig. 2. Alitrunk of a gynandromorph of the ant *Cardiocondyla emeryi* in dorsal view. The individual bears wings on both sides of the body; the lighter, brownish half of the alitrunk is male, the darker, black half is female

other. Two gynandromorphs and two ergatandromorphs were reared in the same colony (B40), the remaining individuals are from different colonies.

In Hymenoptera, sex is determined by haplodiploidy: males develop from unfertilized eggs, and females develop from fertilized eggs. Individuals combining a mosaic of male and female tissue apparently arise either from egg cells with two nuclei, of which only one is fertilized, or from a supernumerary sperm nucleus undergoing mitosis after entering the egg cell (e.g., [10]). The development of sexual mosaics apparently can be induced by severe temperature shock [11]. Gynandromorphs have been seen as evidence that sexual characters in insects are not influenced by circulating hormones [12].

In most ant species, gynandromorphs and ergatandromorphs are typically a rare phenomenon and thus their mere existence is worth a short note [13]. In male polymorphic ants, such as *Cardiocondyla emeryi*, however, the occurrence of gynandromorphs and ergatandromorphs is of special interest in respect with male polymorphism. In other ant species, sexual mosaics randomly combine characters of a winged male with characters either of a wingless worker or a winged queen (e.g., [14]). The endocrine mechanisms controlling caste differentiation in the female sex thus apparently do not affect the morphology of the male parts of these individuals [15]. In contrast, in ergatandromorphs and gynandromorphs of *C. emeryi*, the characters of ergatoid and winged males, females, and workers apparently are not mixed at random. Three individuals were half ergatoid male, half worker, and six individuals were in part winged male and in part winged queen. Furthermore, the only other known *Cardiocondyla* gynandromorph, reported from male-polymorphic *C. batesi*, also combines features of a winged male and a queen [16]. Assuming a random combination of the traits of the two male morphs with those of the two female castes and equal frequencies of winged and wingless morphology, one would expect 50% of gynandromorphs and ergatandromorphs to exhibit morphological characters of either winged queens and ergatoid males or workers and winged males.

The binomial probability that all ten known *Cardiocondyla* ergatandromorphs and gynandromorphs are winged or wingless on both sides of their bodies though characters are mixed at random is approximately 0.001 $(1/2^{10})$. From the actual frequencies of wingedness (0.7) and winglessness (0.3) in the limited material currently known, the probability to find only winged or wingless individuals is approximately 0.028 $(3/10^{10} + 7/10^{10})$. Because of the similarity between workers and wingless males, however, it is likely that several ergatandromorphs have been overlooked and the actual frequency of the wingless trait is larger.

It thus appears that winged and wingless characters are not assorted randomly, but that male morph in polymorphic *Cardiocondyla* is controlled by the same factors which regulate female caste differentiation, i.e., that those parameters which prevent the development of imaginal discs of wings in workers and promote their development in queens also cause winglessness in ergatoid males and the presence of wings in winged males. In many ant species it has been shown that female sexuals are produced only after the colony has become "mature",

i.e., after a certain numerical worker-queen ratio has been surpassed [17]. It is noteworthy that in single-queen colonies of an undescribed *Cardiocondyla* from Japan, ergatoid males were produced at low numerical worker-queen ratios, but winged males were produced only at higher ratios [4], corroborating the hypothesis that the ontogeny of male morph in male-polymorphic *Cardiocondyla* is affected by the social environment.

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Sex Differences in Cerebral Language Dominance in Complex-Partial Epilepsy

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The question of sex-related differences in hemispheric lateralization of language functions has been the subject of controversy [1]. Studies on perceptual laterality in normal persons either reveal no sex differences at all or stronger lateralization for males [2]. Clinical studies have found a lower incidence of aphasia in unilaterally brain damaged women than men [3]. Other groups, however, have not replicated these findings [4].

The intracarotid amobarbital test (IAT) is a more specific tool than approaches used in previous research for determining language lateralization [5]. Surprisingly, data from IAT language testing have rarely been analyzed with regard to sex differences. The only major study on this subject [6] discovered no sex differences in the overall incidence of atypical (right, bilateral) speech patterns in 94 epileptic patients with evidence of left-hemisphere seizure involvement (i.e., unilateral left and bilateral foci). However, these results suggest that the period in which hemispheric reorganization for speech occurs is much shorter in females than in males: speech transfer in females occurs preferentially after an onset of damage in the first year of life. It has been concluded that "plasticity for speech reorganization may be affected by gender" ([6] p. 357). If this is so, one would expect sex differences to be more pronounced in patients with a