

Research article

Permanent loss of wings in queens of the ant *Odontomachus coquereli* from Madagascar

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Received 15 December 2006; revised 26 February 2007; accepted 1 March 2007.
Published Online First 20 March 2007

Abstract. Winged queens are the most common reproductives in ants. They are morphologically specialized for independent colony foundation, with wings for long-range dispersal and metabolic reserves to raise the first brood. However independent foundation can sometimes be selected against and replaced by fission, featuring short-range dispersal on the ground and reproductives that are dependent on the wingless workers for all non-reproductive tasks. We investigated the evolutionary consequences of this transition on the morphology of the reproductives by collecting 30 colonies of *Odontomachus coquereli* from Madagascar, the only species in the genus where winged queens have never been found. Data about colony demography, morphometry, allometry and ovarian dissections showed that the winged queen caste has been replaced by a wingless reproductive caste with distinct body proportions relative to the workers or to congeneric winged queens. The 17 reproductives that we measured exhibited little size variability. A single wingless reproductive was found in each colony, corresponding to 'ergatoids' in literature. Several facts suggest that colonies reproduce by fission, notably the relatively constant colony size (19 ± 11 workers). The developmental origins of wingless reproductive phenotypes need investigation; little genetic change may be involved, as seen when *Odontomachus* larvae are parasitized by nematodes. The sole function of wingless reproductives in *O. coquereli* is reproduction, and they contrast with multi-purpose wingless reproductives found in other ants, where numerous intermorphs occur in each colony and contribute to sterile tasks.

Keywords: Ergatoid queen, morphometry, colony fission, intermorph, caste.

Introduction

Colonial reproduction has a major impact on the morphology of reproductives in ants. Independent colony foundation is performed by winged queens that disperse by flight, mate and found their colony alone (Hölldobler and Wilson, 1990). High mortality of foundresses can cause selection against this strategy and lead to a switch to colony fission, where reproductives are continuously helped by the wingless workers and dispersal occurs on the ground. As a consequence wings become unnecessary, and since associated muscles are costly to produce, wingless reproductives can be selected for (Peeters and Ito, 2001). In some species that reproduce by fission, the wingless reproductives are just workers that have retained the ability to mate and lay eggs (gamergates, Peeters, 1991b). However in many other species, new phenotypes distinct from workers and winged queens have evolved (Peeters, 1991a; Heinze et al., 1995; Heinze, 1998). Their morphology and the demography of the colonies where they occur vary dramatically. Wingless reproductives can range from very similar to workers to highly dimorphic, and colonies can have one or numerous members of the reproductive caste.

The mechanisms of the transition from independent colony foundation to colony fission are poorly known, and so are the selective pressures that favour one type of reproductive phenotype and colonial organization over the other. Ant genera where winged queens are the rule

but where wingless reproductives have sporadically evolved are good models to investigate this question.

The pantropical genus *Odontomachus* (subfamily Ponerinae) consists of 64 species that occur from forests to semi-desert areas, nesting in the ground under stones or logs, or in rotten logs. Winged queens have been reported in all species studied (e.g. Ito et al., 1996) except *O. coquereli* from Madagascar where only wingless reproductives have been found (Brown, 1976; Wheeler, 1910). Mated *Odontomachus* workers have never been found, although they can lay unfertilized eggs (van Walsum et al., 1998). We collected entire colonies of *O. coquereli* and performed morphometry and allometry analyses to describe the phenotype of the reproductives. Using data from dissections and colony demography, we discuss the evolutionary transition from winged queens and independent colony foundation to wingless reproductives and colony fission.

Material and methods

Colonies

30 complete colonies of *Odontomachus coquereli* were collected in December 2004–2005 at various elevations (450 m–775 m) in primary rainforest (Parc National de Marojejy in Madagascar, 14°26.2'S, 49°56.5'E, Table 1). This species nests in rotting branches and logs on the ground. Adults and brood were counted in the field. Voucher specimens are deposited in the California Academy of Sciences (<http://www.antweb.org>).

Morphometry

In 17 colonies, we took photographs of the wingless reproductive and some random workers (0 to 12 workers, i.e. $39 \pm 27\%$ of colony size) with a Leica MZ6 stereomicroscope. We measured the length of the right mandible, the head width above the eyes, the length of the posterior left tibia (the easiest leg part to detach and measure), the volume of the thorax, and the cross-sectional area of the first gaster segment (as an indicator of gaster volume) with ImageJ (<http://rsb.info.nih.gov/ij>) following the method in Molet et al. (2007).

Dissections

We dissected the wingless reproductive from 10 colonies and 14 workers from 5 colonies. Ovarian development and spermatheca were checked. Mature oocytes, i.e. equal to the size of an egg, were counted. The presence of yellow bodies at the base of the ovaries attests to past egg-laying activity (Billen, 1982). The wingless reproductive was removed from 3 colonies to assess the potential of orphaned workers to lay eggs.

Data analysis

In order to determine the growth pattern of the reproductive and worker castes, we chose tibia length as independent variable because it exhibited the strongest correlations with the other variables, unlike head width. We performed allometry analyses between tibia length and four other variables (mandible length, head width, thorax volume and gaster area) in reproductives and workers using standardised major axis linear regressions (Fairbairn, 1997). This regression method takes into

Table 1. Composition of 30 *Odontomachus coquereli* colonies. All but 6 colonies contained one wingless reproductive morphologically distinct from workers. The last column indicates additional data obtained in the laboratory. Demography of colony 13424 was not assessed in the field.

| colony id | workers | pupae | larvae | eggs | measured |
|-----------|---------|-------|--------|------|----------|
| 10980 | 18 | 1 | 6 | 24 | no \$£ |
| 13387 | 30 | 15 | 12 | 2 | no |
| 13388* | 32 | 19 | 18 | 10 | no |
| 13389 | 11 | 4 | 6 | 40 | no |
| 13396 | 18 | 13 | 11 | 5 | yes |
| 13397 | 31 | 6 | 14 | 59 | yes # |
| 13401 | 6 | 3 | 15 | 30 | yes \$£ |
| 13406 | 7 | 4 | 1 | 15 | yes |
| 13408 | 32 | 14 | 13 | 52 | yes \$ |
| 13409 | 23 | 8 | 7 | 27 | yes # |
| 13410 | 30 | 24 § | 21 | 74 | no |
| 13423 | 17 | 10 | 20 | 57 | yes |
| 13424 | – | – | – | – | yes |
| 13427 | 5 | 0 | 0 | 10 | yes |
| 13448 | 24 | 17 | 13 | 22 | yes \$ |
| 13450 | 6 | 7 | 10 | 11 | yes |
| 13451 | 34 | 9 | 16 | 37 | no |
| 13454* | 17 | 13 | 13 | 36 | no |
| 13467 | 7 | 4 | 10 | 7 | yes \$£ |
| 13617* | 15 | 1 | 9 | 1 | no |
| 13618* | 10 | 0 | 0 | 4 | no |
| 13619* | 38 | 6 | 15 | 45 | no |
| 13620 | 6 | 4 | 10 | 10 | yes \$£ |
| 13621 | 36 | 7 | 13 | 7 | no |
| 13622* | 13 | 3 | 8 | 10 | no |
| 13623 | 31 | 8 | 12 | 19 | yes \$£ |
| 13624 | 12 | 11 | 8 | 36 | yes \$ |
| 13625 | 9 | 5 | 9 | 21 | yes \$ |
| 13626 | 9 | 4 | 9 | 29 | no |
| 13627 | 21 | 8 | 18 | 38 | yes \$# |

* No wingless reproductive

§ Reproductive dissected

£ Workers dissected

Worker oviposition followed queen removal

§ One male emerged

account the measurement error in both dependent and independent variables. It is more suitable than the type I regression, which hypothesizes that the independent variable is controlled by the experimenter and is thus error-free. The software (S)MATR 1.0 performs different computations and tests based on standardised major axis linear regressions (Warton and Weber, 2002). We used it to compute allometry coefficients, i.e. the slopes of the regression lines between the logarithms of the morphometric variables. Then we tested whether these coefficients differ from 1, i.e. isometry. If they do, it means that body parts do not grow at the same rate, so individuals of distinct sizes exhibit different body shapes. Finally we compared allometries between body parts and between castes. Details of how test

statistics and P values were computed are available on the (S)MATR website (<http://www.bio.mq.edu.au/ecology/SMATR>). We did not provide the values for these test statistics as they are estimated with random permutations and have no meaning for the readers.

In order to test for differences in size variability between reproductives and workers and between body parts, we first converted all measurements to the same dimension (thorax^{1/3}, gaster^{1/2}, mandible, head and tibia are all in mm) in order to avoid dimensionality issues (Lande, 1977). Then we compared their coefficients of variation (= standard deviation / mean) using the squared-ranks test (STR), a non parametric test which is robust against the distribution of the variable (Funk and Tsang, 1998). We applied a sequential Bonferroni correction using the Dunn-Sidak method to account for multiple comparisons (Sokal and Rohlf, 1995).

Other statistical analyses were performed with Statistica 5.1 (<http://www.statsoft.fr>).

Results

Colony demography and dissection of ovaries

Colonies consisted of one wingless reproductive, 19 ± 11 workers (mean \pm sd), 8 ± 6 pupae, 11 ± 5 larvae and 25 ± 19 eggs (Table 1). Six out of the 30 colonies lacked a reproductive. One male emerged from a cocoon in colony 13410. Both reproductives and workers had 3 ovarioles per ovary. Reproductives were always mated, and their ovaries contained 0 to 4 mature oocytes and yellow bodies. In contrast workers were always virgin and had undeveloped ovaries. With a length of 2.82 ± 0.20 mm and a width of 0.71 ± 0.04 mm ($N=19$), eggs were unusually large compared with other species, e.g. *O. cephalotes* (length: 1.03 ± 0.02 mm, t test: $t_{31}=33.62$, $P<10^{-6}$; width: 0.49 ± 0.02 mm $t_{31}=18.07$, $P<10^{-6}$; $N=14$, unpublished data). The benefits of such big eggs are unknown, since in social insects larvae do not depend on yolk reserves because they are fed by workers (but see Iwata and Sakagami, 1966; Villet, 1990b). Following removal of the reproductive ($N=3$ colonies), male eggs were laid by nestmate workers.

Morphometry

Reproductives have a slightly larger thorax than workers (resp. 4.00 ± 0.34 mm³, $N=17$ vs. 3.17 ± 0.47 mm³, $N=75$, t test: $t_{90}=6.94$, $P<10^{-6}$) but a much larger gaster (4.69 ± 0.36 mm² vs. 1.92 ± 0.21 mm², $t_{90}=42.64$, $P<10^{-6}$), and a slightly shorter tibia (3.22 ± 0.11 mm vs. 3.55 ± 0.13 mm, $t_{90}=9.41$, $P<10^{-6}$) and mandibles (1.83 ± 0.06 mm vs. 1.95 ± 0.06 mm, $t_{90}=7.12$, $P<10^{-6}$). Head width is not different (1.67 ± 0.07 mm vs. 1.69 ± 0.07 mm, $t_{90}=1.09$, $P=0.28$). Reproductives have one anterior ocellus and two vestigial lateral ocelli. The thorax of the reproductives is very simplified relative to winged queens of other species, but distinct from conspecific workers (Fig. 1). Reproductive/worker ratio in thorax volume is thus low (1.26) relative to other species, e.g. *O. cephalotes* (1.74, based on 2 queens and 3 workers, unpublished data). The size of workers

varies between colonies (ANOVA: $F_{1,14}=10.47$, $P<10^{-6}$ for thorax; $F_{1,14}=7.38$, $P<10^{-6}$ for gaster; $F_{1,14}=7.91$, $P<10^{-6}$ for tibia; $F_{1,14}=3.66$, $P=0.0002$ for mandible; $F_{1,14}=1.82$, $P=0.056$ for head).

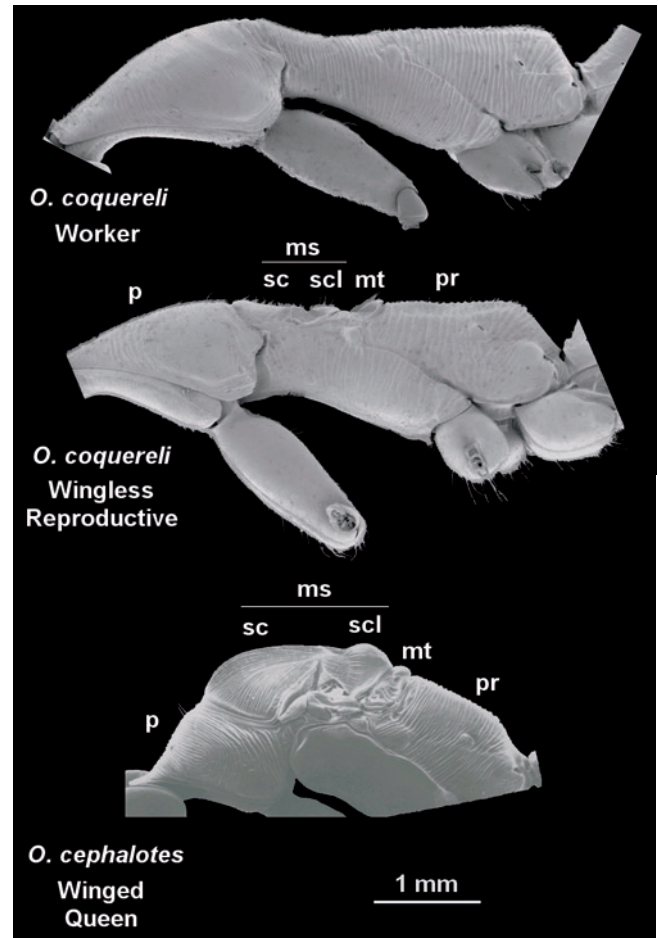


Figure 1. SEM pictures of the thorax of a worker and a reproductive of *O. coquereli* (resp. top and middle), and a dealate queen of *O. cephalotes* (bottom). The pronotum (p) of the reproductive of *O. coquereli* is much enlarged posterodorsad in comparison with the *O. cephalotes* dealate queen, resembling the worker instead. The mesonotum (ms) is divided into a reduced scutum (sc) and scutellum (scl), and delineated from the mesopleura by immovable sutures. This is in contrast to the dealate queen where these plates are large and freely articulated, and the worker where no sutures are present so that there are no boundaries between the different parts. The metanotum (mt) is reduced and separated from the mesonotum and propodeum (pr) by immovable sutures. Again, this is in contrast to the dealate queen where the metanotum is fully articulated, and to workers where there is no discernable metanotum.

The growth of thorax^{1/3} and gaster^{1/2} with tibia is isometric in reproductives (for thorax: Pearson correlation: $r^2=0.52$, $t_{15}=4.07$, $P=0.001$, Fig. 2, test for isometry: $F_{1,15}=1.86$, $P=0.19$; for gaster: $r^2=0.44$, $t_{15}=3.43$, $P=0.004$, $F_{1,15}=3.25$, $P=0.09$) but allometric in workers (for thorax: $r^2=0.80$, $t_{73}=17.22$, $P<10^{-6}$, $F_{1,73}=252$, $P<10^{-4}$; for gaster: $r^2=0.64$, $t_{73}=11.37$, $P<10^{-6}$, $F_{1,73}=299$, $P<10^{-4}$), and signi-

ficatively different between them (for thorax: $P=0.012$; for gaster: $P=0.003$). The growth of mandible with tibia is isometric in workers ($r^2=0.23$, $t_{73}=4.70$, $P<10^{-4}$, $F_{1,73}=1.35$, $P=0.25$, Fig. 2), but there is no correlation in reproductives ($r^2=0.11$, $t_{15}=1.35$, $P=0.20$).

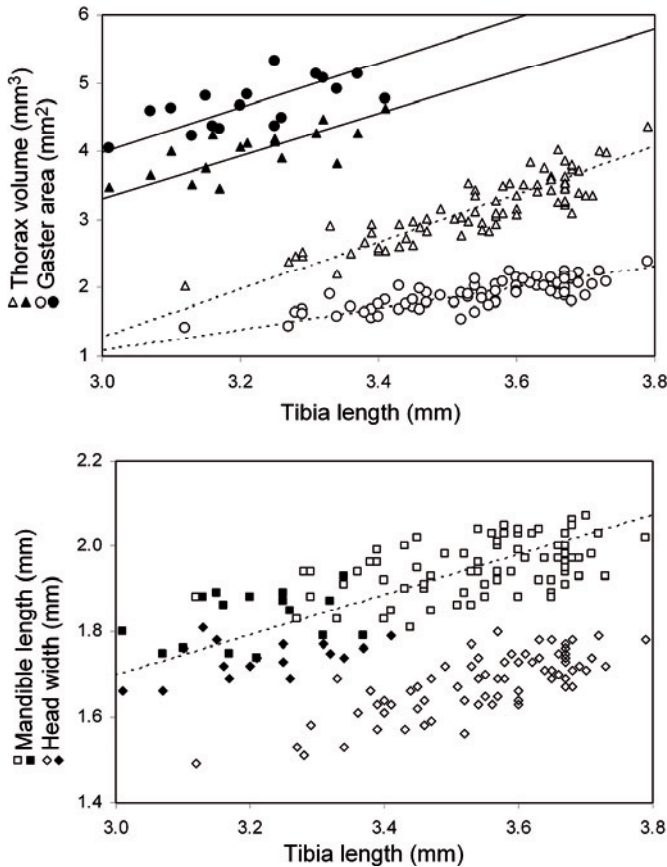


Figure 2. Correlation between tibia length and (a) thorax volume, gaster area, (b) mandible length and head width. Reproductives: black symbols, solid regression lines; workers: white symbols, dotted regression lines. Only significant regression lines are shown.

For each caste, the size variability among colonies is similar in the different body parts when using a Bonferroni correction (Table 2), which means that allometries do not produce a high variability in body shapes because size does not vary much. For each body part, the size variability among colonies is similar in reproductives and workers (coefficients of variation for thorax^{1/3} resp.: 4.4% and 3.0%, STR test for equal CVs: $\chi^2_1=1.50$, $P=0.22$; for gaster^{1/2}: 4.6% and 4.1%, $\chi^2_1=0.45$, $P=0.56$; for mandible: 2.3% and 3.0%, $\chi^2_1=0.63$, $P=0.43$; for head: 2.8% and 4.0%, $\chi^2_1=0.70$, $P=0.40$; for tibia: 3.2% and 3.2%, $\chi^2_1=0.53$, $P=0.47$). These analyses confirm that workers are monomorphic, and similarly that reproductives exhibit little variability.

Table 2. Squared-ranks test for the equality of coefficients of variation of body parts, in reproductives and workers. To include the Bonferroni correction, P has to be compared to the critical P computed with the Dunn-Šidák method, instead of a threshold P of 0.05. Thorax and gaster refer to thorax^{1/3} and gaster^{1/2}.

| | | χ^2 | P | critical P |
|----------------------|----------|----------|-------|--------------|
| Workers | | | | |
| gaster | mandible | 6.419 | 0.011 | 0.005 |
| thorax | mandible | 5.242 | 0.022 | 0.006 |
| thorax | head | 4.597 | 0.032 | 0.006 |
| gaster | head | 4.503 | 0.034 | 0.007 |
| mandible | tibia | 3.198 | 0.074 | 0.009 |
| thorax | tibia | 2.097 | 0.148 | 0.010 |
| gaster | tibia | 2.041 | 0.153 | 0.013 |
| tibia | head | 1.364 | 0.243 | 0.017 |
| mandible | head | 0.185 | 0.667 | 0.025 |
| thorax | gaster | 0.097 | 0.756 | 0.050 |
| Reproductives | | | | |
| gaster | tibia | 1.316 | 0.251 | 0.005 |
| thorax | gaster | 1.085 | 0.297 | 0.006 |
| gaster | mandible | 0.751 | 0.386 | 0.006 |
| gaster | head | 0.552 | 0.457 | 0.007 |
| tibia | head | 0.192 | 0.661 | 0.009 |
| thorax | head | 0.078 | 0.780 | 0.010 |
| thorax | mandible | 0.064 | 0.800 | 0.013 |
| mandible | head | 0.047 | 0.828 | 0.017 |
| mandible | tibia | 0.025 | 0.874 | 0.025 |
| thorax | tibia | 0.006 | 0.938 | 0.050 |

Discussion

Unlike all other species in the genus, winged queens have been replaced by wingless reproductives in *Odontomachus coquereli*. Colonies yield a single member of the reproductive caste, which is always mated and lays eggs, whereas workers remain sterile. However workers can lay male eggs after experimental removal of the reproductive. Reproductives are overall slightly larger than workers, but their gaster is more than twice as big, which allows for higher ovarian development, even though they are not physogastric (Fig. 3). They exhibit little size variability, similarly to workers, and their body is shaped by clear allometric relationships that are different from the workers'. Thus reproductives constitute a well-defined caste. Although permanently wingless, their thorax is not as simplified as the workers' (Fig. 1). Indeed their thoracic sclerites are only partially fused (scutum, scutellum and metanotum are distinct), which makes them intermediate between conspecific workers (completely fused sclerites) and congeneric dealate queens (enlarged mesonotum and metanotum with distinct sclerites). They have one ocellus, while conspecific workers do not have any and congeneric winged queens have three. Interestingly, similar morphs

of wingless individuals with enlarged gaster and one anterior ocellus have been reported in *Odontomachus haematoda* and *O. chelifer* (Wheeler, 1928). They resulted from an infection by the parasitic nematode *Mermis*, which apparently caused a hormonal imbalance that altered larval development. *Mermis* typically prevents female sexuals from developing proper wings and flight musculature, resulting in brachyptery or even winglessness (e.g. in *Solenopsis*: MacInnes and Tschinkel, 1996). Similarly, a shortage of food provided to larvae can affect their development, changing hormonal titers and leading to anomalous adults with intermediate phenotypes between queen and worker, called intercastes (Plateaux, 1970; Peeters, 1991a). Thus hormone-mediated stimuli can lead to the production of wingless reproductives instead of winged queens, without prior genetic change. Hidden developmental plasticity probably provides the potential to evolve wingless reproductives in ants (see West-Eberhard, 2003).

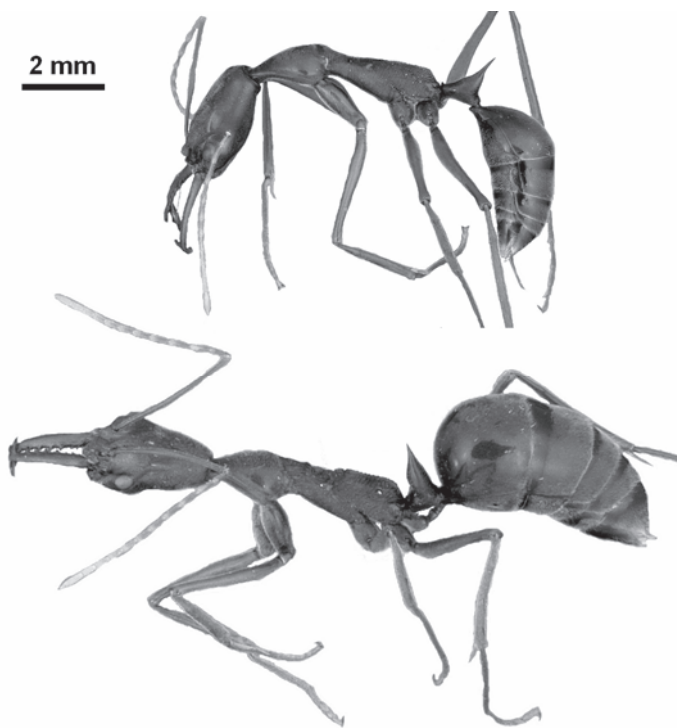


Figure 3. Picture of *O. coquereli* worker (top) and queen (bottom) at the same scale. Note gaster is much larger in the queen. Pictures © Antweb.

Several results suggest that the strategy of colonial reproduction in *O. coquereli* has switched from non claustral independent foundation (typical of ponerine species and observed in *O. troglodytes*: Colombel, 1971) to fission. First, wingless reproductives lack wing muscles that can be metabolised after dispersal, so they would need to forage even more frequently in order to feed the first generation of workers, thus exposing themselves to

predators and parasites. Second, since reproductives cannot perform long-range dispersal, founding alone would likely be selected against given the large benefits gained from the help of workers during colony foundation (e.g. Hee et al., 2000). Last, no isolated foundress was found and the smallest colonies consisted of at least 5 workers (Table 1). The largest colonies never exceeded 40 workers, indicating a threshold size at which a colony divides in two daughter colonies. In contrast, *O. troglodytes* colonies can reach 1300 workers (Colombel, 1971). In conclusion, colonies of *O. coquereli* are very likely to reproduce by fission, but this behaviour is hard to observe in nature for any ant.

Ants with wingless reproductives that are morphologically distinct from workers exhibit two types of colonial organization. In some species many members of an intermorph caste are present in each colony. A few of them reproduce and others perform tasks that are normally restricted to workers, including brood rearing and foraging (e.g. *Eutetramorium mocquerysi*: Heinze et al., 1999; *Mystrium*: Molet et al., 2007). Such multipurpose caste is analogous to the gamergate strategy in species where workers can mate. In sharp contrast, other species have a single member of the reproductive caste in each colony, and her sole function is reproduction. Some sole-purpose reproductives called “dichthadiiform” are very dimorphic relative to workers, often physogastric and highly fertile (e.g. Bolton, 1990). Other sole-purpose reproductives called “ergatoid” are not much bigger than workers (e.g. *Megaponera foetens*: Villet, 1990a; *Platythyrea conradti*: Molet and Peeters, 2006). In fact a continuum exists, with dichthadiiform and ergatoid reproductives representing two ends. The reproductives of *Odontomachus coquereli* correspond to the latter because they are not physogastric and queen/worker size dimorphism is relatively low. We did not find any young virgin member of the reproductive caste, but there was only one male, indicating that our colonies were collected outside the mating period. Generally in ants, winged gynes perform independent colony foundation and experience a high mortality during dispersal, mating, nest excavation and brood rearing. Accordingly they need to be produced in large numbers (Hölldobler and Wilson, 1990). In contrast, wingless reproductives restricted to egg-laying survive better because they mate close to their natal nest and all dangerous tasks are performed by workers during fission, so only a few reproductives need to be produced and investment is diverted towards more workers (Pamilo, 1991).

Dichthadiiform, ergatoid and intermorph reproductives evolved in different taxa as solutions to selection against independent colony foundation. However their respective developmental origins are still unknown. Species exhibiting winged queens together with either wingless reproductives or brachypterous (= short-winged) queens (e.g. *Myrmecia regularis*: Haskins and Haskins, 1955, an oriental *Odontomachus* species: F. Ito, pers. comm.) are good models to investigate the genetic and

developmental components of winglessness in ant reproductives (e.g. Miyazaki et al., 2006).

Acknowledgments

We thank Brian Fisher's team in Madagascar for field assistance, Gérard Mascarell and Alain Couté for scanning electron microscopy at the Muséum National d'Histoire Naturelle (Paris), Alexandra Sébastien for help in the laboratory, Roberto Keller for description of thorax morphology, and Fuminori Ito for critical comments on the manuscript. This work was supported in part by National Geographic Society grant n° 7617-04, National Science Foundation grant n° DEB-0344731 to B.L. Fisher and P.S. Ward, and Laboratoire d'Ecologie CNRS UMR 7625. Research and Export permits were issued by Association Nationale pour la Gestion des Aires Protégées, République de Madagascar. Data on *O. cephalotes* were obtained in Ross Crozier's laboratory while C. Peeters was supported by the ARC.

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