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Alternative Dominance Mechanisms Regulating Monogyny in the Queenless Ant Genus *Diacamma*

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Compared to other ants, the genus *Diacamma* (subfamily Ponerinae) is morphologically extraordinary, because all

workers eclose with a single pair of tiny bladder-like appendages attached laterally on the thorax ([1, 2], Fig. 1). These

“gemmae” are normally recessed into a distinct cavity, although they can be bitten off during dominance interactions. In *D. australe*, the gemmae are filled with glandular cells which are connected to minute pores opening to the outside [3].

Queens (which constitute a morphologically specialized caste in ants) do not exist in *Diacamma*, and instead members of the worker caste are able to mate and reproduce (“gamergates” [4]). In *D. australe* and *D. rugosum*, there is only one gamergate in each colony, and other workers are inhibited from laying eggs. The gamergate is the only individual which keeps the gemmae – new workers which emerge in her presence are soon mutilated [5, 6]. Workers without gemmae have never been found to be inseminated, which suggests that the gemmae are essential to mate. Their exocrine secretions may function as sexual attractants. Furthermore, mutilation of the gemmae has a dramatic effect on individual behavior, which soon changes from aggressive to timid. Although mutilation of the gemmae is an essential component of reproductive dominance in *D. australe* and *D. rugosum*, we report here that it does not occur in an Indian species of *Diacamma*.

We collected ten colonies of *D. vagans* from Masunigodi, Tamil Nadu, southern India. We immediately noticed that all the workers retain the gemmae in this species (except for sporadic individuals in some colonies). A histological investigation revealed that a gemma of *D. vagans* contains much fewer glandular cells (about 50) than in *D. australe* (about 500); the external morphology (Fig. 1) is similar, although there are fewer pores. Dissection of a sample of 390 workers from

Fig. 1. Scanning electron micrograph of a gemma in *D. vagans*. Arrow indicates the narrow stalk which is attached to the thorax. Note the long sensory hairs on the gemma's upper surface

five colonies, together with experimental fission of colonies, indicated that there is only one gamergate per colony. The other workers, only a few of which were mutilated, all had empty spermathecae, and exhibited undeveloped ovaries in the presence of a gamergate.

We studied four large colony fragments without a gamergate [7]; these groups consisted of 50–250 workers marked with individual color codes. In two orphaned groups, frequent aggressive interactions occurred among a proportion of the workers. Various individuals were repeatedly bitten and jerked, or were held captive for long periods of time. Examination of the pattern of aggressive interactions indicated that one worker was clearly dominant in each group. Subordinate workers who were aggressive towards each other behaved timidly when attacked by the top-ranked worker. Many workers laid eggs, but these were often cannibalized by the dominant individual. In contrast, her eggs were never eaten. When dissected, many workers involved in dominance interactions had active ovaries (no workers were inseminated).

In another two orphaned groups, comparatively little aggression was observed. A dominant worker was also recognized, who frequently patrolled through the nest, with body held up high (“strutting”). She directed antennal boxing or mandible threats towards nest mates, who often avoided her. Eggs were not laid by other workers, and dissections confirmed that only the dominant worker had active ovaries. The latter was distinguished by another behavior – she frequently rubbed both hind legs against her posterior abdominal tergites, both inside and outside the observation nest. Since a pygidial gland occurs in this region, this conspicuous behavior may represent sexual calling. In *Rhytidoponera metallica*, the pygidial gland has been shown to be involved in mate attraction [8]. This form of sexual calling was never observed in *D. australe* or *D. ru-*

gosum (Peeters, unpublished), and instead a sex attractant emanating from the gemmae may be more important.

The different patterns of aggression documented in the orphaned colonies of *D. vagans* seem to correspond to various stages involved in the establishment of a stable dominance hierarchy. Over time, the interactions between a dominant worker and her subordinates become less physical, and this is associated with the cessation of ovarian activity in the latter. Eventually, the top-ranked worker may exhibit sexual calling, and we presume that she will mate and become the gamergate when foreign males visit the nest. When the dominant worker was removed from a colony in which no aggression was occurring, after 1 day violent fighting started among a small number of workers.

The gemmae of *Diacamma* workers are unique structures among the ants. The sensory nature of the hairs on their upper surface (Fig. 1), and the branching pattern of their afferent axons in the central nervous system [9], suggest homology with the first pair of wings found in ant queens. However, the glandular cells present inside have evolved de novo, but it is not clear whether they have a pheromonal function in all species. Furthermore, in *D. vagans*, there is no association between the presence or absence of the gemmae, and the level of aggressiveness. In the absence of phylogenetic data on the relationships within the genus *Diacamma*, it is not yet possible to determine whether the noninvolvement of the gemmae in reproductive control is the ancestral condition, or a secondary modification.

The occurrence within the genus *Diacamma* of two different mechanisms regulating the incidence of mating is of great evolutionary interest. The dominance interactions in *D. vagans* are similar to those observed in other queenless ponerines, where they also function to regulate egg laying, and ultimately insemination [10, 11]. In contrast, the situation in *D. australe*

and *D. rugosum* is exceptional, since both sexual attractiveness and dominance status are controlled solely by the mutilation of the gemmae.

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