

# Evolution of advanced social traits in phylogenetically basal ants: striking worker polymorphism and large queens in *Amblyopone australis*

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**Abstract** The ecological success of ants results notably from their ability to derive several phenotypes from the same genotype. In higher ants, polyphenism can be extreme: high queen–worker size dimorphism and worker polymorphism allow for better success at colony founding by lone queens, better division of tasks, and ultimately access to new ecological niches. However in basal ants, polyphenism is much more limited, restricting them to narrow niches. It is often assumed that basal ants lack the ability to produce a pronounced polyphenism. In *Amblyopone*, most species nest and hunt centipedes in soil and leaf litter, and polyphenism is weak, e.g. *A. pallipes*. Here we studied *A. australis*, which forages and nests in rotten logs. Using analyses of morphometry and allometry, we showed that queen–worker dimorphism and worker polymorphism are much higher in *A. australis* than in *A. pallipes*. Workers of *A. australis* exhibit various sizes and shapes, and large individuals could be better adapted for digging galleries in rotten logs. Moreover, larger queens are probably more efficient during non-claustral colony foundation. We conclude that the evolution of advanced social traits typical of higher ants is also possible in basal ants, but it is not often selected for.

**Keywords** Allometry · Amblyoponinae · Ponerinae · Queen–worker size dimorphism

## Introduction

Ants (over 12,000 species) exhibit tremendous diversity in lifestyles and ecological profiles. Two important adaptations contribute to modulating the complexity of their colonial organization, i.e. degree of queen–worker dimorphism, and size polymorphism among workers. Increases in these traits can allow more efficient colony founding and division of labour. Indeed larger queens have more metabolic reserves, so there is less need to forage outside the nest during the founding phase. Moreover, if worker size can vary, then queens can produce small workers (minims) during the founding phase, which speeds up initial colony growth. Finally, polymorphic workers in mature colonies are more efficient at specific tasks. These traits are often linked with increased size of colonies and access to a wider range of ecological resources. Hence high queen–worker dimorphism and worker polymorphism are thought to be pillars of the ecological success of higher ants (formicoids), where they frequently occur (Passera and Aron, 2005).

Nonetheless there exist extant ants with relatively simple societies, where size-polymorphic workers and large queens are absent. Recent phylogenies show that the poneroid subfamilies Amblyoponinae and Ponerinae are basal (e.g. Brady et al., 2006), i.e. closer to solitary vespoid wasps. Some species can thus give an insight into the early steps towards more advanced societies. A small degree of dimorphism between queens and workers has often been interpreted as a ‘primitive’ character (e.g. Peeters, 1997). As phylogenies based on molecular data become more detailed and robust, it will become possible to test the

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general assumption that there are developmental constraints in basal ants preventing the evolution of advanced traits.

We studied a case of unexpectedly derived colonial organization in *Amblyopone*, a genus repeatedly cited as an example of ant societies at an early stage of evolution (e.g. Haskins, 1970; Wilson, 1971; Thorne and Traniello, 2003). This genus (69 species) belongs to the Amblyoponinae (7 genera; formerly tribe Amblyoponini in subfamily Ponerinae), the basal position of which has never been contested. Species of *Amblyopone* are found throughout the world in tropical and temperate areas. Only few species (*A. pallipes*, *A. pluto*, *A. silvestrii* and *A. reclinata*-group) have been investigated in the field (Haskins, 1928; Traniello, 1982; Gotwald and Lévioux, 1972; Masuko, 1993; Ito, 1993a) and they are highly specialised predators of centipedes. Brown (1960) reported a lack of worker polymorphism in the genus. Unlike congeneric species, *Amblyopone australis* can be locally common and is regularly encountered throughout Australia, as well as in New Caledonia and New Zealand (Shattuck, 1999). Colonies are diffuse and difficult to collect completely. We performed a detailed morphometric analysis of all female adults (queens and workers) in one large colony. For comparison, measurements were also taken for all members of a colony of the New World *A. pallipes*. We review the scattered distribution of polymorphic workers and large queen–worker dimorphism in Amblyoponinae and Ponerinae.

## Materials and methods

One complete colony of *A. australis* was collected in September 2005 from Mary Cairncross Park, near Maleny, Queensland (26.78°S, 152.88°E). The ants nested in a big, isolated rotten log lying on the soil of a subtropical rainforest. Large central chambers were lacking and instead many small pockets of workers and brood were scattered in the wood. A total of 78 workers, 2 dealate queens (found together in one of the last pockets), 6 cocoons and 417 larvae of all sizes were found. This log was also inhabited by *Rhytidoponera chalybaea*, *Hypoponera* sp., unidentified termites and several beetles (larvae and adults). The galleries of these different species were very close to one another. Several nests of *A. pallipes* were collected by T. Monnin in June 2003 from Saint Augustin and Sainte Foy, Québec.

All adults from the colony of *A. australis* (72 workers and 2 queens) and one colony of *A. pallipes* (20 workers and 1 queen) were measured (head width, mandible length, thorax volume and gaster area) with ImageJ (<http://rsb.info.nih.gov/ij>) following Molet et al. (2007b). In order to increase the sample size of queens, four *A. australis* queens

and three *A. pallipes* queens from other colonies were measured as well.

Variations in the shape of individuals result from combining 1/ variation in size and 2/ allometric growth (i.e. differential growth rates across body parts). We assessed size variation in the worker caste of both species by computing and comparing the coefficients of variation of head width (Molet et al., 2007a). In order to assess allometry between body parts, we transformed measures of length, area or volume to a single linear dimension and log-transformed them (Table 1). Then we performed a correlation analysis to determine whether queen and worker castes have significant growth rules. If so, a regression line could be computed, its slope being the allometry coefficient. When this coefficient equals one, both body parts grow at the same rate, i.e. isometry. Otherwise growth is allometric, i.e. body shape changes with size. A test for isometry is provided in Table 1. Finally, we determined whether worker castes of both species exhibit different growth rules by comparing slopes and intercepts of their regression lines. Any difference in either of these reveals a difference in growth rules. We did the same for queen castes of both species. We used (S)MATR 1.0 (Warton and Weber, 2002; <http://www.bio.mq.edu.au/ecology/SMATR/>) to perform all statistical analyses related to allometry (see Molet et al., 2007b). All other statistical analyses were performed with Statistica 7.1.

## Results

Workers of *A. australis* are larger than those of *A. pallipes* [e.g. head width resp.  $1.72 \pm 0.03$  mm (mean  $\pm$  SE) and  $1.01 \pm 0.01$  mm, *t* test:  $t_{117} = 12.8$ ,  $P < 10^{-6}$ ]. *A. australis* workers exhibited a much higher size polymorphism than *A. pallipes* workers (coefficient of variation for head width 18% against 7%, respectively; squared ranks test  $\chi_1^2 = 141$ ,  $P < 10^{-6}$ , Fig. 1). In both *A. australis* and *A. pallipes* workers, the size of body parts was correlated, indicating that workers exhibit clear growth rules with marked allometry (Table 1). These growth rules did not differ significantly between species: comparing four regression lines revealed no difference in slopes (i.e. allometry coefficients) and only one difference in intercepts (head width vs. mandible length, Table 1).

The concomitant allometric growth and large size variation in *A. australis* resulted in a variety of worker shapes. For instance the ratio *head width/thorax volume*<sup>1/3</sup> varies from 1.25 in small workers to 1.70 in large workers, so large workers have enlarged heads (Fig. 2). Similarly, the ratio *mandible length/head width* varies from 0.75 in small workers to 0.55 in large workers, so large-headed workers have relatively short mandibles. In contrast, size variation

**Table 1** Allometry analysis between pairs of transformed morphological variables (independent variable vs. dependent variable): log(head width), log(mandible length), log(thorax volume <sup>1/3</sup>), log(gaster area <sup>1/2</sup>)

Species	Caste	N	Correlation analysis		Regression line		Test against isometry		
			Pearson's $r^2$	P	Slope = allometry coefficient*	Intercept*	$F_{(1, N-2)}$	P	Conclusion
Gaster area vs. thorax volume									
<i>A. australis</i>	Queen	6	0.07	0.61	–	–	–	–	
	Worker	72	0.96	<0.001	1.02 a	0.045 a	0.97	0.33	Isometry
<i>A. pallipes</i>	Queen	4	0.82	0.094	–	–	–	–	
	Worker	20	0.49	<0.001	1.04 a	0.046 a	0.049	0.83	Isometry
Head width vs. mandible length									
<i>A. australis</i>	Queen	6	0.83	0.012	1.58 a	–0.37 N/A	5.18	0.085	Isometry
	Worker	72	0.94	<0.001	0.89 b	–0.16 a	15.96	<0.001	Allometry
<i>A. pallipes</i>	Queen	4	0.4	0.37	–	–	–	–	
	Worker	20	0.68	<0.001	0.84 b	–0.12 b	1.73	0.20	Isometry
Head width vs. thorax volume									
<i>A. australis</i>	Queen	6	0.56	0.086	1.02 ab	–0.08 a	0.003	0.96	Isometry
	Worker	72	0.96	<0.001	0.85 b	–0.15 b	47.7	<0.001	Allometry
<i>A. pallipes</i>	Queen	4	0.98	0.010	1.28 a	–0.05 c	6.49	0.13	Isometry
	Worker	20	0.41	0.003	0.7 b	–0.14 b	4.07	0.059	Iso/allometry
Head width vs. gaster area									
<i>A. australis</i>	Queen	5	0.38	0.27	–	–	–	–	
	Worker	72	0.97	<0.001	0.83 a	–0.19 a	72.6	<0.001	Allometry
<i>A. pallipes</i>	Queen	4	0.89	0.059	1.24 a	–0.12 b	0.80	0.46	Isometry
	Worker	20	0.47	<0.001	0.67 a	–0.18 a	5.62	0.029	Allometry

\*Results of the multiple comparisons tests: same letter means no significant difference

was low in *A. pallipes*, so allometric growth could not alter shape much. Size distribution was unimodal in both *A. australis* and *A. pallipes* workers (head width: Shapiro–Wilk test, respectively,  $W = 0.98$ ,  $P = 0.18$  and  $W = 0.96$ ,  $P = 0.50$ ), which means that there were no worker subcastes.

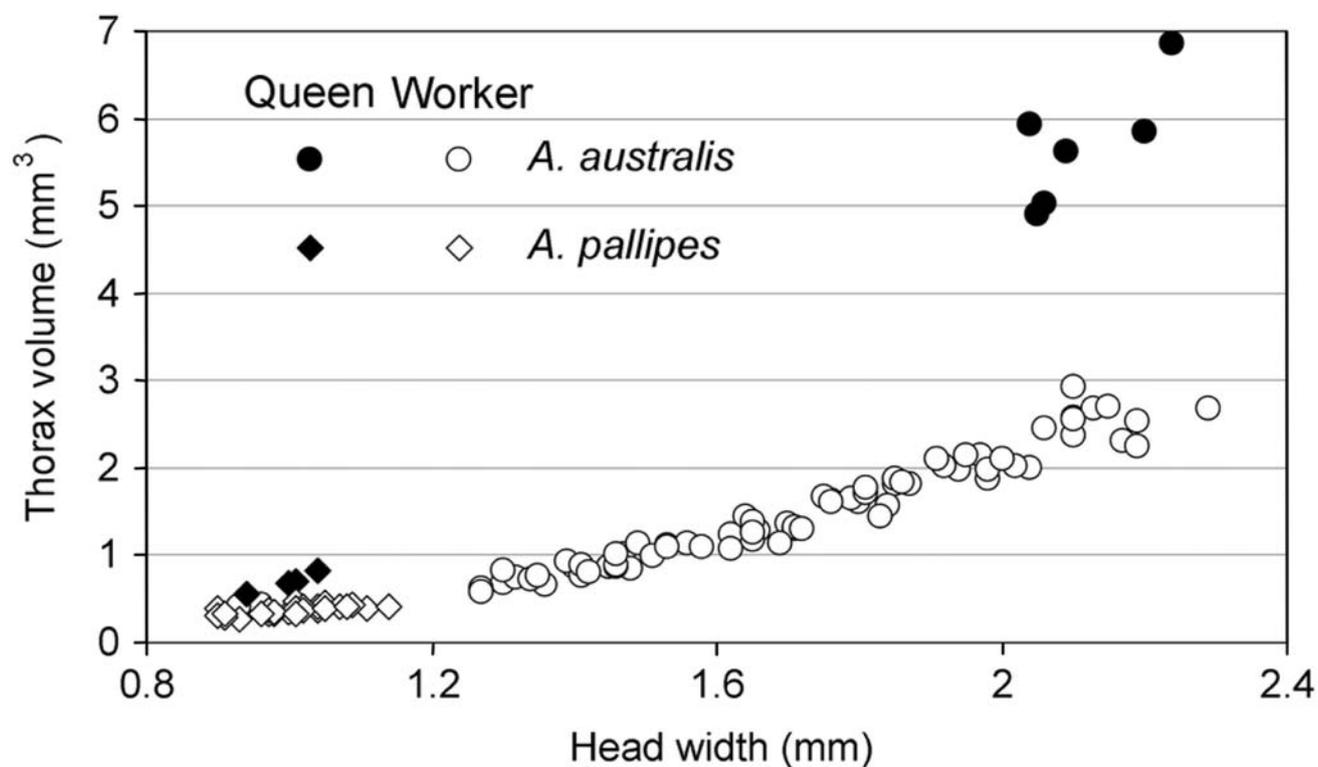
Queen/worker size dimorphism was much higher in *A. australis* than in *A. pallipes* (Fig. 3). It was, respectively, 3.83 and 1.86 for thorax volume, 2.09 and 1.30 for gaster area, 1.27 and 1.02 for mandible length, and 1.24 and 1.00 for head width. In queens of both species, the correlation between the size of body parts was not significant for various pairs of variables, probably because of low sample sizes (Table 1). In the only instance where queens of both species showed statistically significant growth rules (head width vs. thorax volume, Table 1), the regression lines were significantly different (no difference in slopes but difference in intercepts), indicating that the growth rules are distinct.

## Discussion

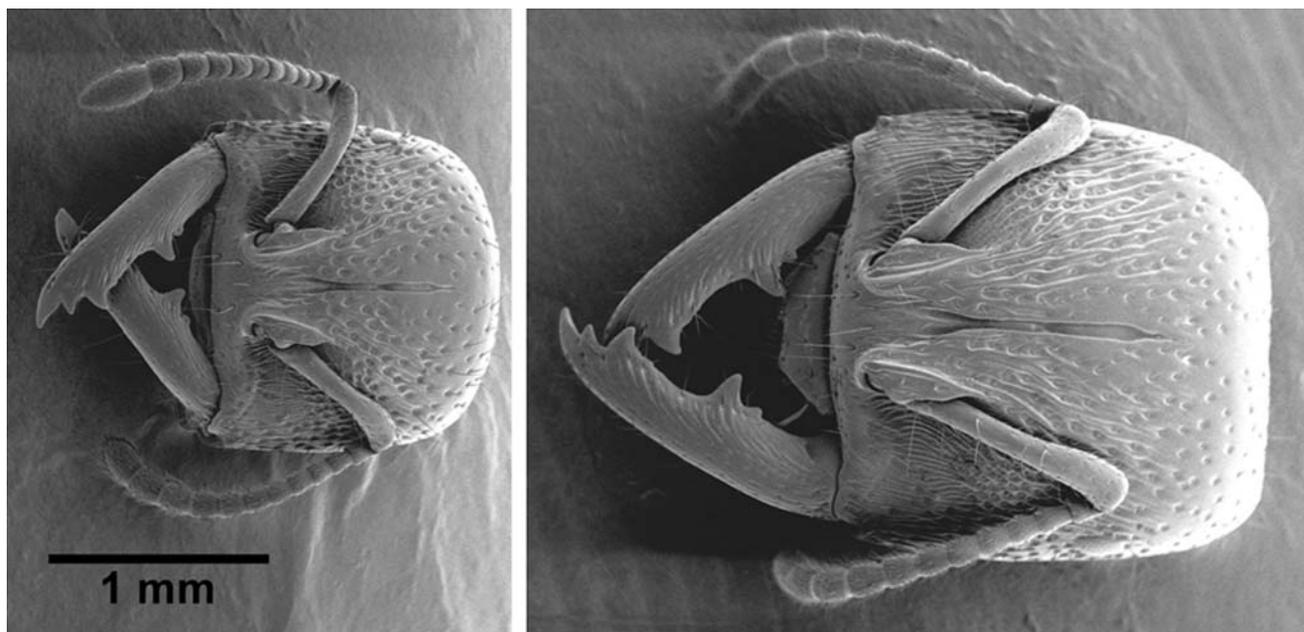
Our morphometric analysis of the queen and worker castes in two species of *Amblyopone* revealed a conspicuous difference in two key aspects of colonial architecture. First,

the queens of *A. australis* are significantly bigger than conspecific workers, unlike in *A. pallipes* (Fig. 3). Second, the workers of *A. australis* exhibit a considerable range of sizes, unlike in *A. pallipes* (Fig. 1). This is accompanied by differences in body shape, the large workers of *A. australis* notably having an enlarged head. The existence of worker polymorphism suggests differences in polyethism, but behaviours inside rotten logs are difficult to study.

Similarly to *A. pallipes*, many species of *Amblyopone* have monomorphic workers that hunt centipedes exclusively. Worker polymorphism is low in *A. pluto* [total length of workers is 5.66–6.38 mm ( $n = 15$ ), queens 6.43–6.78 mm ( $n = 5$ ); Gotwald and Léveux, 1972]. In the Japanese *A. silvestrii*, head widths of workers varied by 8–18% (Masuko, 1996), close to the value of 27% that we found in *A. pallipes*, and in striking contrast with the 146% in *A. australis*. Workers of *A. pallipes*, *A. pluto* and *A. silvestrii* are cryptic predators in soil and leaf litter and seldom forage above ground. *A. pallipes*, *A. silvestrii* and at least seven species of *Amblyopone* in SE Asia have small underground nests in soil, under stones or logs (Haskins, 1928; Masuko, 2010; F. Ito, pers. comm.). *A. australis* differs markedly because it feeds on a range of soft-bodied arthropods and nests in logs above ground (Shattuck, 1999;



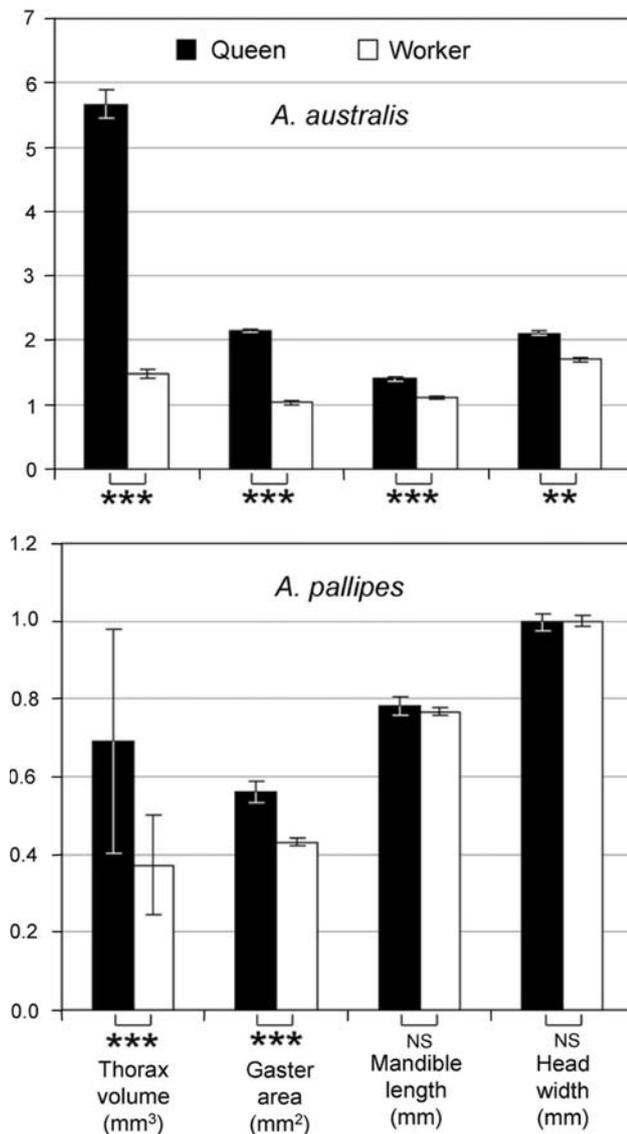
**Fig. 1** Growth of thorax relative to head in *A. australis* and *A. pallipes* queens and workers. Worker size variation and queen/worker size dimorphism are much higher in *A. australis*



**Fig. 2** Heads of a small (*left*) and large (*right*) worker of *A. australis*. Due to allometry, a 35% increase in head width is associated with a 25% increase in mandible length. A longer head may correspond to more powerful mandibular muscles

Wheeler, 1933). Thus it is the exception in the genus. In the absence of a detailed species-level phylogeny, we assume that *A. australis* is derived because the behavioural traits of

*A. pallipes* and other species are widespread in the genus. Colonies of *A. australis* may also be larger, although field data are limited due to the diffuse arrangement of



**Fig. 3** Comparison of the size of body parts between queens (*black*) and workers (*white*) in *A. australis* (top) and *A. pallipes* (bottom). Bars indicate mean  $\pm$  SE. Results of the *t* tests are reported at the bottom of each pair of bars \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , <sup>NS</sup> $P \geq 0.05$

galleries. Other species have smaller colonies, e.g. 9–16 workers in *A. pallipes*,  $12.2 \pm 11.3$  workers in *A. silvestrii* ( $n = 90$  colonies) (Traniello, 1982; Masuko, 2003). Only in the *A. reclinata*-group do colonies reach 100 workers (Ito, 1993a). It cannot be excluded that the size variation shown among *A. australis* workers occurs only in large colonies.

The absence of pronounced queen–worker dimorphism, together with lack of worker polymorphism, have generally been held to be consistent with a basal phylogenetic position among ants. The existence of both these traits in *A. australis* contradicts this view. Our results suggest that these two traits are an adaptation to the unusual ecology of

*A. australis*, which alone in the genus escaped a narrowly specialised feeding niche. In parallel to becoming more generalized predators, and shifting from underground nests to rotten logs richly endowed with insect inhabitants (including termites and beetles), a greater variability in worker sizes and shapes has evolved. One possible reason for producing larger workers is that they are better able to excavate galleries in the wood, due to bigger and more forceful mandibular muscles inside their expanded heads (Paul and Gronenberg, 1999). Moreover, the three apical teeth on the mandibles (Fig. 2) make these clearly different from the mandibles of congeneric species (see <http://www.antweb.org>), and they appear more suited for chewing wood, not hunting (K. Masuko, pers. comm.). An alternative is that the ants take over the tunnels already dug by other wood-feeding insects, and the production of workers with varying sizes could allow exploiting tunnels with a range of fixed diameters.

Similar adult polymorphism occurs in two other Amblyoponinae taxa. In *Myopopone castanea*, head width of one winged queen (3.00 mm) contrasts with 1.48–2.18 mm in 33 workers (Ito, 2010). This polymorphism is correlated with marked ovarian differences: 32 ovarioles versus 6–22 ovarioles in workers. The remarkable size variation of *Myopopone* workers may be an adaptation for searching prey (mainly coleopteran larvae; Wilson, 1971) in tunnels of various sizes inside decaying wood. In *Mystrium rogeri*, workers exhibit marked size variability, and they perform all tasks from brood care to hunting (Molet et al., 2009). However in *M. oberthueri*, infertile ergatoid queens care for the brood and the workers only hunt. Accordingly there are only large workers: the production of small workers has been selected against because infertile queens took over their function (Molet et al., 2007c).

Worker polymorphism is also known in very few species of Ponerinae (Peeters, 1997). In *Megaponera analis*, major workers are twice as big as minors, with a clear bimodal distribution combined with allometry (Crewe et al., 1984). All size classes participate in raids on termites; minors enter underground galleries and sting prey, while majors carry bundles of termites back to the nest (Longhurst and Howse, 1979). Minors are more active than majors (248 vs. 135 acts/h, resting excluded; Villet, 1990). In *Centromyrmex*, another genus of specialised termite predators, worker polymorphism is encountered in two highly related Afrotropical species (*C. bequaerti* and *C. secutor*), while the workers are monomorphic in all other species-groups (Bolton and Fisher, 2008). Colonies of *C. bequaerti* exceed 500 workers, and the queens (about 20 mm long) are 1.6 times bigger than the largest workers (12 mm long) (Dejean and Fénelon, 1996). Largest workers are twice as big as the smallest (5 mm long), but size distribution is unimodal and there is allometry. Workers of

all sizes attack termites, albeit at different frequencies (Dejean and Fénéron, 1996). Since these ants nest inside the mounds of termites that they prey upon, it should be investigated if the existence of workers of different sizes simply allows a more efficient utilization of termite galleries differing in diameter. Other ponerine ants that have polymorphic workers (together with large colony size) are *Brachyponera senaarensis* and *Termitopone* species (Dejean and Lachaud, 1994; Wheeler, 1936).

Why were bigger winged queens selected for in *A. australis*? Independent colony foundation (ICF) is non-claustral (Haskins and Haskins, 1951; Wheeler, 1933). Lone foundresses rely on their hunting ability to feed the first generation of workers. Bigger queens may be better hunters. Moreover their enlarged flight thorax (Fig. 3) carries bigger wing muscles which function as metabolic reserves, meaning that hunting trips can be less frequent. In *A. pallipes*, limited evidence suggests that gynes mate close to their natal nests and then return to it; wings may be shed before or after mating (Haskins, 1928, 1978). Data on colony growth, nest distribution and nest structure hint that newly mated queens leave the natal colony accompanied by a group of nestmate workers, i.e. dependent colony founding (DCF) (Traniello, 1982). Accordingly *A. pallipes* queens never hunt alone, and we found that they exhibit a distinct allometry rule compared to *A. australis* queens, whereas workers of both species exhibit similar rules. Although caution is needed, this result suggests that queens exhibit distinct traits as a corollary of selection for either DCF or ICF. We did not study whether the increase in size of *A. australis* queens results in higher fertility. Peeters (1987) recorded eight ovarioles in both castes.

Comparative data reveal that non-claustral ICF was often selected against in Amblyoponinae, all species of which are specialised predators. Solitary hunting may be a challenge for foundresses. Winged queens have been replaced by gamergates (i.e. mated reproductive workers) in all species of the *A. reclinata*-group (Ito, 1993b, 1993c), while in *Onychomyrmex* and three species of *Mystrium*, ergatoid queens occur instead (Brown, 1960; Molet et al., 2009). Loss of winged queens is generally associated with obligate DCF (Peeters and Molet, 2010). In contrast, ICF persists in *Myopopone castanea*, *Mystrium rogeri* and *Prionopelta amabilis* (Ito, 2010; Molet et al., 2009; Hölldobler and Wilson, 1986), and all these exhibit a pronounced size dimorphism between queens and workers. Thus larger queens (as also found in *A. australis*) probably succeed better during independent foundation.

Our results show that the evolution of polymorphic workers and large queen–worker dimorphism, two traits typical of ‘higher’ ants, is possible in basal ants. While the morphological characters of individuals tend to be evolutionarily conservative (e.g. basal ants remain morphologically

similar to the wasp ancestors), colony-level traits such as inter-individual variability in size and shape seem to have the potential to evolve readily. Since a few scattered basal ants exhibit derived colonial architecture, possible developmental constraints cannot be invoked to explain the general lack of polymorphic workers or large queens. Thus modifications during larval development can produce variation in adult size, but this is apparently not often selected for in basal ants. Energetic constraints at colony-level may be a better explanation for the weak queen–worker dimorphism typical of amblyoponine and ponerine ants (see Peeters, 1997). Colony size affects the amount of resources that can be gathered and invested annually in the production of sexuals. Colonies of most basal ants are small, and we suggest that they cannot afford producing many large gynes. Given that many gynes need to be produced annually for ICF to succeed (Peeters and Molet, 2010), this puts a constraint on the degree of caste dimorphism. Furthermore, it may be that morphological and behavioural specialisations for predation on specific prey or specific nesting sites constrain workers to a limited range of sizes, holding back the evolution of group traits. However, *A. australis* changed its predatory and nesting habits, allowing for the evolution of advanced social traits in that single species. It has long been known that behaviour is highly labile and gives only limited information about the direction of evolutionary change. Similarly, it appears best to interpret colonial architecture traits through phylogeny, rather than using these traits to derive phylogenetic relationships.

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## References

- Bolton B. and Fisher B.L. 2008. Afrotropical ants of the ponerine genera *Centromyrmex* Mayr, *Promyopias* Santschi gen. rev. and *Feropena* gen. n., with a revised key to genera of African Ponerinae (Hymenoptera: Formicidae). *Zootaxa* **1929**: 1-37
- Brady S.G., Schultz T.R., Fisher B.L. and Ward P.S. 2006. Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proc. Nat. Acad. Sci. USA* **103**: 18172-18177
- Brown W.L. 1960. Contributions toward a reclassification of the Formicidae. III. Tribe Amblyoponini (Hymenoptera). *Bull. Mus. Comp. Zool.* **122**: 143-230
- Crewe R., Peeters C. and Villet M. 1984. Frequency distribution of worker sizes in *Megaponera foetens* (Fabricius). *S. Afr. J. Zool.* **19**: 247-248

- Dejean A. and Lachaud J.P. 1994. Ecology and behavior of the seed-eating ponerine ant *Brachyponera senaarensis* (Mayr). *Insect. Soc.* **41**: 191-210
- Dejean A. and Féron R. 1996. Polymorphism and oligogyny in the ponerine ant *Centromyrmex bequaerti* (Formicidae: Ponerinae). *Insect. Soc.* **43**: 87-99
- Gotwald W.H. and Lévieux J. 1972. Taxonomy and biology of a new West African ant belonging to the genus *Amblyopone* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* **65**: 383-396
- Haskins C.P. 1928. Notes on the behavior and habits of *Stigmatomma pallipes* Haldeman. *J. N.Y. Entomol. Soc.* **36**: 179-184
- Haskins C.P. 1970. Researches in the biology and social behavior of primitive ants. In: *Development and Evolution of Behavior* (L. Aronson, E. Tobach, D. Lehrman and J. Rosenblatt, Eds), Freeman, San Francisco. pp 355-388
- Haskins C.P. 1978. Sexual calling behavior in highly primitive ants. *Psyche* **85**: 407-416
- Haskins C.P. and Haskins E.F. 1951. Note on the method of colony foundation of the ponerine ant *Amblyopone australis* Erichson. *Am. Midl. Nat.* **45**: 432-445
- Hölldobler B. and Wilson E.O. 1986. Ecology and behavior of the primitive cryptobiotic ant *Prionopelta amabilis* (Hymenoptera: Formicidae). *Insect. Soc.* **33**: 45-58
- Ito F. 1993a. Observation of group recruitment to prey in a primitive ponerine ant, *Amblyopone* sp. (*reclinata* group) (Hymenoptera: Formicidae). *Insect. Soc.* **40**: 163-167
- Ito F. 1993b. Social organization in a primitive ponerine ant: queenless reproduction, dominance hierarchy and functional polygyny in *Amblyopone* sp. (*reclinata* group). *J. Nat. Hist.* **27**: 1315-1324
- Ito F. 1993c. Queenless reproduction in a primitive ponerine ant *Amblyopone bellii* (Hymenoptera: Formicidae), in southern India. *J. N.Y. Entomol. Soc.* **101**: 574-575
- Ito F. 2010. Notes on the biology of the Oriental amblyoponine ant *Myopopone castanea*: queen-worker dimorphism, worker polymorphism and larval hemolymph feeding by workers (Hymenoptera: Formicidae). *Entomol. Science* (in press)
- Longhurst C. and Howse P. 1979. Foraging, recruitment and emigration in *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae) from the Nigerian Guinea savanna. *Insect. Soc.* **26**: 204-215
- Masuko K. 1993. Predation of centipedes by the primitive ant *Amblyopone silvestrii*. *Bull. Assoc. Nat. Sci. Senshu* **24**: 35-44
- Masuko K. 1996. Temporal division of labor among workers in the ponerine ant, *Amblyopone silvestrii* (Hymenoptera: Formicidae). *Sociobiology* **28**: 131-151
- Masuko K. 2003. Analysis of brood development in the ant *Amblyopone silvestrii*, with special reference to colony bionomics. *Entomol. Science* **6**: 237-245
- Masuko K. 2010. Nest density and distribution of subterranean ants in an evergreen broadleaf forest in Japan with special reference to *Amblyopone silvestrii* (Hymenoptera: Formicidae). *Entomol. Science* (in press)
- Molet M., Peeters C. and Fisher B.L. 2007a. Permanent loss of wings in queens of the ant *Odontomachus coquereli* from Madagascar. *Insect. Soc.* **54**: 174-182
- Molet M., Peeters C. and Fisher B.L. 2007b. Winged queens replaced by reproductives smaller than workers in *Mystrium* ants. *Naturwissenschaften* **94**: 280-287
- Molet M., Peeters C., Follin I. and Fisher B.L. 2007c. Reproductive caste performs intranidal tasks instead of workers in the ant *Mystrium oberthueri*. *Ethology* **113**: 721-729
- Molet M., Fisher B., Ito F. and Peeters C. 2009. Shift from independent to dependent colony foundation and evolution of 'multi-purpose' ergatoid queens in *Mystrium* ants (subfamily Amblyoponinae). *Biol. J. Linn. Soc.* **98**: 198-207
- Paul J. and Gronenberg W. 1999. Optimizing force and velocity: mandible muscle fibre attachments in ants. *J. Exp. Biol.* **202**: 797-808
- Passera L. and Aron S. 2005. *Les Fourmis. Comportement, Organisation Sociale et Evolution*. Presses Scientifiques du CNRC, Ottawa, Canada. 480 pp
- Peeters C. 1987. The diversity of reproductive systems in ponerine ants. In: *Chemistry and Biology of Social Insects* (J. Eder and H. Rembold, Eds), Verlag J. Peperny, Munich. pp 253-254
- Peeters C. 1997. Morphologically "primitive" ants: comparative review of social characters, and the importance of queen-worker dimorphism. In: *The Evolution of Social Behavior in Insects and Arachnids* (J.C. Choe and B.J. Crespi, Eds), Cambridge University Press, Cambridge. pp 372-391
- Peeters C. and Molet M. 2010. Colonial reproduction and life histories. In: *Ant Ecology* (L. Lach, C. Parr and K. Abbott, Eds), Oxford University Press, New York. pp 159-176
- Shattuck S.O. 1999. *Australian Ants—Their Biology and Identification*. CSIRO Publishing, Melbourne. 256 pp
- Thorne B.L. and Traniello J.F.A. 2003. Comparative social biology of basal taxa of ants and termites. *Annu. Rev. Entomol.* **48**: 283-306
- Traniello J. 1982. Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche* **89**: 65-80
- Villet M. 1990. Division of labour in the Matabele ant *Megaponera foetens* (Fabr.) (Hymenoptera Formicidae). *Ethol. Ecol. Evol.* **2**: 397-417
- Warton D.I. and Weber N.C. 2002. Common slope tests for bivariate errors-in-variables models. *Biom. J.* **44**: 161-174
- Wheeler W.M. 1933. *Colony-Founding among Ants with an Account of Some Primitive Australian Species*. Harvard University Press, Cambridge. 179 pp
- Wheeler W.M. 1936. Ecological relations of ponerine and other ants to termites. *Proc. Am. Acad. Arts Sci.* **71**: 159-243
- Wilson E.O. 1971. *The Insect Societies*. Harvard University Press, Cambridge. 548 pp