

THE REPRODUCTIVE CYCLE OF THE QUEENLESS ANT
PRISTO MYRMEX PUNGENS

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Reçu le 17 octobre 1983.

Accepté le 20 décembre 1983.

SUMMARY

The life cycle of the myrmicine ant *Pristomyrmex pungens* was investigated. Colonies of this species are usually composed of several thousand small workers, although a few males (2.3 %) occasionally appear during June and July in mature colonies, and large workers with ocelli and abortive spermathecae (here termed *ergatoid queens*) were observed extremely rarely. We found that the virgin small workers can lay eggs and that these develop into further small workers. Cerebral ganglion cells and oogonal cells had the diploid chromosome number ($2n = 24$), but the haploid number ($n = 12$) was observed in oocytes at pachytene, and also in spermatocytes from the rare males. Males have functionally normal copulatory organs and their spermatogenesis is normal, but they probably do not mate, because small workers have no spermatheca and their copulatory organs are degenerative. These observations indicate that reproduction in *P. pungens* is carried out predominantly or, probably, wholly by the small workers and hence is thelytokous. We discuss the evolution of the *P. pungens* life cycle, pointing out the difficulty of applying the "queen" concept to this species or even in deciding whether or not it is "eusocial". In view of the apparent genetic isolation between colonies, the mode of selection maintaining sociality in this case is probably interdemic group selection rather than kin selection.

RESUME

Cycle reproductif d'une colonie sans reine de *Pristomyrmex pungens*

Nous avons étudié le cycle biologique de la fourmi myrmicine *Pristomyrmex pungens*. En général, les colonies de cette espèce se composent de plusieurs milliers de petites

ouvrières, tandis qu'un petit nombre de mâles (2-3 %) apparaissent occasionnellement en juin et juillet dans les colonies mûres et que de grandes ouvrières à ocelles et spermathèque abortive (*reines ergatoïdes*) ont pu être observées très rarement. Nous avons démontré que les petites ouvrières vierges peuvent pondre des œufs qui donnent d'autres petites ouvrières. Les cellules des ganglions cérébroïdes et les ovogonies des ouvrières sont diploïdes ($2n = 24$), mais la formule haploïde ($n = 12$) a pu être observée chez les ovocytes au stade pachytène ainsi que chez les spermatozytes des mâles. Ces mâles possèdent des organes copulateurs normaux et leur spermatogénèse est normale, mais ils ne fécondent probablement pas les petites ouvrières, lesquelles sont dépourvues de spermathèque et d'organes copulateurs fonctionnels. Ces observations indiquent que la reproduction chez *P. pungens* est assumée de façon prépondérante, et probablement complètement, par les petites ouvrières, de façon par conséquent thélytoque. Nous discutons l'évolution du cycle biologique de *P. pungens*, en soulignant la difficulté d'appliquer à cette espèce le concept de « reine » ou même de décider si elle est « eusociale » ou non. Au regard de l'isolement génétique présumé entre colonies, le mode de sélection maintenant dans ce cas une structure sociale est probablement davantage une sélection de groupe interdémique plutôt qu'une sélection de parentèle.

INTRODUCTION

The myrmicine ant *Pristomyrmex pungens* is one of the commonest species in Japan. It is well known to form prominent roadside raiding columns which are sometimes longer than several hundred meters. The life history closely resembles that of army ants, except for some puzzling differences: The colony is usually composed only of small workers, and both queens and males have seldom been observed. The only record of a queen was made by TERANISHI (1923). He found a slightly larger worker with ocelli and identified it as an ergatogyne (ergatoid queen). IMAI (1966) observed the chromosomes of both males and workers in this species, and found $n = 12$ and $2n = 24$, respectively. This observation indicates that the males of *P. pungens* developed parthenogenetically from unfertilized eggs (i.e., arrhenotoky) (for detailed accounts of the reproductive cycle of ants see WILSON, 1971, and CROZIER, 1975). More recently, MIZUTANI (1980) and ONO (1983) found that workers develop from eggs laid by workers. These preliminary findings suggested two possibilities for the *P. pungens* life cycle: (1) production of workers by workers, via diploid parthenogenesis (thelytoky), together with occasional male production by such workers via arrhenotoky; (2) mating of workers or ergatoid queens, with normal arrhenotokous production of both workers and males. Cycle (1) above has been found in *Cataglyphis bicolor* by CAGNIANT (1982) and *Apis mellifera capensis* (see ROTHENBUHLER *et al.*, 1968), while cycle (2) is known from many *Rhytidoponera* species (HASKINS and WHELDEN, 1965) and in *Hypoponera eduardi* (LE MASNE, 1956). The present paper deals with the *P. pungens* reproductive cycle from both the morphological and cytological aspects.

MATERIALS AND METHODS

The ants used in this work were collected mainly from the campus of Shizuoka University during 1978-1982, but some colonies collected from Odawara (Kanagawa-ken), Nagashima (Mie-ken), Yamaguchi (Yamaguchi-ken) and Amami Oshima (Kagoshima-ken) were also used for examining colony composition and chromosome observations. Because *P. pungens* does not have a fixed nest, we could only use bivouac colonies, which were located under fallen leaves or in rotten wood. For this reason, the estimate of colony composition, especially the number of workers, is probably biased (underestimated). We consider, however, that any such bias is negligible for the purposes of this study.

To examine worker oviposition, we took 100 workers from each colony and bred them for several months in plastic cages containing sterilized soil and fallen leaves, in an incubator at 27°C. *Tubifex* sp., *Chironomus* larvae, and honey diluted with water were supplied as food every week. When the first batch of larvae turned to young adults (callows), they (i.e., workers of the 2nd generation) were isolated from the starting colony. Old workers were discriminated from young ones by being marked with white enamel paint on their abdomens. The workers of the 2nd generation bred again without males. We continued the breeding experiments for up to three generations in the same manner. The number of progeny decreased gradually in each successive generation. We stress, however, that this decline in progeny did not result from unfavourable culture conditions, but rather from the breeding system we employed, i.e., only the first batch of offspring was used.

To determine the condition of worker ovaries, we dissected them out in insect Ringer's solution and counted the number of mature eggs, which were identified by their size and the amount of yolk. Ovaries of some workers were fixed in Carnoy's solution or FAA (formalin, 70 % ethanol, absolute acetic acid ; 5: 15: 1), embedded in celloidin and paraffin, and then sectioned (10-20 μ m) for histological analysis.

Chromosome observations were made using cerebral ganglia of worker prepupa, ovaries of worker pupae, and testes of male pupae, using an air-drying technique (IMAI *et al.*, 1977).

RESULTS

Colony composition of *Pristomyrmex pungens*

To investigate the occurrence of ergatoid queens (ergatogynes) as reported by TERANISHI (1923), we examined the seasonal change of colony composition in 9 mature colonies collected on the campus of Shizuoka University. As summarized in *table I*, all colonies except one were composed only of small workers. The size of workers was quite uniform (head width taken across the compound eyes = 0.72 ± 0.02 mm S.D.). No morphological polymorphism involving so-called large workers, soldiers or queens was observed. The same result was obtained also for pupae. *Table I* suggests that the breeding season of this species begins in April and continues until the end of September. The majority of pupae reared during the breeding season were small workers.

With respect to males, we found two colonies containing a few adult males (July 2, 1982) or pupae (2.5 % ; July 1, 1980). One of us (IMAI) collected (June 2, 1972) a colony with males from Amami Oshima, in which the frequency of male pupae against worker pupae was 3.3 %. These data suggest

Table I. — Seasonal change of colony composition in *Prisomyrmex pungens* from the campus ground of Shizuoka University.Table I. — Seasonal change of colony composition in *Pristomyrmex pungens* from the *pungens* provenant du campus universitaire de Shizuoka.

Date of observation		Eggs	Larvae	Pupae		Adults	
				Male	Small worker	Male	Small worker
April 12,	1981	0	0	0	0	0	1,000 <
April 24,	1981	+	0	0	0	0	1,000 <
May 1,	1981	++	+	0	0	0	1,000 <
June 9,	1979	+++	++	0	0	0	1,000 <
July 1,	1980	+++	9,020	26	1,033	0	3,780
July 2,	1982	+++	+++	0	+++	3	1,000 <
August 1,	1980	++	1,737	0	2,993	0	5,095
September 6,	1980	0	91	0	1,416	0	10,846
November 4,	1982	0	0	0	0	0	3,814

+ = a few; ++ = several tens; +++ = several hundreds.

that in *P. pungens* a few males (2-3 %) are produced occasionally in some mature colonies during June and July.

The third author (KUBOTA) recently found some unusual colonies which included many large workers as well as the small ones described above (fig. 1). One of these large workers was collected in rotten wood at Nagashima. The worker size distribution is strongly bimodal, so that we can describe the "workers" as being dimorphic (fig. 2 A). The large workers are characterized by the possession of three well-developed ocelli (fig. 1 E), two pairs of ovarioles, a spermatheca (though it is more or less degenerate), and morphologically normal copulatory organs (fig. 3 A). In contrast, the small workers have no discernible spermatheca, and their copulatory organ is somewhat degenerate (fig. 3 B). These morphological characteristics suggest that the "large workers" could be described as ergatoid queens rather than true workers; following the description by TERANISHI (1923). We therefore term this category "ergatoid queen" (Qe). The frequency of ergatoid queens was 49.0 % in the Nagashima colony, but lower in other colonies, i.e., 33.3 % in the colony collected at Odawara and 3.0 % in that from Yamaguchi. We then excavated more than 50 colonies in the campus ground of Shizuoka University, but none of these had ergatoid queens. Given that the three colonies with ergatoid queens were collected over 500 km from each other, and that their distribution range includes the Shizuoka University site, with numerous colonies lacking ergatoids, it seems likely that colonies with ergatoid queens are widespread in Japan but present at low frequency.

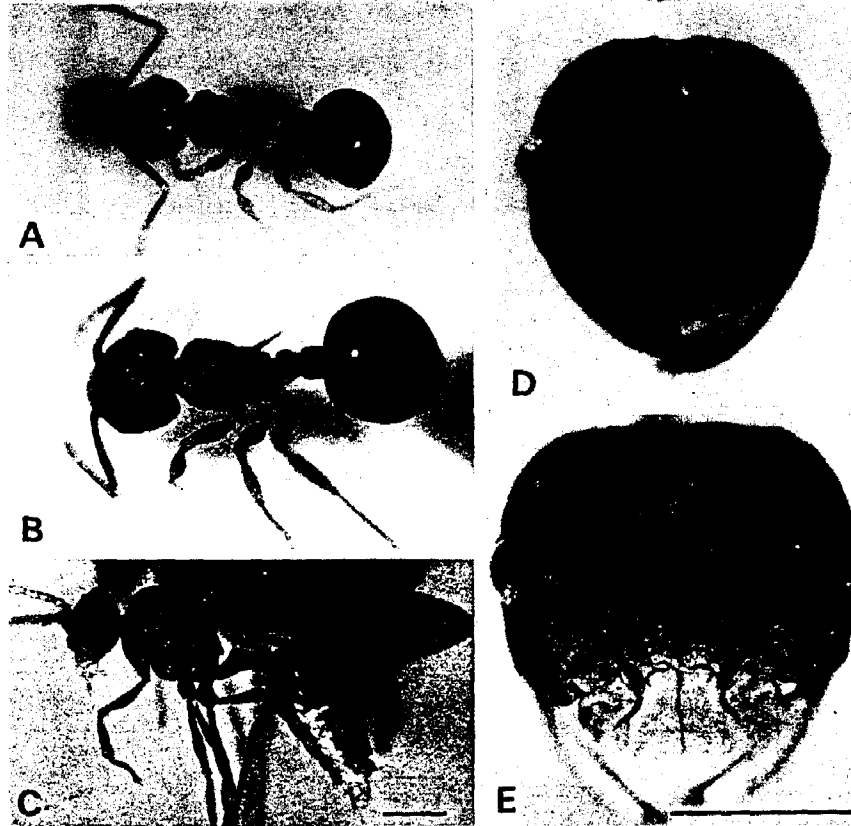


Fig. 1. — Castes found in *Pristomyrmex pungens*. A, small worker ; B, ergatoid queen (large worker) ; C, male. The ergatoid queen has ocelli (E) but the small worker has not (D). Scale: 0.5 mm.

Fig. 1. — Castes trouvées chez *Pristomyrmex pungens*. A, petite ouvrière ; B, reine ergatoïde (grande ouvrière) ; C, mâle. La reine ergatoïde possède des ocelles (E), contrairement aux ouvrières (D). Echelle: 0,5 mm.

Oviposition of workers

MIZUTANI (1980) and ONO (1983) have reported that workers of *P. pungens* held in an artificial nest can lay eggs, and that eggs laid by workers develop into workers. To confirm these observations, 100 workers (fig. 1 A and D) were selected from each of 12 colonies collected in the field, and they were reared in plastic cages at $27 \pm 2^{\circ}\text{C}$. In all such groups workers laid eggs within a few weeks and most of those eggs began to develop normally. An

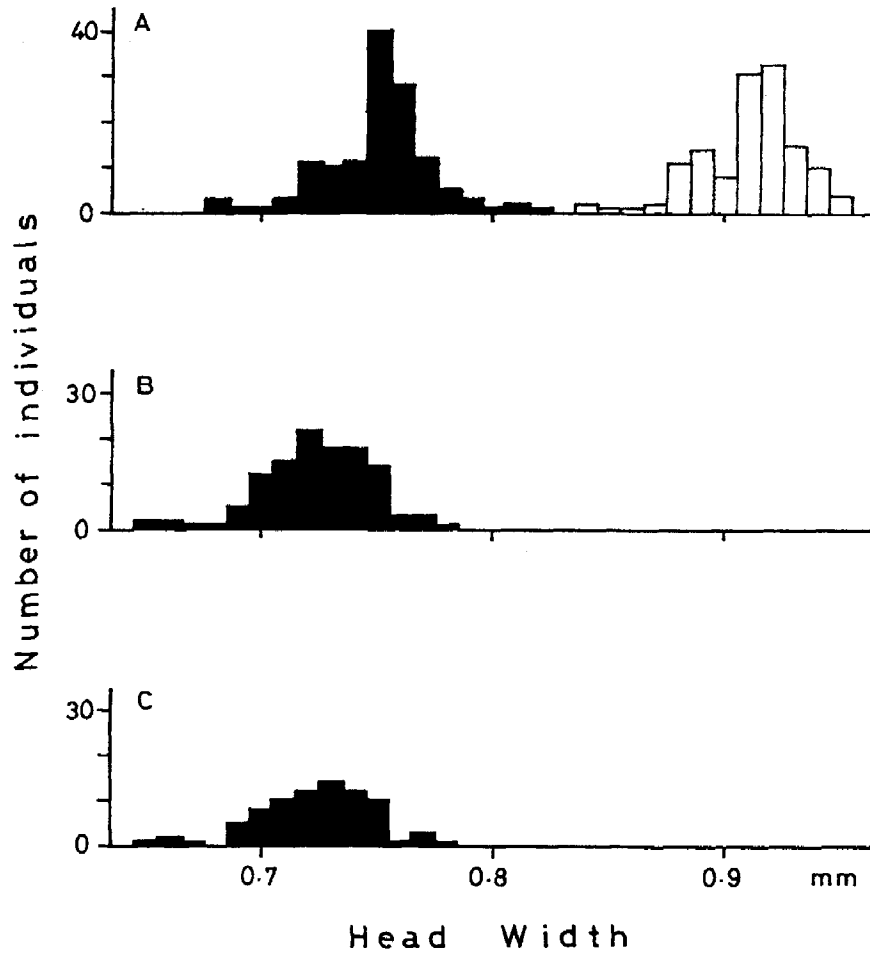


Fig. 2. — Size distribution of head width in three colonies of *P. pungens*. A, A colony involving both small workers (black column) and ergatoid queens (white column); B, A colony comprising of monomorphic workers; C, Workers developed from the eggs laid by virgin workers.

Fig. 2. — Distribution de la largeur de la tête chez trois colonies de *P. pungens*. A, colonie ayant à la fois de petites ouvrières (colonne noire) et des reines ergatoïdes (colonne blanche); B, colonie comprenant des ouvrières monomorphes; C, ouvrières issues d'œufs pondus par des ouvrières vierges.

example of these experiments is detailed in *figure 4 A*, in which 48 eggs or larvae are demonstrated. We obtained functionally normal workers (mean 19.8 workers/colony) one or two months later (*table II*). Note that the head width of these workers developed from worker laid eggs is almost the same as that of workers collected in field (*fig. 2*). We could not identify any ergatoid queens or males.

Table II. — Reproduction by workers of *Pristomyrmex pungens*.

Table II. — Reproduction des ouvrières de *Pristomyrmex pungens*.

Colony	Workers collected in field	Progeny grown up from the eggs		
		Worker	Ergatoid queen	Male
1	100	50	0	0
2	100	4	0	0
3	100	8	0	0
4	100	3	0	0
5	100	15	0	0
6	100	10	0	0
7	100	19	0	0
8	100	20	0	0
9	100	24	0	0
10	100	14	0	0
11	100	28	0	0
12	100	43	0	0
Mean	100	19.8	0	0

These investigations suggest the occurrence of diploid parthenogenesis by workers. There is, however, an alternative possibility, i.e., workers might have been previously inseminated by males in the field, as known in *Diacamma* (WHEELER and CHAPMAN, 1922), *Rhytidoponera* (HASKINS and WHELDEN, 1965) and *Ophthalmopone* (PEETERS, 1982). To test this possibility, we used worker pupae instead of adults in further experiments. We used 50 and 44 worker pupae respectively from two different field colonies. These two groups were nursed by 10 marked adult workers, which were removed when the pupae eclosed as adults. The workers used in this experiment, therefore, were completely virgin (denoted here as virgin workers of the 1st experimental generation). The virgin workers laid eggs, from which 12 and 34 virgin workers (the 2nd generation) developed, respectively. In the same manner, 4 and 16 virgin workers (the 3rd generation) were obtained from eggs laid by virgin workers of the 2nd generation. The ergatoid queens can also lay eggs, but these did not yield pupae for reasons unknown.

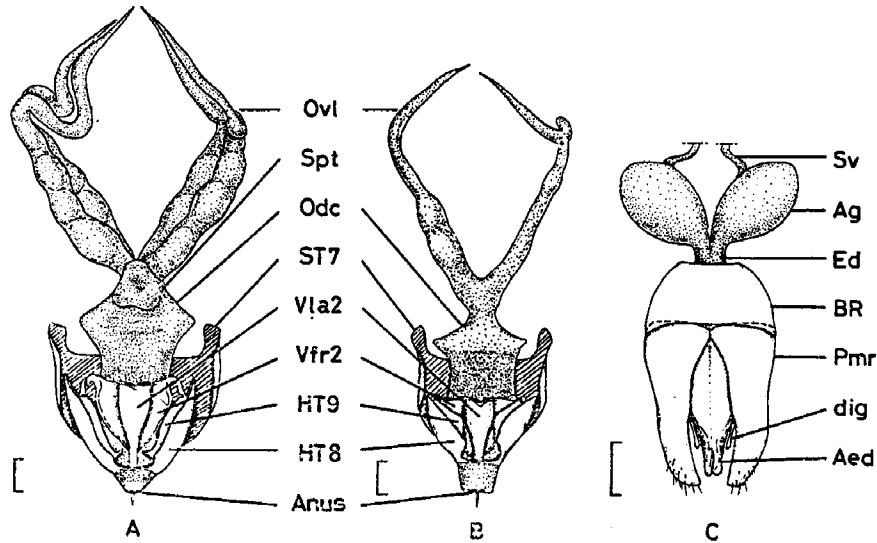


Fig. 3. — Reproductive organs of the ergatoid queens (A), small worker (B), and male (C) of *P. pungens* (dorsal view). *Aed*, aedeagus; *Ag*, accessory gland; *BR*, basal ring; *dig*, digitus; *Ed*, ejaculatory duct; *HT8*, hemitergite 8; *HT9*, hemitergite 9; *Odc*, common oviduct; *Ovl*, ovariole; *Pmr*, paramere; *Spt*, spermatheca; *ST7*, sternite 7; *Sv*, seminal vesicle; *Vfr2*, second valvifer; *Vla2*, second valvulac. Scale: 0.1 mm.

Fig. 3. — Organes reproducteurs de la reine ergatoïde (A), de la petite ouvrière (B) et du mâle (C) de *P. pungens* (vue dorsale). *Aed*, édéage; *Ag*, glande accessoire; *BR*, anneau basal; *dig*, digitus; *Ed*, canal séminal; *HT8* et *HT9*, hémitergites 8 et 9; *Odc.*, oviducte commun; *Ovl.*, ovariole; *Pmr*, paramère; *Spt.*, spermathèque; *ST7*, sternite 7; *Sv*, vésicule séminale; *Vfr2*, seconde valve; *Vla2*, seconde valvule. Echelle: 0,1 mm.

Table III. — The number of maturated eggs in ovarioles of workers of *Pristomyrmex pungens*.

Table III. — Nombre d'œufs mûrs dans les ovarioles des ouvrières de *Pristomyrmex pungens*.

Colony	Month of observation	Number of maturated eggs			Number of dissected workers
		2	1	0	
1	June	15 (52 %)	8 (28 %)	6 (21 %)	29 (100 %)
2	July	5 (7 %)	21 (31 %)	42 (62 %)	68 (100 %)
3	December	0 (0 %)	0 (0 %)	75 (100 %)	75 (100 %)

To determine whether or not such worker oviposition actually occurs under natural conditions, we examined the ovaries of workers from three colonies collected in June, July and December. Most of these workers had one or two matured eggs (mean 1.3 ± 0.8 per worker) in June (*fig. 3 B*, *table III*). The workers collected in July also had mature eggs (mean 0.5 ± 0.6 per worker). These seemed to be functionally normal, in that we did not observe any abnormality, either in egg size and yolk content, or in a histological examination (*fig. 4 C*). On the other hand, no mature eggs were seen in workers dissected in December. These series of observations, and the seasonal change of colony composition shown in *table I*, strongly suggest that workers of *P. pungens* can lay eggs without previous insemination by males during summer, and that 97-98 % of such worker-laid eggs are destined to become workers.

Chromosomes of *P. pungens*

The chromosome number was $2n = 24$ in the cerebral ganglion cells of workers (*fig. 5 A*). Chromosomes were also observed from males collected at Amami Oshima (June 2, 1972). A total of 24 spermatocytes obtained from three male pupae showed the haploid chromosome number $n = 12$ (*fig. 5 C*). There were no abortive spermatocytes, and both spermatids and sperms were observed in the late pupal stage, so that spermatogenesis seems to proceed normally in this species. The copulatory organ is also normal (*fig. 3 C*). These results agree exactly with the previous observations by IMAI (1966). We observed chromosomes in ovaries from worker pupae, and found many oocytes at pachytene, in which homologous chromosomes are associated completely, and 12 pairs of bivalents ($n = 12$) can be identified (*fig. 5 B*).

DISCUSSION

Ants belong to the order Hymenoptera, and, like other members of the order, are male-haploid. In general males develop from haploid, unfertilized eggs and females from diploid fertilized ones (CROZIER, 1975 : 1-2). There is good evidence that sex-determination in many hymenopterans, especially in the Aculeata to which ants belong, involves individuals heterozygous at one or more specific loci, which become female, and hemi- and homozygotes, which become male (CROZIER, 1977). As in other social Hymenoptera, male ants are restricted to a reproductive role, and are rare compared to females. Females are divided, roughly, into mated, highly-fertile reproductive specialists, the queens, and the great bulk of the colony, the workers, which are generally virgin and sterile, or at any rate of low fertility. The workers are also often subdivided into specialist castes, such as soldiers (OSTER and WILSON, 1978 : 130-143).

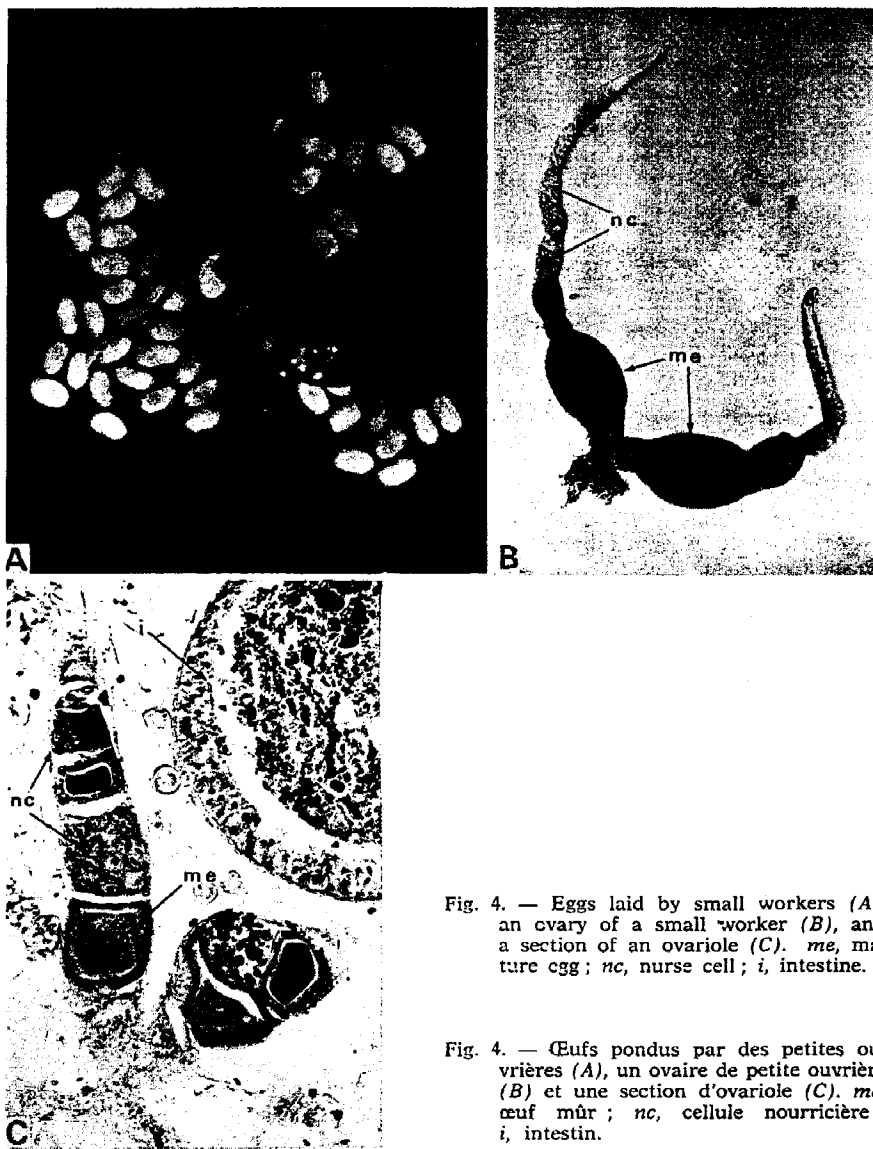


Fig. 4. — Eggs laid by small workers (A), an ovary of a small worker (B), and a section of an ovariole (C). *me*, mature egg; *nc*, nurse cell; *i*, intestine.

Fig. 4. — Œufs pondus par des petites ouvrières (A), un ovaire de petite ouvrière (B) et une section d'ovariole (C). *me*, œuf mûr; *nc*, cellule nourricière; *i*, intestin.

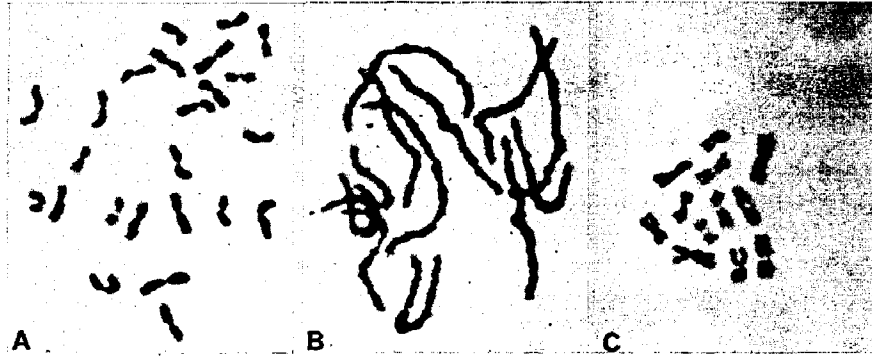


Fig. 5. — Chromosomes of *P. pungens*. A, A cerebral ganglion cell at metaphase ($2n = 24$); B, An oocyte at pachytene ($n = 12$); C, A spermatocyte at 1st meiotic metaphase ($n = 12$).

Fig. 5. — Chromosomes de *P. pungens*. A, cellule de ganglion cérébroïde en métaphase ($2n = 24$); B, ovocyte en pachytène ($n = 12$); C, spermatocyte en première métaphase de méiose ($n = 12$).

The above overview serves to focus attention on these issues, but it clearly involves some oversimplification. When we understand that the origin of sociality in ants involved the evolution of workers from within a category of females all of which were reproductively competent (e.g., CROZIER, 1982), it is not surprising that we find intergrades between queens and workers (e.g., WHEELER, 1905), or that the degree of this inter-female difference varies widely between species (WILSON, 1953; OSTER and WILSON, 1978: 6). Ant evolution can in fact be described as evolution of the allometric growth curve, so that socially-valuable individual morphology will result at all sizes attained at maturity, and that appropriate size frequency distributions obtain. Thus, not only are intergrades between queens and workers observed in many species, but also we might expect that the potential for producing such intergrades remains in genera where they are not currently observed.

Intergradation between queens and workers can involve more than morphology, and extends also to reproduction. In some genera, such as *Solenopsis* (WILSON, 1971: 320), the workers lack ovaries and hence are totally non-reproductive, but in most ants they not only possess ovaries but lay some eggs. Often these eggs are so-called "trophic" eggs, used for feeding other colony members (e.g., FREELAND, 1958), but true eggs are also frequent. Worker-laid eggs provide a fraction of the males in many species, sometimes being responsible for all of them (CROZIER, 1977).

That males should result from worker-laid eggs is expected, under the general picture that ants are arrhenotokous and workers are virgin, but females also arise from worker-laid eggs. In some species this is a rare

occurrence, reflecting only the sporadic thelytoky found in Hymenoptera in general (CROZIER, 1975 : 16-18). But in some instances female-production by workers is prolific. Such female production by workers need not involve thelytoky, because in some genera workers mate and can therefore lay fertilized eggs. In *Ophthalmopone berthoudi* (PEETERS, 1982), *Diacamma* (WHEELER and CHAPMAN, 1922) and most species of *Rhytidoponera* (e.g., *R. metallica*, HASKINS and WHELDEN, 1965) differentiated queens are absent altogether and reproduction is by mated workers.

While invariable arrhenotoky is thought to be the rule in most ants, in some species worker thelytoky has been suggested as being important in the life cycle. Such a central role for worker thelytoky has been implied for species of *Cataglyphis* (CAGNIANT, 1982), *Crematogaster* (SOULIE, 1960) and *Oecophylla* (BHATTACHARYA, 1943 ; LEDOUX, 1950, 1954). The *Oecophylla* reports, however, could not be confirmed (WAY, 1954 ; VANDERPLANK, 1960 ; CROZIER, 1970). If we accept that, as we have shown here for *Pristomyrmex pungens*, worker thelytoky does have a key role in some ant life cycles, then it is tempting to regard it as acting to extend the female-producing life of the colony in these instances, as in the comparatively well-known case of the Cape Honey Bee, *Apis mellifera capensis*.

In the case of *Pristomyrmex pungens*, we have clearly demonstrated that worker thelytoky occurs, because we used workers reared in the laboratory in the absence of males. We can also exclude the possibility that the mechanism of thelytoky is ameiotic (as suggested by LEDOUX for *Oecophylla*), because we observed bivalents in worker meioses ; nor therefore does it involve pre-meiotic doubling of the chromosome number. Further work, possibly using isozymes, is required to determine which of the possible types of meiotic thelytoky occurs in *P. pungens*. Given that the various types have quite different consequences in terms of maintaining heterozygosity and releasing genetic variability (CROZIER, 1975 : 15), such work is clearly desirable.

The production of males in *P. pungens* accords with the general phenomenon of occasional male production by otherwise thelytokous Hymenoptera (CROZIER, 1975 : 18). The lack of spermathecae in the small workers indicates that these males do not have a habitual or obligatory role in colony reproduction, but the possession of spermathecae by the ergatoids suggests that occasional outbreeding may occur. The possible parallel is with the case of females of the "thelytokous" sibling of the aphelinid *Aphytis mytilaspidus*. These females sometimes mate with males of the bisexual sibling species and produce fertilized eggs (ROESSLER and DEBACH, 1973).

Some *Rhytidoponera* species have a polymorphism between colonies, in which some are headed by alate queens and others lack such queens, but persist via oviposition by mated workers (WARD, 1981, 1982). Such a polymorphism has been suggested as being primitive for ants (WHEELER, 1922 : 113 ; WARD, 1983), and this is plausible in view of our arguments about ant

evolution expressed above. Models are known in the form of species which have winged/wingless polymorphisms, such as the bethylid *Cephalonomia perpusilla* (EVANS, 1963), the chalcidoid *Melittobia chalybii* (SCHMIEDER, 1938) and the beetles *Ptinella aptera* and *P. errabunda* (TAYLOR, 1978). In such cases, production of winged forms allows dispersal to new habitats, but may be energetically expensive wingless individuals may require less food to produce and be more efficient in exploiting hypogenic modes of existence. For these conditions to lead to worker evolution and eusociality requires the occurrence of appropriate cost-benefit ratios and opportunity for kin-kin altruism (CROZIER, 1982).

The lack of winged queens in ants is thus clearly secondary, and it is tempting to suggest that it occurs most readily where there is little need for dispersal and claustral colony foundation. Mating within the nest and subsequent colony reproduction by fission, thought to be the situation in many *Rhytidoponera* and *Ophthalmopone* species, provide one scenario, as does colony foundation by social parasitism, as observed in *Harpagoxenus* (BUSCHINGER, 1968).

The *Harpagoxenus* case is particularly instructive. Although we have followed precedent in terming the large workers of *P. pungens* "ergatoid queens", this distinction between them and normal workers is probably trivial. Thus, BUSCHINGER describes all mated egg-layers in *Harpagoxenus* as ergatoids, but these are included among the larger members of a continuum of workers, with the crucial difference being the possession of a spermatheca (BUSCHINGER and WINTER, 1975, 1978). In *Rhytidoponera* and *Ophthalmopone* not even this difference exists: all workers have spermathecae and, in *Ophthalmopone*, mating is determined by the presence or absence of males at eclosion. Clearly, the terminology of "queenless" is entering a difficult stage, and quibbling over such details is unlikely to aid understanding.

The general outlines of the evolution of the *P. pungens* life cycle are given in figure 6. This, however, says little about the selective forces favoring thelytoky, which are more than unusually obscure in this case. We lean towards the general view that thelytoky is generally an evolutionary dead-end, but that when thelytokous lineages arise they may occasionally "trap" a genotype fitting them to a particular specialised mode of life and persist for as long as that mode of life is present. Whether *P. pungens* is such a specialist awaits further study, particularly of its ecology, but the apparently normal arrhenotokous nature of its Australian congeners (TAYLOR, 1965) is noteworthy.

Given the reproductive cycle as we have described it, we also predict that, in comparison with related but arrhenotokous ants, *P. pungens* should show marked differences between colonies and uniformity within them (to the extent that this is not masked by all the colonies in the same area belonging to the same clone). The expected uniformity within, but differences

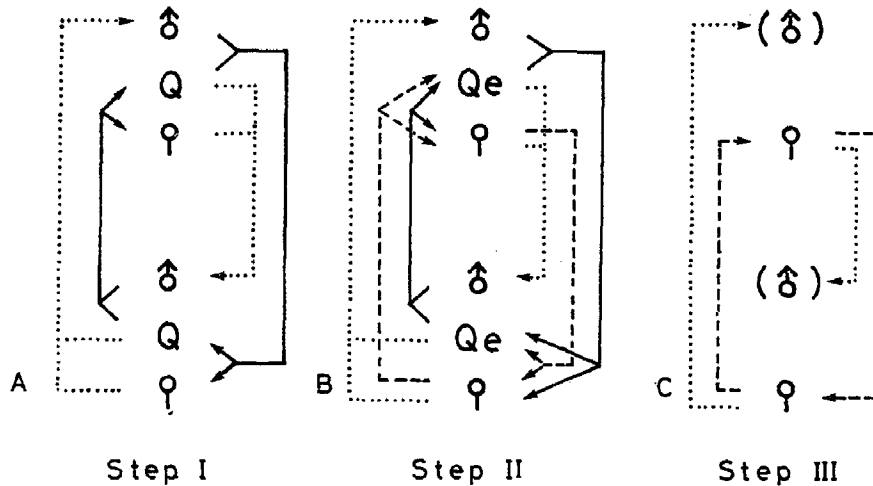


Fig. 6. — A scheme for evolution of thelytoky in *P. pungens*. A, The basic life cycle of ants; B, Life cycle expected in an hypothetical and involving thelytokious workers and ergatoid queen; C, Life cycle of *P. pungens*. ♂, male; Q, queen; Qe, ergatoid queen; ♀, worker. Dotted lines: arrhenotoky. Broken lines: thelytoky. Solid lines: bisexual reproduction (haplo-diploidy). Males appearing occasionally are represented in parentheses.

Fig. 6. — Schéma de l'évolution de la thélytoquie chez *P. pungens*. A, cycle biologique de base des fourmis; B, cycle biologique hypothétique impliquant des ouvrières thélytoques et une reine ergatoïde; C, cycle biologique de *P. pungens*. ♂, mâle; Q, reine; Qe, reine ergatoïde; ♀, ouvrière. Lignes pointillées: arrhénotoquie; lignes brisées: thélytoquie; lignes continues: reproduction sexuée (haplodiploïdie). Les mâles apparaissant occasionnellement sont représentés entre parenthèses.

between, colonies leads to the conclusion that the mode of selection maintaining sociality in *P. pungens* is not longer describable as kin selection but rather as a form of group selection. Colonies that are "well-tuned" and made up of highly-cooperative workers will flourish, increase in size and reproduce by fission; whereas those with more selfish and less cooperative workers will not do so well, and ultimately die out.

Finally, we note that it is an open question as to whether *Pristomyrmex pungens* is still eusocial or not, at least in the case of those colonies made up exclusively of small workers. Eusociality has been defined (MICHENER, 1969; WILSON, 1971: 4-5) as involving a reproductive division of labor in which offspring assist parents. It is uncertain how much reproductive division of labor there is in *Pristomyrmex pungens*, or indeed what criteria to apply to settle this point — would, for example, deviation from a Poisson distribution of eggs laid per individual be sufficient to demonstrate reproductive specialization?

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