

## Research article

# Evolution of wingless reproductives in ants: weakly specialized ergatoid queen instead of gamergates in *Platythyrea conradti*

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**Abstract.** *Platythyrea conradti* is the only species in this genus with ergatoid (= permanently wingless) queens. Colonies lack gamergates (unlike other species in this genus), yet aggressive interactions among queen and workers define a hierarchy. A single fertile queen has the top rank and high-ranking workers do not lay eggs, except when the queen dies. Colonial reproduction by both alate queens (independent foundation) and gamergates (fission) seems the ancestral state in *Platythyrea*. Independent foundation can be selected against in some species, causing the loss of alate queens for economic reasons. Thus gamergates become the only reproductives, except in *P. conradti* in which queens became ergatoid. Gamergates and ergatoid queens are two mutually redundant reproductive phenotypes that allow colonial reproduction by fission.

**Keywords:** Aggression, hierarchy, ergatoid queen, gamergate, queen/worker dimorphism, reproduction, fission.

## Introduction

Social Hymenoptera start new colonies using two dramatically different strategies. A reproductive female can raise her first generation of offspring alone (independent foundation), or she can be completely dependent on sterile relatives (colony fission). Fission is an evolutionarily derived strategy that allows all the advantages of group living to be retained throughout colony ontogeny, in contrast to independent foundation which obligatorily involves a solitary stage (Peeters and Ito, 2001). Contrary to wasps and bees, ant workers lack wings, and thus species that have shifted to colony fission are restricted to dispersal on foot. Consequently flying reproductives are no longer needed and in a large number of species, permanently wingless 'ergatoid' queens have evolved

(Peeters, 1991). In other species restricted to the Poneromorph complex, workers have retained the ability to mate and some of them reproduce (= gamergates) instead of or in addition to queens (Peeters and Ito, 2001).

Ergatoid queens are the ultimate specialization for colony fission. They have lost the option to disperse and found a colony alone because they lack wing muscles and thus sufficient metabolic reserves. Their success is entirely determined by the number of workers that accompany them during a fission event. In several species ergatoid queens exhibit ovarian specialization for increased fecundity and they produce large colonies (Peeters, 1993). Nevertheless different degrees in this specialization can be seen among ants.

The Poneromorph complex includes the most basal ant genera and exhibits the greatest diversity of reproductive strategies. The 37 species of the Ponerinae genus *Platythyrea* can be found in tropical areas throughout the world (Brown, 1975). Among the seven species that have been studied, three have both alate queens and gamergates: *P. quadridenta*, *P. tricuspidata* (Ito, 1995) and *P. arnoldi* (Villet, 1993). Another three lack the queen caste and have gamergates only: *P. lamellosa* (Villet et al., 1990), *P. schultzei* (Villet, 1991b) and *P. cf. cribrinodis* (Villet, 1991a). Finally, alate queens are quite rare in *P. punctata*, gamergates occur but workers can also reproduce by thelytokous parthenogenesis (Heinze and Hölldobler, 1995; Schilder et al., 1999). Thus each of the species studied so far in this genus has gamergates.

We focused on *Platythyrea conradti*, an arboreal species living in warm and humid West African forests. It nests in hollow branches and tree cavities, and hunts insects although it also feeds on nectar (Dejean and Suzzoni, 1997; Lévieux, 1976a). Lévieux (1976b) described the queen as ergatoid and very similar to workers. We determined whether gamergates occur in *P. conradti*. We observed the aggressive interactions between workers and queen and described ovarian morphology and activity. We discuss the reasons why, contrary to all

other *Platythyrea* species, an ergatoid queen strategy could evolve in *P. conradti*.

## Methods

14 colonies of *Platythyrea conradti* were collected at the Lamto Ecological Station, Ivory Coast (6°13' N, 5°01' W), in December 2001 (colonies #1–5), April 2002 (colonies #6–9), June 2002 (colonies #10–12) and October 2005 (colonies #13–14). Whole branches containing the nests were carefully wrapped with plastic, sawn off and opened in the laboratory in order to avoid ants escaping. Details about these colonies are reported in Table 1. The ants were housed in plaster nests with glass roof, and maintained humid at 25 °C. Food was added daily outside the nest and consisted of mealworm pupae or larvae, crickets and diluted honey. Colony #5 was split into two colonies #5a and #5b in the laboratory.

All ants in each colony were marked individually with colour paint dots. Colonies #5a, #5b, #7 and #9 were regularly observed for 30 min sessions over a period of about two months. Every aggressive interaction was recorded. Social structure was manipulated by removing specific ants for dissection as well as adding cocoons in cocoonless colonies so that new workers could emerge and interact with other individuals.

Many of these ants were dissected under a Leica MZ6 stereomicroscope at 40x magnification to check ovarian development and spermatheca, either during the experiments to confirm the reproductive status of individuals with interesting behaviours, or at the end of the experiments to check for inseminated workers and to compare workers' and queens' ovaries and spermatheca. Four mating experiments were carried out with females (workers or gynes) and males from different colonies. We computed thorax volume and gaster area dimorphism between queen and worker. Because ant thorax has a complex shape, we did not consider it as a simple prism, but approximated its volume as the mean of two volumes: dorsal width times lateral area and lateral height times dorsal area. The cross-section of the first segment of the gaster was assimilated to an ellipse, the diameters of which are lateral height and dorsal width. To perform these measurements, only a lateral and a dorsal picture of the individuals are needed (see <http://www.biologie.ens.fr/ecologie/comportement/molet/dimorphism.html>).

Statistical analyses were performed with Statistica 5.1.

## Results

### *External morphology and ovaries of queens and workers*

Queens and workers of *P. conradti* are similar in their external morphology (Fig. 1). Indeed ergatoid queens lack flight sclerites and have the same thorax volume as workers ( $7.79 \pm 0.37 \text{ mm}^3$  (mean  $\pm$  SD)  $N = 6$  against  $7.57 \pm 0.46 \text{ mm}^3$   $N = 6$ , Student  $t = 0.89$   $p = 0.39$ ). However queens have a larger gaster area than workers ( $3.63 \pm 0.18 \text{ mm}^3$  against  $2.81 \pm 0.28 \text{ mm}^3$ ,  $t = 6.03$   $p = 0.0001$ ). Moreover, queens have a shorter and broader head than workers, their pronotum is swollen, their dorsal alitrunk has marginally better defined sclerites, and their petiole node is shorter and stouter (B. Bolton, pers. comm.). The queens do not have ocelli, as also described for alate queens in some congeneric species (Brown, 1975).

We dissected 106 workers and 8 queens (3 from the field and 5 born in the laboratory). They had the same number of ovarioles per ovary ( $9.9 \pm 2.0$  and  $8.9 \pm 1.9$ ,  $t = 1.45$   $p = 0.15$ ). Both queens and workers had a spermatheca.

**Table 1.** Composition of 14 *P. conradti* colonies collected at various times of year.

Colony	Workers	Queen	Males	Pupae	Emerged queens *	Month
# 1	173	0	0	34	0	December
# 2	75	1	0	yes	0	
# 3	118	0	0	16	1	
# 4	157	0	0	2	0	
# 5 ?	242	0	44	28	1	
# 6 ‡	24	1	0	0	0	April
# 7	131	1	1	184	0	
# 8	74	1	2	83	0	
# 9	67	0	0	150	3	June
#10	15	0	0	27	0	
#11	49	0	5	93	1	
#12	139	1	0	134	0	October
#13	19	1	0	32	0	
#14	>79	0	15	32	0	

\* Queens that emerged in the laboratory.

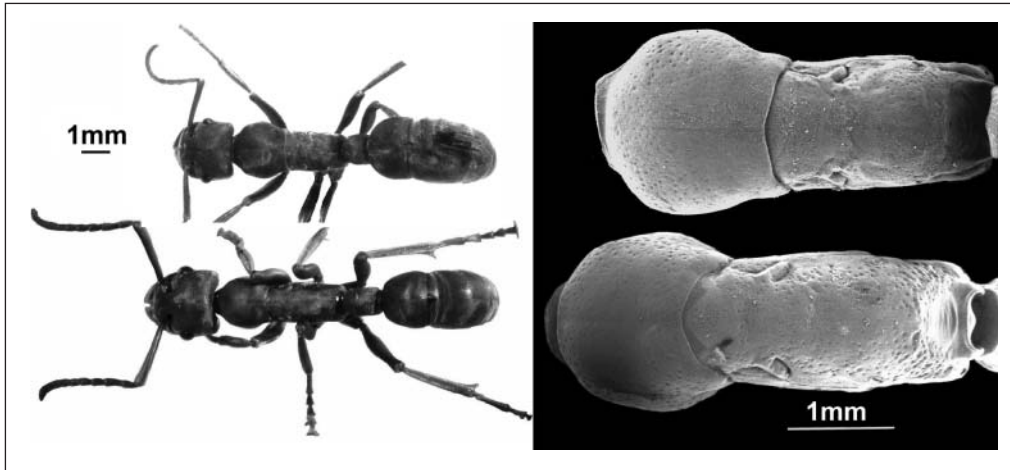
‡ Split into two artificial colonies of the same size.

‡ Incipient colony in a nest with little construction.

### *Hierarchy and reproduction*

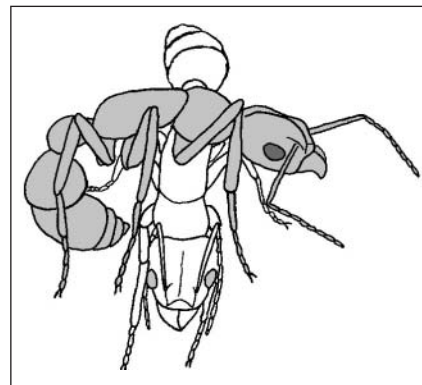
Colonies consisted of  $99 \pm 66$  workers (Table 1). Both workers and queens interacted in the different colonies with two kinds of aggressive behaviours. 'Antennal boxing' has been reported in many ant species (e.g. Gobin et al., 1998), but 'coxal hit' (Fig. 2) has never been described. An aggressive individual climbs over its opponent and repeatedly moves back and forth with its gaster folded under the thorax. During these movements, the base of the anterior legs violently hits the opponent, sometimes even causing it to roll over. Neither the gaster nor the mandibles touch the opponent. The opponent often behaved submissively. This aggression was usually accompanied by antennal boxing. Because antennal boxing is not easily quantified, we used only coxal hits to define a hierarchy in every colony. The hierarchy included one to four regularly aggressive workers called high-rankers, as well as workers that exhibited occasional aggressions. High-rankers were clearly identifiable because they performed most of the coxal hits.

Egg-laying activity was restricted to one high-ranker (the queen in stable queenright colonies) or shared among several high-rankers. Young individuals were more likely to become high-rankers (5 young workers out of 7 aggressive workers in colony #7 and 3 out of 3 in colony #9), and old high-rankers could then become excluded from the hierarchy. In queenless colonies, aggressions were common (1.6 and 5.1 coxal hits per hour in colonies #5a and #5b, Fig. 3). Aggression increased following queen emergence (2.0 and 7.2 coxal hits per hour in colonies #5a and #5b). The three queens

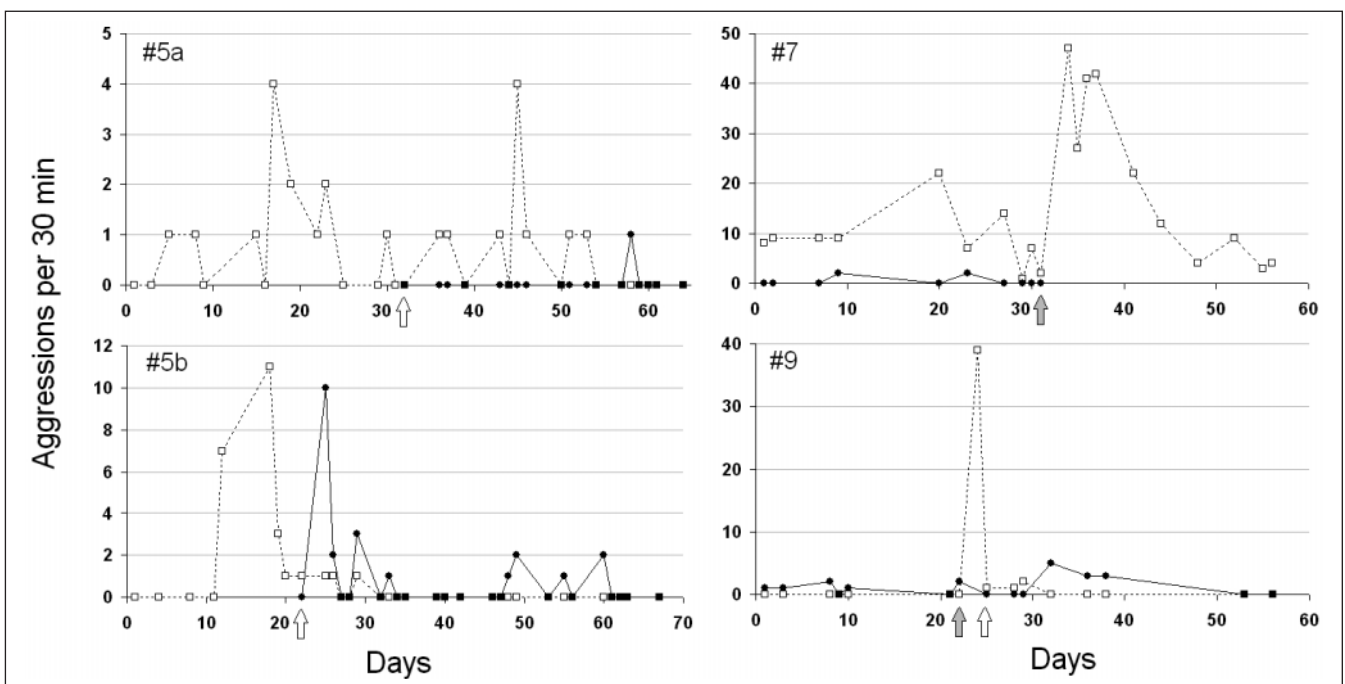


**Fig. 1.** Morphology of a queen (top) and a worker (bottom). Their sizes are similar (left) even if SEM photographs (right) reveal differences in thorax segmentation.

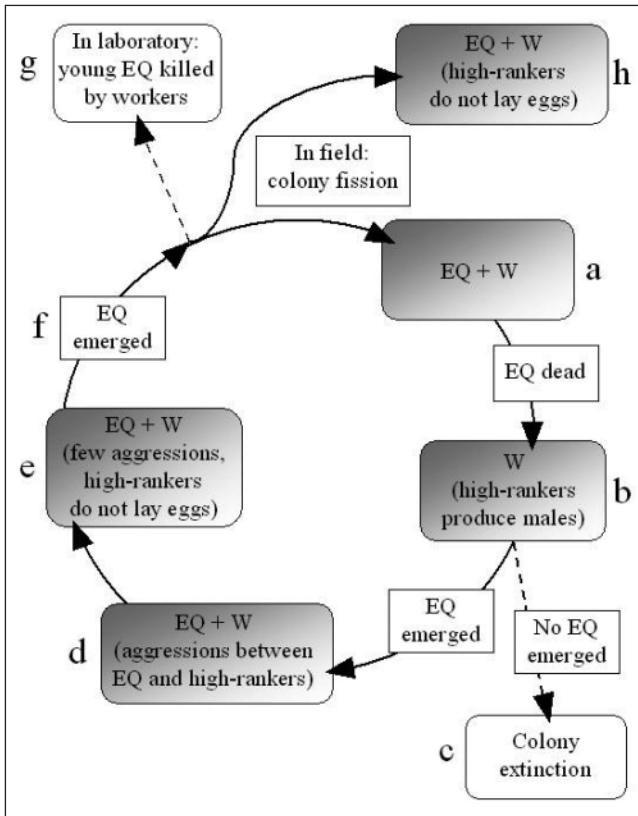
emerged in the laboratory were frequently aggressed by high-rankers but quickly became aggressive, reached the top rank of the hierarchy after three days to two weeks (Fig. 3) and then monopolized egg-laying. In colonies with an established queen, aggressions were less frequent (0.3 and 0.7 coxal hits per hour in colonies #5a and #5b) and mainly performed by the queen, who dominated all high-rankers. However the few interactions among workers still defined a clear hierarchy, although high-rankers never laid eggs in the presence of a queen. Following the death of the queen, aggressions became extremely frequent (switching from 9.2 to 22 and from 1.5 to 39 coxal hits per hour in colonies #7 and #9, Fig. 3).



**Fig. 2.** Drawing of a dominant worker (grey) performing a 'coxal hit' aggression. The victim (white) takes a submissive position with her body flattened on the ground.



**Fig. 3.** Aggressions performed by workers (empty squares/dashed line) and by queens (filled circles/continuous line) in four colonies. White arrows indicate queen emergence and grey arrows indicate queen death. Colonies #5a, #5b, #7 and #9 were observed during 16h30, 16h30, 10h and 8h respectively.



**Fig. 4.** Life cycle of *P. conradti* colonies based on demography in the field, laboratory observations of aggressive interactions, and dissections. Abbreviations are EQ for ergatoid queen and W for workers. (a) In a stable colony, a hierarchy between queen and workers occur. The queen dominates high-rankers. She lays eggs unlike workers. (b) If the queen dies, a peak of aggressions occurs and high-rankers start laying eggs. (c) If no new queen emerges from the brood of the dead queen, the colony becomes extinct. (d) If a new queen emerges, many aggressions occur between the high-rankers and the queen, who (e) becomes dominant and starts laying eggs while high-rankers stop. (f) If another queen emerges, (g) she is killed by workers in the laboratory, (h) but in the field colony fission could occur.

All 8 dissected queens had active ovaries. The 3 queens originally present in the colonies were inseminated, whereas none of the 106 dissected workers was although they had a spermatheca. Thus queens could lay diploid and haploid eggs developing into workers, queens and males, whereas workers could only lay haploid eggs developing into males.

#### Mating experiments

We introduced alien males in some colonies. They were accepted without aggressions but we did not observe matings. We then isolated two males in small boxes with two high-rankers but no copulation occurred. Another two males were isolated with two virgin queens, and they mated during a few seconds. One of these two queens was dissected and her spermatheca was full.

#### Discussion

Caste dimorphism is very limited in *P. conradti*: the ergatoid queens and workers have the same thorax volume and a mean of 9–10 ovarioles per ovary. Hence a queen may be only slightly more fertile than a worker. Dissections and mating experiments did not yield any evidence for mating ability in workers, and we conclude that there are no gamergates in *P. conradti*.

A hierarchy based on aggressive interactions occurs whether a queen is present or not (Fig. 4). Hierarchies that regulate sexual reproduction are common in queenless ants (e.g. Ito and Higashi, 1991; Monnin and Peeters, 1999), including other *Platythyrea* species (Heinze and Hölldobler, 1995). In species with a queen, hierarchies among workers that cannot mate have been described in *Pachycondyla apicalis* (Oliveira and Hölldobler, 1990). However, in *Platythyrea conradti*, the queen herself is involved. Among species without gamergates, this has only been reported in the slave-making ant *Protomognathus americanus*, where the queens and the workers compete to lay male eggs (Franks and Scovell, 1983). In *Pachycondyla tridentata*, aggressions among multiple queens and workers occur but most workers are mated (Sommer and Hölldobler, 1992; Sommer et al., 1994). In *Platythyrea conradti*, high-rankers perform only 8 to 66% of aggressions. If the queen is included this reaches 66 to 100%, which matches the level of aggression performed by high-rankers in other queenless species (89 to 97%, Monnin et al., 2003). *P. conradti* queens are aggressive but never as much as high-ranking workers. They may be aggressed by workers when their ovaries have not yet developed, but they quickly become dominant; once they monopolize reproduction they stop being aggressive (Fig. 4). When a fertile *P. conradti* queen is present, workers do not lay eggs and the hierarchy only has a predictive role should the queen die. A fertility signal may be involved, informing the workers about the egg-laying status of the queen, as in the queenless Ponerinae *Diacamma ceylonense* where a change in cuticular hydrocarbons of the gamergate occurs as ovaries become active (Cuvillier-Hot et al., 2002). Queens also influence the intensity of the conflicts among workers. Indeed when a young queen becomes fertile, aggressions decrease among workers, while the death of a queen leads to a peak of aggressions. Young workers are more likely to join the hierarchy than older ants. The high-rankers lay eggs in queenless colonies or if the queen is not yet fertile, as may also occur in a *Plectroctena* species with ergatoid queens (Peeters and Crewe, 1988). Thus they gain an individual benefit from male production. High-rankers are very aggressive as long as their ovaries are undeveloped, but their aggressions decrease as soon as they start laying eggs. This predictive hierarchy in *P. conradti* is costly at the colony level because high rankers spend the majority of their time in aggressive interactions (up to 38 aggressions per hour) instead of working. It is plausible that such a hierarchy is a behavioural legacy from an ancestor in which the workers competed to be gamergates.

Ergatoid queens lack wing muscles which account for a large part of the metabolic reserves, because in winged insect



females their histolysis increases brood production (Roff, 1990). Since alate queens in Poneromorph ants are all restricted to semi-claustral independent colony foundation (Peeters, 1997), if ergatoid queens were to found new colonies independently, they would need to forage outside the nest even more than alate queens. Besides, the lack of wings prevents queens from dispersing very far. Therefore they would gain no benefit from independent colony foundation relative to fission. New *P. conradti* colonies are likely to be founded by fission. We found an incipient colony in the field (Table 1: colony #6) consisting of one inseminated queen, 24 workers, eggs and small larvae, but neither cocoons nor older larvae. The tree cavity in which it nested was small and had not been modified yet in spite of the many workers. Thus, this colony probably emigrated there recently after splitting from the mother colony.

Colonies are monogynous since at most one queen was recovered in each nest, and a young queen that emerged in a queenright colony in the laboratory was killed by workers. In the field the emergence of queens could trigger colony fission. The production of males and young queens is not seasonal (Table 1) so throughout the year colonies can easily regain a queen after orphanage or fission. We did not find any queen in 8 of the 14 colonies in the field. Even though the nests were collected carefully, we cannot exclude that the queen sometimes escaped. Colonies have been suggested to be polydomous by Léviéux (1976b). He observed that workers leaving the nest on one day were fewer than workers returning, and claimed that some spent the night in other nests of the colony. Yet the only nest studied was observed during three non consecutive days. It is possible that the missing workers simply spent the night outside in the canopy. Léviéux performed aggression tests to find out whether two nests belonged to the same colony. However intruders can sometimes enter a foreign nest without being attacked (pers. obs.). Finally, queen lifespan is likely to be short, like other Ponerinae species (e.g. Liebig and Poethke, 2004), which may explain the large proportion of queenless colonies.

One 'queen' that emerged in the laboratory was excluded from the morphological comparison between queens and workers. Not only did she have a smaller thorax than other queens, but also than workers (5.57 mm<sup>3</sup>). Yet her gaster area was not different from that of normal queens (3.6 mm<sup>2</sup>) and her ovaries had 7 and 8 ovarioles. She behaved aggressively like any other queen and quickly started laying eggs. Her morphology may have resulted from a developmental accident, indicating that thorax and gaster growth can be dissociated. This illustrates that even cheaper ergatoid queens with enlarged gaster relative to thorax can be produced (Peeters, 1991).

In a species exhibiting such a low queen-worker dimorphism, it is surprising that workers cannot mate as in all other *Platythyrea* species studied so far. Although no complete phylogeny of the genus is available yet (but see Hartmann et al., 2005), we can speculate on the evolution of reproductive strategies in this genus. Alate queens are found in many species (Brown, 1975), and gamergates have been reported in all the species studied in detail (Villet, 1992). Reproduction by alate queens together with gamergates is likely

to be ancestral in *Platythyrea*. Hence colonies could take advantage of two alternative reproductive strategies: independent colony foundation by alate queens offers the benefits of long range dispersal, while reproduction by gamergates following queen death allows a turnover of reproductives and a rapid short-range colonization by fission (Peeters and Ito, 2001). Because of their low success rate linked to the risky independent foundation, many alate queens need to be produced annually, which is costly. Thus in habitats where fission is more successful than independent colony foundation (e.g. predation on queens or high competition for suitable nesting sites), the alate queen strategy may disappear. Such selection for colony fission clearly occurred in *Platythyrea* and led either to the queenless species with gamergates, or to the only species with ergatoid queens but no gamergates *P. conradti*.

Gamergates offer a cheaper alternative than weakly specialized ergatoid queens because they are morphologically workers, so they can either work or reproduce. Furthermore gamergates have a similar fertility as a *P. conradti* queen, and polygyny reduces the probability of orphanage and colony extinction. Thus it is very unlikely that ergatoid queens would have replaced gamergates in any *Platythyrea* species. The evolution of ergatoid queens in *P. conradti* could have been driven by the loss of gamergates in an ancestor with alate queens, followed by the loss of wings in the queen caste. *P. conradti* is the only species of the genus that exhibits arboreal nesting and foraging (Brown, 1975). The specific constraints of this habitat could be responsible for the initial loss of the gamergates and the subsequent evolution of ergatoid queens. This assumes a switch in selective pressures: first fission was selected against, and then independent foundation.

Ant species with both ergatoid queens and gamergates have never been described yet. Our results confirm this in a genus where all previously described queens are alate (Brown, 1975) and where gamergates are ubiquitous, even in the parthenogenetic species *P. punctata* (Hartmann et al., 2005). This suggests that contrary to alate queens and gamergates that are complementary because of the alternative colony founding strategies that they offer, ergatoid queens and gamergates are two mutually redundant wingless reproductive forms.

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