

## Striking polymorphism among infertile helpers in the arboreal ant *Gesomyrmex*

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**ABSTRACT.** *Gesomyrmex* (subfamily Formicinae) is a poorly known arboreal ant from the Oriental tropics. We sampled colonies in three localities (NE Thailand, peninsular Malaysia, and Sabah) and examined inhabitants of ten nests inside living branches. None of the nests had a reproductive dealate queen, indicating colonies are polydomous. We distinguished three sterile castes using discrete morphological traits, morphometry and total body size. Observations of behaviour are challenging in tree canopies, and we use functional morphology to predict the specialised functions of different castes. Disproportionately large eyes and piercing mandibles are consistent with workers being agile hunters. Soldiers and supersoldiers share robust mandibles, but the latter have a rectangular head and substantially larger body size, like the queens. This suggests both supersoldiers and queens have the muscular power necessary to chew entrance tunnels in healthy wood. Queens and supersoldiers also share frontal lobes (protection for antennal bases), suggesting that they block nest entrances with their heads. When founding a nest, newly mated queens need to chew an entrance tunnel that reaches the innermost soft pith. Supersoldiers are mostly restricted inside nests where they store nutrients in their gaster, but they may also chew the entrance tunnels of additional nests as the colony expands.

**Keywords:** functional morphology, soldiers, supersoldiers, repletes, phragmotic, ovaries, mandibles, mosaics

### INTRODUCTION

Many thousands of ant species are arboreal. This crucial evolutionary shift away from ground-living ancestors underlies much of the ecological success of subfamily Formicinae. Food is abundant in tree canopies since honeydew from sap-sucking insects or secretions from extraflo-

ral nectaries can be supplemented with hunting and scavenging. Nests occur in a variety of micro-habitats, including cavities in dead branches or living wood, under bark, inside domatia and epiphytes, or structures built outside trees (carton nests, leaf nests, ant gardens) (Klimes et al. 2015; Peeters & Wiwatwitaya 2014; Tanaka et al. 2010). Dozens of ant species can coexist in single

trees, partly due to micro-environmental heterogeneity (temperature and humidity) inherent to three-dimensional canopy structures (branches, epiphytes, lianas) (Tanaka et al. 2010). One major challenge for arboreal species is to secure a nest that can be defended against other ants. Several genera inhabiting tree cavities have adults with head shapes specialized to block nest entrances, e.g. *Cephalotes*, *Colobopsis* (Powell 2016, Laciñy et al. 2017).

A poorly known resident of tree canopies in the Oriental tropics is *Gesomyrmex* Mayr, 1868 (subfamily Formicinae). This genus was established for fossil large-eyed ants in Baltic amber (Mayr 1868). *G. chaperi* was described (André 1892) for a worker from Sabah, similar to the fossils. Soldiers were classified as another genus, and described as “dimorphic” with heads of similar shape but different sizes (André 1892). Wheeler (1929a, 1929b) recognized three castes (*maxima*, *media*, *minima*) in a colony from teak forests in Java. In addition to Sabah (André 1892), Java (Wheeler 1929a) and Philippines (Wheeler 1930), known distribution is NE India (Assam State; Cole 1949), northern Thailand (Doi Inthanon, Chiangmai province; AntWeb), southern China (Xishuangbanna, Yunnan province; Cong Liu pers. comm.), Vietnam (Hoa Binh province; Dubovikoff 2004), Cambodia (DeGreef 2007), southern Thailand (mangrove forest in Ranong province; Joachim Offenberger pers. comm.) and Singapore (fallen *Ficus* tree in Nassim Road; collector D.H. Murphy). *Gesomyrmex* is one of the five isolated, long-branched evolutionary lineages (*Oecophylla* is another) that do not fit in any established tribes of the Formicinae (Ward et al. 2016).

Great diversity is left to be discovered in tropical tree canopies (Moffett 1993), but behavioural observations are hindered by the practicalities of canopy access, in addition to rareness of many focus insects. An alternative is to study morphology using specimens freshly collected or deposited in a museum collection. In insect research, morphological data are used almost exclusively for taxonomic identification. Unfortunately, its great potential for explaining function and inferring behaviour has been neglected. Morphology attempts to explain why body parts have evolved their current structure, and to understand

their relation to one another (Snodgrass 1935). In doing so, morphology seeks explanations about how an organism is able to perform given functions and how structure impacts behaviour. In this paper we use functional morphology to predict the specialised functions of different castes in *Gesomyrmex*. Based on the examination of ten complete live nests in Malaysia and NE Thailand, we infer colony structure and life history (foundation and polydomy).

## MATERIAL AND METHODS

We collected ten nests belonging to three *Gesomyrmex* colonies in primary forests of SE Asia: (1) Phu Luang, Loei province, Thailand (6 Sep. 2009), 1200m elevation; (2) Danum Valley Field Centre, Sabah, Malaysia (25 Aug. 2010); (3) Ulu Gombak, Selangor State, peninsular Malaysia (26 March 2012 and 27 January 2016). Whole branches were sawn off, and carefully split open in the laboratory before exact counts of adults and brood. All life stages were documented with photographs. Attempts to maintain ants in plaster nests were unsuccessful, with very high mortality of workers. We dissected the different castes and counted the number of ovarioles.

Extreme polymorphism among *Gesomyrmex* adults has led to great taxonomic confusion, and different castes have been described as up to six nominal species (<http://www.antcat.org>); 18 fossil species are recorded on AntWeb (<https://www.antweb.org>). Marked colour variations further complicate alpha taxonomy. Our three populations are treated separately in Results, although they may all be the same species. Gary Alpert (pers. comm.) is of the opinion that all described species of *Gesomyrmex* belong to *G. chaperi* (the name with priority). Wheeler (1929a) already suggested that extant species may correspond to “sub-species or varieties”.

### Morphometry

We photographed 104 individuals from the Thai colony, including 77 workers, 15 soldiers and 10 supersoldiers, using a stereomicroscope coupled with a digital camera. Two queens from Ulu Gombak (peninsular Malaysia) were added for comparison. We measured head width, head

length, thorax volume and cross-sectional area of the first gaster segment (abdominal segment III) using ImageJ software (<http://rsb.info.nih.gov/ij/>), following Molet et al. (2014).

Stacked images of all castes (Sabah and Ulu Gombak colonies) were created and are deposited on AntWeb (CASENT0839000–0839004). Specimens from Thailand were examined with scanning electron microscopy. Voucher specimens (all three populations) are deposited in the Museum of Comparative Zoology (Harvard Univ., Cambridge MA).

## RESULTS

### Nest description and colony structure

In all three populations, inhabited chambers occupied the very center of the heartwood in living branches of small diameter (3–8 cm) (Fig. 1). A single entrance (diameter 2.5–2.7 mm, N=2) had been chewed through the wood, leading into a narrow (0.3–0.4 cm) cavity of variable length (4–10.5

cm) excavated in the innermost softer pith (Electronic Appendix Fig. S1). When several nests occurred in the same or nearby branches, they were considered to belong to the same colony. All ten nests (three colonies) contained several castes together with brood (Table 1), but we found no dealate reproductive queens. This strongly suggests that mature colonies are polydomous (Greek for ‘many homes’), and that we simply missed the queen nests. Eggs were not found inside half of the nests (Table 1), even though these were 100% complete. This is support for a single queen laying all eggs in one of the nests of a polydomous colony. Only the Ulu Gombak colony yielded young winged queens, although males were present in two colonies. Across all populations, three categories of wingless adults were clearly recognizable using body size and morphology of several body parts: workers and two size classes of soldiers (Fig. 2). We use the term “supersoldier” (e.g. Rajakumar et al. 2012) to distinguish large soldiers from small ones.

**Table 1.** Demographics of ten *Gesomyrmex* sp. nests from three localities in SE Asia. Each nest was confined to one segment of a branch, resulting in exact counts of brood.

nest	supersoldiers	soldiers	workers	males	pupae	larvae	eggs
Thailand							
E	0	4	14	8	3	2	2
G	4	3	25	17	34	37	0
H	4	2	14	0	0	0	0
J	1	2	21	1	6	20	1
K	1	3	7	32	3	22	0
<i>total</i>	<i>10</i>	<i>14</i>	<i>81</i>	<i>58</i>	<i>46</i>	<i>81</i>	<i>3</i>
Sabah							
	8	16	78	0	52	109	31
Gombak							
2012	13	12	175	1	na	na	na
Gombak 2016							
FI16-50	6	29	118	4	8	15	0
FI16-55	9	11	27	13	20	7	6
FI16-63	16	5	26	8	0	0	0
<i>total</i>	<i>31</i>	<i>45</i>	<i>171</i>	<i>25</i>	<i>28</i>	<i>22</i>	<i>6</i>

na: not counted



**Fig. 1.** Nests of *Gesomyrmex* sp. in innermost pith (Thailand colony). Different branches were cut longitudinally and in cross-section. Inner walls (blackish colour) are very hard.



**Fig. 2.** Two size classes of *Gesomyrmex* sp. soldiers (above), and workers (Sabah colony). Pupae are naked (Wheeler 1923a), thus cocoons have been lost as in *Oecophylla*.

In **NE Thailand**, *Gesomyrmex* foragers were found on a branch that had fallen on the road due to elephant damage. We cut live branches 8-10m high up in this tree using a saw attached to the end of a long bamboo pole (Electronic Appendix Fig. S2). Five nests were found, but none contained a queen. A total of over 100 adult females, 58 males and all brood stages were collected (Table 1).

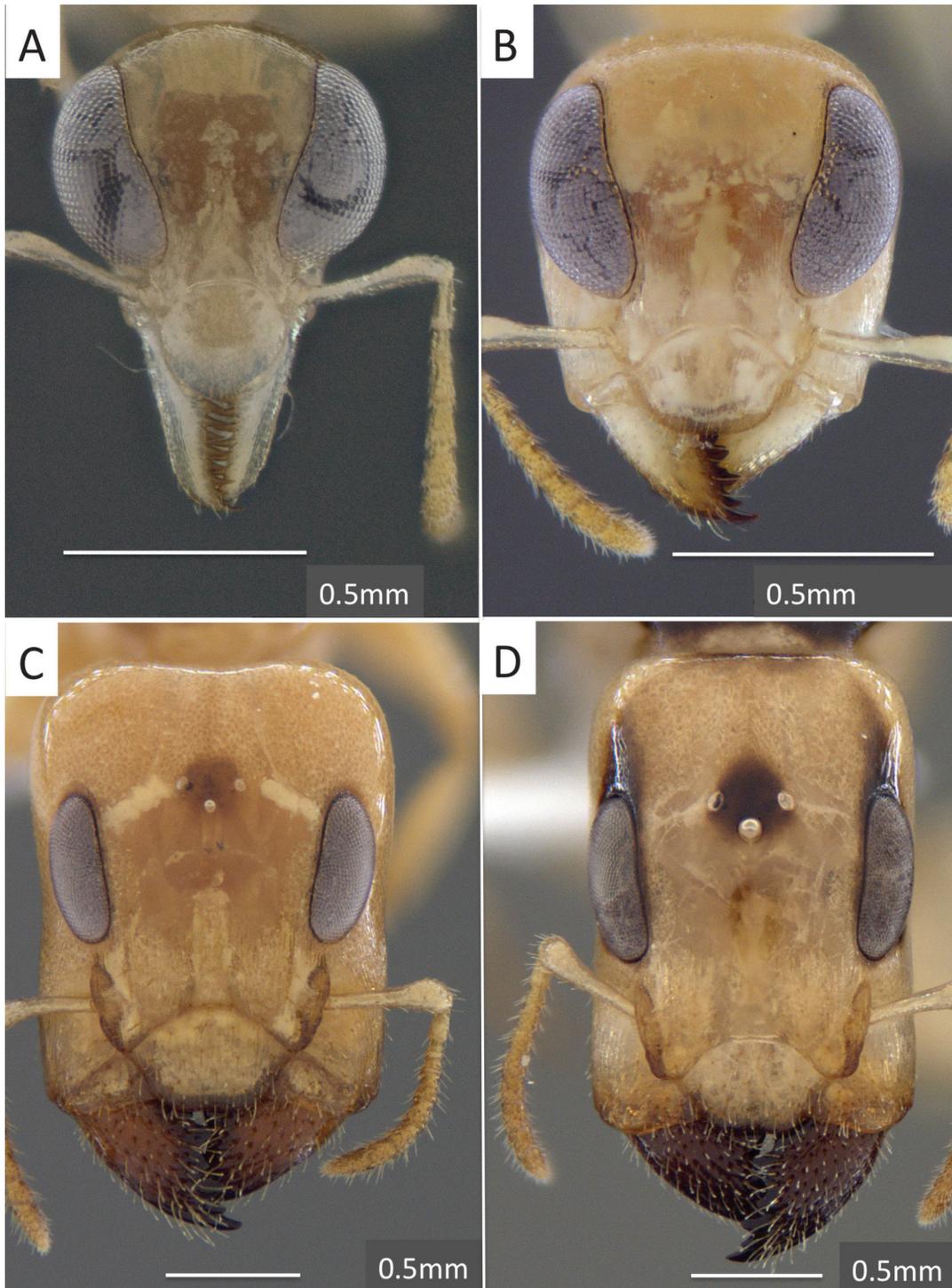
In **Sabah**, foragers were seen in a small tree (*Saraca declinata*; Fabaceae) about 4m high, and their nest was in a live stem about 3cm in diameter. There were over 100 adult females, all brood stages but no sexuals (Electronic Appendix Fig. S3).

In **Peninsular Malaysia**, a colony in a big tree on the forest edge in Ulu Gombak was first sampled in 2012. A total of 13 supersoldiers, 12 soldiers, 175 workers, 1 male and three alate queens were collected. In 2016 another three

nests were taken from the same tree after a big branch fell on the ground (Table 1).

#### **Morphological differences among castes**

Workers have triangular heads, unlike the square heads of soldiers and rectangular heads of supersoldiers and queens (Fig. 3). Indeed, soldiers have distinctly shorter heads than supersoldiers. Workers have thin elongated mandibles with a narrow base and a wide masticatory margin bearing 8-9 sharp teeth; the distal ends curve down. Soldiers, supersoldiers and queens share mandibles with a wider base (Fig. 3). The clypeus in workers is rounded, whereas it is ovoid in all other castes. SEM revealed the existence of setae with peculiar spiky ends on both clypeus and mandibles of soldiers and supersoldiers, but not workers (queens were not examined with SEM) (Fig. 4 and Electronic Supplementary Material Fig. S4). Both supersoldiers and queens have frontal lobes

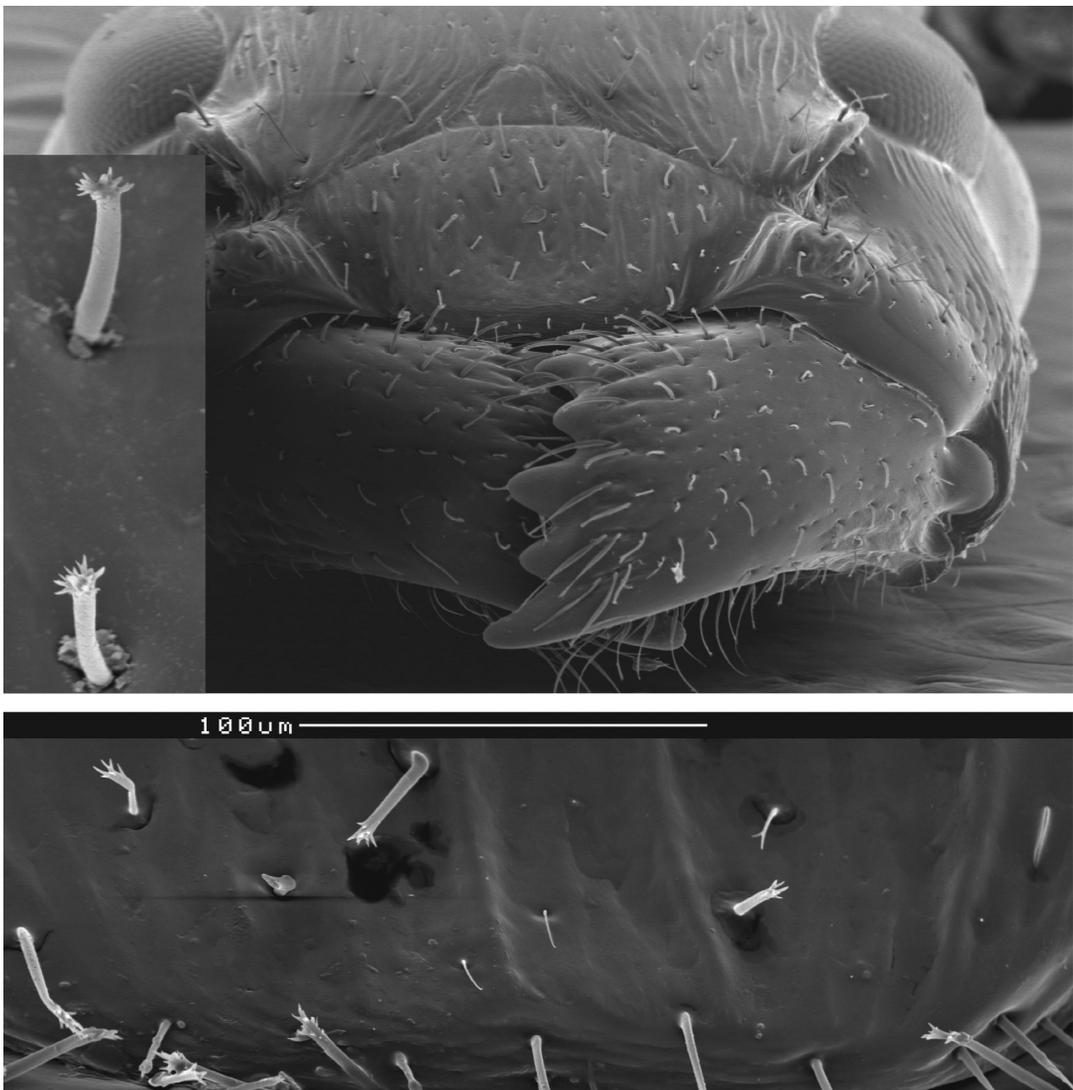


**Fig. 3.** Heads of all four castes of *Gesomyrmex* sp. shown at different scales (A: worker, B: soldier, C: supersoldier (Sabah colony); D: queen from Ulu Gombak). Note differences in ocelli, clypeus, mandibles and frontal lobes (covering the antennal sockets).

(lateral projections of cuticle that cover the antennal sockets; Keller 2011) protecting the base of antennae (Fig. 3). These are completely absent in workers, and present as traces in soldiers. Important differences are also seen in relative eye size. All castes have compound eyes with similar surface areas, but they are disproportionately large in workers because of their much smaller heads (Fig. 5). Eyes look smaller in soldiers and even more so in supersoldiers and queens that have heads at least twice longer. Queens have three

conspicuous raised ocelli, these are reduced but distinct in supersoldiers; soldiers have two vestigial ocelli and workers none.

Thorax sclerites of queens are consistent with flying ability, the mesonotum is conspicuously much higher than in non-flying castes. However the prothorax is unusually large compared to Formicinae queens generally (Electronic Appendix Fig. S5). Abdomen size is larger in both supersoldiers (Fig. 6) and queens.



**Fig. 4.** SEMs of “spiky” setae occurring on mandibles and clypeus region of supersoldier caste in *Gesomyrmex* sp. (Thailand colony). Insets show magnified setae. Additional SEMs of worker and soldier are shown in Electronic Supplementary Material Fig. S4.



**Fig. 5.** Heads of *Gesomyrmex* sp. worker and soldier drawn at the same scale, showing differences in relative eye sizes.

Measurements of four body parts showed distinct allometries among the four castes of the Thai colony (Fig. 7). Differences in body size are clearly seen in Fig. 6, but there is much variability among the four castes (Fig. 7). In particular, soldiers and supersoldiers can be similar in body size. In the Ulu Gombak nest, workers were 3.4 – 3.7 mm in length, soldiers 4.1 – 4.5 mm, and supersoldiers 5.5 – 6.0 mm. This is a close match to individuals of *G. kalshoveni* measured in Java (Wheeler 1929a): *minima* (2.8 – 3.2mm), *media* (3.5 – 4.5mm), *maxima* (5 – 6.6mm). Similarly, a queenright nest of *G. luzonensis* from the Philippines (Wheeler 1930) included *minima* (2.5 – 3.5mm), *media* (4.5 – 6mm), *maxima* (6.5 – 7mm) and a dealate queen (9mm). In our sample of nests, supersoldiers constituted roughly 10% of female adults (range 7.8 – 12.5%). Soldiers were often more numerous than supersoldiers (Table 1).

#### **Behavioural differences among non-flying castes**

In the field, workers were active only under strong sunshine. One individual was observed retrieving a winged insect (S. DeGreef pers. comm., Elec-

tronic Appendix Fig. S6). Soldiers were active on the bark of trees. Supersoldiers were neither seen nor collected outside nests. In Thailand we observed their heads inside nest entrances, presumably blocking it (Fig. 8). Supersoldiers with swollen gasters occurred in a few nests. In Thailand, when sweet food with a red colour dye was presented, within an hour some workers had a red spot in the gut, and one soldier acquired a completely red gaster (Electronic Appendix Fig. S7).

#### **Ovarian differences among castes**

Two alate queens from Ulu Gombak (2012) had 18-18 and 17-17 ovarioles. Workers had 1-1 ovarioles (N= 34), while soldiers had 1-1 or 2-2 (N= 12). In nest FI16-55, 8 of 9 soldiers had 1-2 developing oocytes. Dissection of a supersoldier with a swollen gaster (Sabah colony) revealed active ovaries with 4-4 ovarioles and 2 large oocytes (Electronic Appendix Fig. S8). A spermatheca was not found.



**Fig. 6.** Differences in body size among worker, soldier and supersoldier castes of *Gesomyrmex* sp. (Thailand colony).

## DISCUSSION

### Caste differences and Polyethism

Bulging eyes allow overlapping fields of view that result in 3D and lateral vision. Together with nimble piercing mandibles, this confirms that workers hunt live prey in the canopy (already suggested by Dlussky et al. 2009). Workers run with a jerky zigzag gait (Wheeler 1930) and are very agile on tree trunks (Cole (1949) in India).

Wheeler (1930) described a small group of workers greedily imbibing juices from a ripe banana before returning to their nest, indicating that sweet secretions are also exploited.

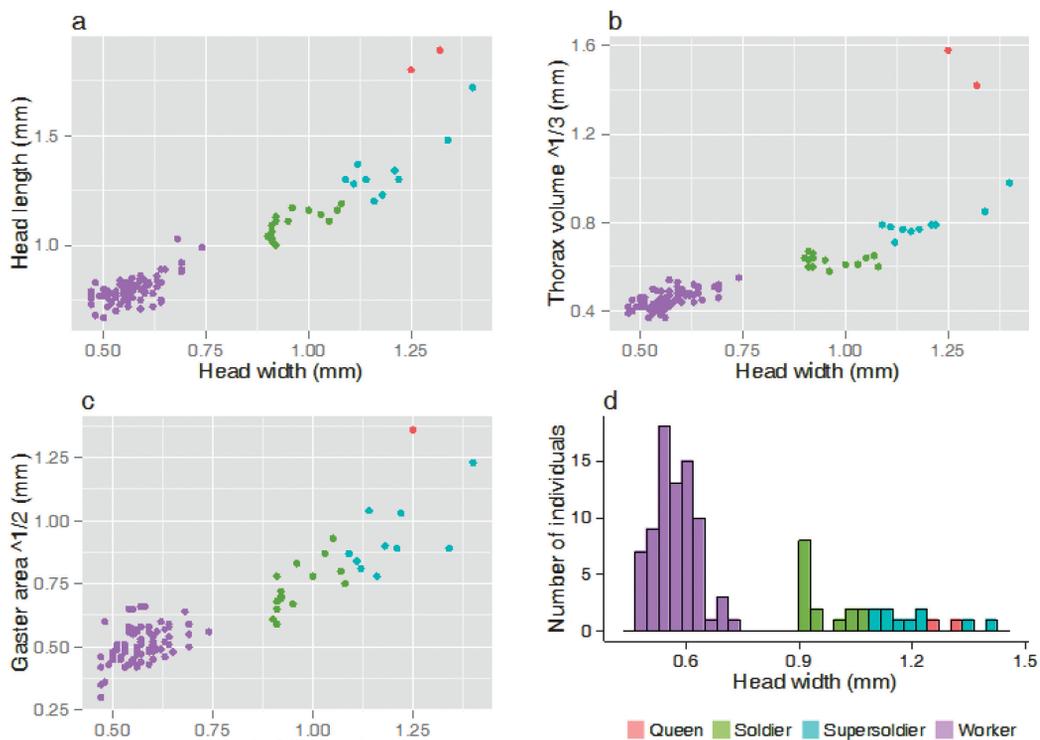
Soldiers appear to share the good vision of workers and their agility to move around quickly outside the nests. Soldier mandibles are more similar to supersoldiers than to workers, hence soldiers presumably defend foraging workers and the nest from intruders (e.g. other

ants, spiders). Being equipped with formic acid also contributes to defence capability, but we did not check the poison gland across castes. Soldiers may also block entrances, especially when two individuals stand together; they have spiky setae on the head although frontal lobes are lacking.

Supersoldiers and queens have massive mandibles with broad articulation and molar-like teeth, becoming blunt with age. Given that the rectangular head of supersoldiers is packed with mandible muscles (J. Billen, pers. comm.), this is evidence of the ability of both castes to chew through hard living wood. In contrast, workers have thinner elongate mandibles, with acute teeth that are more adapted for prey capture. Supersoldiers are mostly confined inside the nests except when they are required to chew the entrance hole during settlement of additional nests (see below). Other functions include blocking nest entrances and food storage. A physogastric supersoldier from Sabah had large oocytes in the ovaries (Electronic Appendix Fig. S8), suggest-

ing the production of trophic eggs to share nutrients among nestmates. This trophic function is supported by a higher ovariole number relative to soldiers. It is possible that soldiers store sweet liquid food in their crop, while supersoldiers lay trophic eggs.

Supersoldiers and queens show well-formed frontal lobes and stronger sclerotization of the anterior region of the head, all suggestive that they engage in phragmotic behavior. Phragmosis is supported by the novel spiky setae (“stubby hairs”; Dlusky 2009) on the clypeus and mandibles of soldiers and supersoldiers, but not workers (Fig. 4 and Electronic Supplementary Material Fig. S4). Their function is currently unknown, and we speculate that they are chemosensory sensillae, allowing the detection of cuticular hydrocarbons forming the colonial odour, and removing the need to expose antennae out of the entrance hole during identification of incoming nestmates.



**Fig. 7.** Morphometry and allometry for 77 workers, 15 soldiers and 10 supersoldiers (Thailand colony). Two queens from peninsular Malaysia were added for comparison. Pairwise allometric relationships between head width and (a) head length; (b) thorax volume; (c) gaster area. Frequency distribution of head width (d).



**Fig. 8.** Supersoldier head blocking the entrance of a *Gesomyrmex* sp. nest (Thailand colony). Worker head is shown in the same entrance for comparison (below).

*Gesomyrmex* shows clearly the expression of modular body traits across castes. For example, supersoldiers share several morphological modules with winged queens, including rectangular heads with sturdy mandibles and frontal lobes, except that supersoldiers are wingless. This supports the hypothesis (Molet et al. 2012, 2014) that worker and queen traits can be recombined to evolve novel mosaic phenotypes. In several species of *Pheidole* having both soldiers and supersoldiers, their developmental programs share many modules (e.g. vestigial wing discs, body size; Rajakumar et al. 2012).

### Ability to chew living wood and colony foundation

All inhabited nests we examined had one small entrance hole leading to the very center of living branches. When newly mated queens start a nest in a suitable branch, they must chew through up to 1cm of healthy wood to gain access to the pithy center (Fig. 1). The combination of rectangular head and strong mandibles in *Gesomyrmex* queens confirms that foundresses are capable of this essential task. It is possible that they start chewing in spots where the wood has decayed or is weakened by wood-boring insects. As opposed to ants where workers tunnel through robust wood and live in the tunnels (e.g. *Melissotarsus*, Fisher & Robertson 1999), *Gesomyrmex* queens only need to chew an entrance gallery. Afterwards, removing the soft pith is relatively easy, and soldiers may carry out this task. Since foundation is claustral (see below), queens do not need to come in and out with prey, and a rudimentary entrance tunnel can be broadened over time.

Given the very hard nature of living wood, specialised cutting tools are needed to gnaw through it. Ant mandibles can generate a variety of movements, ranging from extremely fast (e.g. trap-jaw species) to highly powerful (wood-chewing species) (Gronenberg et al. 1997). The force and speed of mandible muscles depend on the geometry of their attachment to the cranium and internal cuticular apodemes, together with the ratio between fast and slow fibres (Paul 2001). Species that perform fast mandible movements generally have long head capsules to accommodate long muscle fibres that attach at small angles

to the closer apodeme, channeling force to the mandibles. Differences in head shape have been documented across ant species (Paul 2001), but in *Gesomyrmex* these occur among castes. The triangular heads of *Gesomyrmex* workers versus the quadrilateral heads of the other castes is due to an increase in the frontal area that forms the mandibular articulation (Figs. 3 and 5). Since the rectangular heads of queens and supersoldiers are associated with power instead of speed, this shows that the space inside head capsules of any shape can be optimized with different configurations of muscles and apodemes.

### Phragmosis

Attempts to induce *Gesomyrmex* workers to exit a nest were unsuccessful, indicating that their defence strategy consists simply in withdrawing inside their fortress (Wheeler 1930). If phragmosis is broadly defined as blocking nest entrances with a body part (Fischer et al. 2015), two extremes are distinct across ants: (i) in *Cephalotes*, *Colobopsis* and a few other genera, soldiers have highly modified heads that match exactly the shape of nest entrances (Powell 2008, 2016, Laciny et al. 2017); (ii) in *Cataulacus* and others, blocking behaviour is not associated with dramatic modifications in head shape. In *Gesomyrmex*, conspicuously rectangular heads reflect enlarged mandible muscles, but the dorsal cranium is not used to plug the nest entrance. Instead, a broader head together with sturdy mandibles combine to block entrances (Fig. 7). A compromise is thus apparent between powerful mandibles and evolving plug-shaped heads. *Cephalotes* ants have highly specialised soldiers that block nest entrances, but these have relatively small mandibles, hence a limited capacity to chew hard wood and expand the nest cavity, incl. entrances that are selected on the basis of existing size (Powell 2016).

### Claustral colony foundation

Ant queens generally start new colonies without any help from workers (independent colony founding, ICF). In *Gesomyrmex*, this implies that lone foundresses must first chew an entrance tunnel to the pith, and then guard the entrance against intruders for several weeks while they raise the first generation of worker larvae to adulthood. Since supersoldiers have been observed to block

nest entrances with their head (Fig. 7), one can assume that queens behave similarly when starting new colonies. Indeed, queens and supersoldiers share frontal lobes (for protection of antennal bases) and sclerotized mandibles. In all ICF species, the challenge for newly mated foundresses is to rear a first generation of workers as quickly as possible. It is probable that soldiers and especially supersoldiers are reared only after colonies have reached a critical size.

Among Formicinae, *Gesomyrmex* queens have an unusually large pronotum (Electronic Appendix Fig. S5). The contrast with *Oecophylla* is particularly striking, where queens have a predominant mesonotum and a highly reduced pronotum. Instead, *Gesomyrmex* queens have a prothorax that is closer in size to that of the non-flying castes, similarly to queens in Ponerinae and several other subfamilies (Keller et al. 2014). A large prothorax reflects worker-like neck muscles that allow such queens to forage during colony founding (i.e. non-claustral ICF) (Keller et al. 2014). Nonetheless, we think *Gesomyrmex* foundresses do not forage outside (i.e. ICF is claustral), because their mandibles are unsuitable for hunting. Hence the strong neck muscles associated with the unusually large prothorax of *Gesomyrmex* queens appear necessary for chewing wood and/or phragmosis. The large difference in body size between queens and workers (Fig. 7) is consistent with claustral ICF, because founding queens can rear workers much smaller than themselves using stored metabolic reserves.

### Colony expansion and polydomy

Many arboreal ants nest in structures that are built next to or partly within trees. This allows for space expansion as colonies grow in size (e.g. carton nests of *Crematogaster*). In *Gesomyrmex*, the drawbacks of highly secure nests inside living branches is the impossibility to gain additional living space. Provided a colony has sufficient foraging workers, its queen can become very fecund as evidenced by a large number of ovarioles. Monogyny is presumed (as in *Oecophylla*) but needs confirmation. There was a large variability in the number of inhabitants of the nests we collected, ranging from a dozen adults to more than 100 (Table 1). Indeed, the single Sabah nest was as populous as the combined five nests of

the Thailand colony. This variability may be related to physical characteristics of the cavities. In the Philippines, a chamber (12.5 cm long) in the pithy center of a green branch yielded about 150 adults, one dealate queen, larvae and eggs (Wheeler 1930). Growing colonies are forced to expand into additional nests, leading to polydomy. This strategy allows for optimal use of spatial resources (Robinson 2014) and has evolved in many unrelated ants (including *Oecophylla*; Crozier et al. 2010). Arboreal species that are polydomous apparently require closed cavities as nest sites, e.g. inside large branches or epiphytes, and the scarcity of these may restrict competitive ability (Tanaka et al. 2010).

This raises the question of how additional nests begin in a colony of *Gesomyrmex*? An entrance tunnel must be chewed, but the single reproductive queen is very unlikely to take risks by leaving the safety of her nest. We speculate that supersoldiers carry out the specialized task of chewing the entrance tunnel of a new nest, and they may be recruited by scouting workers. This likely explains the retention of large eyes in supersoldiers, given they are otherwise restricted to the inside of nests.

*Gesomyrmex* presents an intriguing division of labour: workers are the active hunters, with very distinct mandibles. Queens (and both kinds of soldiers) have different mandibles, indicating that they do not hunt during colony foundation. However, a foundress needs to chew an entrance tunnel through living wood, and then block this nest entrance for many months until the colony is strong enough to produce the first soldiers. Supersoldiers are presumably reared even later in colony ontogeny, because they are more costly. Relatively few supersoldiers are present and they show two queen-like behaviours: they stay inside nest chambers and block the entrances, and they chew entrance holes when starting other nests belonging to the same colony. Supersoldiers also store nutrients (trophic eggs) in their gaster. These multiple functions bring sufficient benefits to the colony to balance their higher cost of manufacture. There are many examples of other ants having soldiers that combine specialist activities involving large heads, powerful mandibles and food storage (Peeters & Ito 2015). In *Crematogaster* (*Orthocrema*), soldiers

also have a trophic function, but they lack specialized mandibles (Peeters et al. 2013).

Fossils of *Gesomyrmex* are very diverse from the middle to late Eocene, then disappear from the geological record. This genus illustrates the very early evolution of soldiers (Dlussky et al. 2009), and it has undergone no significant modification since 40MY (Wheeler 1929a). It is presently restricted to forests of tropical Asia, a relict of an Eocene distribution across the Old World (Dlussky et al. 2009). Current records (Introduction and this study) show a very broad distribution across SE Asia, and its perceived rareness may simply be a consequence of restriction to the high canopy of evergreen forests (Electronic Appendix Fig. 2). Its closest relative appears to be *Oecophylla*, which is ecologically dominant in forest canopies across three continents (Crozier et al. 2010). Why is *Gesomyrmex* much less successful? Many similarities are seen in lifestyles and colony structure, but also important differences. Too little is known about foraging biology and other ecological factors in *Gesomyrmex* to assess its competitive abilities relative to other arboreal ants. Our predictions about division of labour based on functional morphology need to be validated with field observations.

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