

Worker laying in the absence of an ergatoid queen in the ponerine ant genus *Plectroctena*

C.P. Peeters

School of Zoology, University of New South Wales, P.O. Box 1, Kensington N.S.W., 2033 Australia

R.M. Crewe*

Department of Zoology, University of the Witwatersrand, 1 Jan Smuts Avenue, Johannesburg, 2050 Republic of South Africa

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Ergatoid queens (without wings and worker-like) occur in *Plectroctena mandibularis* and *P. conjugata*. Five nests of these species were incompletely excavated, and an ergatoid was collected in only one of them. The orphaned groups of workers were kept in the laboratory for several months, during which time many eggs were laid. Some of these developed into males. Thus workers can lay haploid eggs in the absence of an ergatoid queen. This was confirmed by dissecting 60 workers from various nests: many of them had mature oocytes in their ovaries, and inseminated individuals were not found. Various data on foraging behaviour and male activity are also presented.

Ergatomorfiese koninginne (sonder vlerke en soos werkers) kom voor onder *Plectroctena mandibularis* en *P. conjugata*. Vyf neste van hierdie spesies is gedeeltelik oopgegrawe en 'n ergatomorfiese koningin is in net een van hulle gevind. Die groepe weeswerkers is vir 'n paar maande in die laboratorium gehou en 'n aantal eiers is gelê. Party van hulle het in mannetjies ontwikkel. Dit is dus moontlik vir werkers om haploïde eiers te lê in die afwesigheid van die ergatomorfiese koningin. Hierdie verskynsel is d.m.v. disseksie van 60 werkers van die verskillende neste bevestig. Baie van hulle het volwasse oösiete in hul eierstokke gehad, en daar het geen bevrugte individue voorgekom nie. Data oor voedingsgedrag en aktiwiteit van mannetjies word ook gegee.

*To whom correspondence should be addressed

Many species in the phylogenetically primitive ant subfamily Ponerinae lack alate queens: either the queen caste has been replaced by mated laying workers (Peeters & Crewe 1985), or the queens have become permanently wingless (Haskins & Welden 1965). The latter have a simplified thorax, and are called 'ergatoid' because of their worker-like appearance. The biology of ergatoid queens in the ponerines is poorly understood, and it is necessary to establish whether they have retained the attributes of a specialized reproductive caste (Peeters 1987).

Plectroctena is a small (17 known species) ponerine genus restricted to the Ethiopian region. It was revised by Bolton (1974): alate females have been described in nine species, and ergatoid females in five species. There are three species-groups in *Plectroctena* (Bolton 1974), and ergatoids occur in two of these. This distribution indicates that the loss of the winged condition has evolved independently at least twice in this group of ants. The selective pressures responsible for this evolutionary modification remain unclear. However, if ergatoids are a specialized reproductive caste, then one of their attributes should be control over reproduction by workers (Fletcher & Ross 1985). In the absence of a queen or under conditions of inefficient queen control, workers often lay haploid eggs that develop into males and the presence of these laying workers is indicative of a lapse in reproductive control. In this article we explore the reproductive potential of workers in colonies without queens.

Methods

Nests of *Plectroctena mandibularis* F. Smith and *P. conjugata* Santschi were collected from the same locality in Mkuzi Game Reserve (north-eastern Natal) from 1980 to 1982. It is unlikely that there are microhabitat differences between these two species. The nests consisted of long vertical tunnels connecting various chambers, with occasional side tunnels. The majority of ants were found in the deeper levels of the nest (about 80 cm–1,20 m deep). Most nests were probably incompletely excavated, because the hard clay soil made these deep chambers difficult to reach. Thus an ergatoid queen was collected in only one of the nests (Table 1). *P. mandibularis* workers are of similar size and are easily distinguished from the larger ergatoid. However, in *P. conjugata*, there is a marked worker size polymorphism and the ergatoid is less likely to be recognized (although it has a distinctive external appearance, Bolton 1974). Observations of activity and foraging behaviour of workers, and activity of males at nest entrances were made prior to nest excavation.

The ants were kept in artificial nests in the laboratory, consisting of shallow depressions in low mounds of soil covered with a sheet of red perspex. They were fed on millipedes and *Tenebrio* larvae.

Oviposition and brood development were monitored over several months. Cocoons were opened to sex pupae. Small samples of workers from some nests were dissected: ovarian development was assessed and spermathecae were examined.

Results

Orphaned groups of workers were kept in the laboratory, and after some time large numbers of eggs were laid. A few males developed to the adult stage. Although these data were not collected as part of systematic experiments, they showed that worker laying occurs in the absence of ergatoid queens.

The data presented in Table 1 record the contents of the colonies at the time of excavation. The data given below indicate what brood was reared by the colonies that were successfully established in the laboratory.

P. mandibularis

(i) September 1980: queenright colony (Table 1). A group of 120 workers was isolated without the queen, and by November over 100 eggs had been laid. Very few of these eggs were reared to maturity, but two male pupae were found.

(ii) April 1981: colony without a queen. By January 1982, there were 107 eggs and 41 larvae. Two male pupae were found in March. Eighteen workers were dissected, and all had oocytes in their ovaries. Many had one or more mature basal oocytes (i.e. as large as an egg). The spermatheca was found in five workers, and each was empty.

P. conjugata

(i) January 1981: Oviposition occurred in this colony and 24 workers were dissected. Eight of these had well-developed and presumably active ovaries (i.e. with one or more mature basal oocytes, and with several smaller yolky oocytes in each ovariole. However, the occurrence of yellow bodies was not recorded). Another nine workers had only a few developing oocytes in their ovaries, while seven had undeveloped ovaries. Seven of the laying workers were checked for sperm and all were unmated. The 24 workers dissected were placed in two size classes (on the basis of head and gaster measurements) and of the eight laying workers, six were of the larger size class and two of the smaller.

Table 1 Composition of various nests belonging to two species of *Plectroctena* at the time of excavation. An ergatoid queen was only collected in the September 1980 nest. Data on oviposition in the laboratory are presented in the text

Date of excavation	No. of ergatoids	No. of workers collected	Brood composition
<i>P. mandibularis</i>			
September 1980	1	275	larvae and eggs
January 1981	—	110	no brood
April 1981	—	172	4 larvae only
<i>P. conjugata</i>			
January 1981	—	178	42 cocoons, 155 larvae
March 1982	—	192	no brood

(ii) March 1982: Neither queen nor brood was found when this nest was excavated. Oviposition started in August–September 1982; 280 eggs were laid in a group of 111 workers. This delay in the start of egg laying was confirmed by the dissection of 18 workers in May 1982 of which 11 had swollen ovarioles containing only non-yolky oocytes and sometimes small yolky ones. In October 1982, 50 randomly chosen workers were isolated, and another 70 eggs were laid within one month. In total, 29 male pupae or adults developed.

Various aspects of the ecology of this genus are summarized in Bolton (1974) and Bolton, Gotwald & Leroux (1976). In this study we made the following observations: (i) workers are only active outside their nests after rain. In Mkuzi (with a semi-arid climate), workers were not seen to be active throughout the year, and nest entrances became eroded and partly obstructed. After rain, large numbers of foragers soon became active, e.g. 64 foragers in one nest of *P. conjugata*. (ii) Small millipedes made up most of the ants' diet, but other arthropods were also retrieved to the nests, e.g. termites, small beetles, crickets, and ant sexuals. (iii) Workers usually hunt alone, but there is occasional cooperation. Fletcher (1973) noted that, in *P. mandibularis*, group retrieval was necessary for the transport of large prey. However, this behaviour was seldom observed in this study. Instead, foraging parties (with 10–15 workers) left the nests and headed towards a particular area; they were led by a worker laying a trail on the ground. The group eventually broke up, and the workers searched, captured, and retrieved prey independently. (iv) In *P. conjugata*, an episode of male activity was observed in March 1982. Male dispersal occurred after a rainy night followed by hot sunny weather. By 11 h 00, over 20 males had flown singly out of one nest. At the time 82 workers were active outside the nests, either because of the favourable foraging conditions or as a result of the male exits.

Discussion

It is probable that ergatoids were present but not found in the various queenless nests of *Plectroctena* that were excavated. After a few weeks, oviposition occurred in all the orphaned groups of workers kept in the laboratory, which suggests that ergatoid queens normally inhibit the reproductive activity of workers. Eggs were reared to maturity in three nests, and new workers were never produced. Only male (haploid) eggs were laid, which was consistent with the failure to find inseminated workers.

Inhibition of worker laying by reproductives is widespread in the social Hymenoptera (Fletcher & Ross, 1985) and has been documented in a few ponerine species with alate queens, e.g. *Rhytidoponera purpurea* (Haskins & Whelden 1965) and *Odontomachus troglodytes* (Colombel 1971). In the latter it appears that dealate queens exert their inhibition partly through a pheromonal effect. The present work on *Plectroctena* suggests that ergatoid queens inhibit worker laying. In the myrmicine slave-making *Harpagoxenus sublaevis*,

unmated workers can lay in the presence of the single ergatoid individual (Winter & Buschinger 1986). However, these ergatoid individuals appear to be intercastes and they are not the queen caste. In contrast, *Plectroctena* ergatoid queens form a specialized reproductive caste, the properties of which should be evaluated and compared with those of alate queens.

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