

Queen polymorphism in *Acanthomyrmex careoscrobis* Moffett, 1986 in Peninsular Malaysia (Hymenoptera: Formicidae: Myrmicinae), with descriptions of hitherto unknown female castes and males

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ABSTRACT. The present study presents biological observations on colony characteristics of *Acanthomyrmex careoscrobis* Moffett, 1986 in Ulu Gombak (Selangor, Malaysia), with redescription of the minor worker and descriptions of the hitherto unknown female castes and males. The colony of *A. careoscrobis* can produce both alate and ergatoid queens. Ergatoid queens may function as cheap secondary reproductive females, whereas it is at present unclear whether they engage in dependent colony foundation or not. Ergatoid queens have the same number of ovarioles as alate queens, and show variable intermediate external morphology between major workers and alate queens. The colony redistributes nutrients via trophic eggs among colony members. Reviewing current available data for other *Acanthomyrmex* species, this study highlights the great prevalence and diversity of ergatoid queens in this poorly-studied genus.

Keywords: ant, ergatoid queen, polyphenism, phenotypic plasticity, trophic egg.

INTRODUCTION

In most ant species, the queen possesses the full complement of flight sclerites and muscles, and deciduous wings, i.e., the ability to fly while she has wings (hereafter this normal queen type is referred to as an alate/dealate queen). In contrast, permanently wingless reproductive females (ergatoid queen, brachypterous queen, and gamergates) evolved independently in more than 50 genera belonging to 16 ant subfamilies, with the result of either winged/wingless queen

polymorphism or complete loss of alate queens and replacement by the wingless reproductives (Peeters & Molet 2010; Peeters 2012). However, our knowledge of such females is still incomplete because the reproductives and life histories of the majority of ant species remain undescribed, and also because different types of queens may be rare or conditionally expressed.

The myrmicine ant genus *Acanthomyrmex* Emery, 1893 is primarily restricted to the Oriental realm, with one exceptional species *A. notabilis* (Smith F., 1860) which is distributed on both

sides of the Weber's Line (Holt et al. 2013; Janicki et al. 2016; Antmaps.org), consisting of 17 valid extant species (Bolton 2018); 11 species were recognized in a taxonomic revision by Moffett (1986), and since six new species have been described (Terayama 1995; Terayama et al. 1998; Zhou & Zheng 1997; Eguchi et al. 2008). Colonies of this genus are commonly small (usually with less than 100 workers), and nests are found in cavities in dead twigs or rotten wood, under or between stones and in litter on the forest floor. The nests of *Acanthomyrmex* species usually contain tiny seeds; *A. ferox* Emery, 1893 exclusively gathers fig seeds from bird feces (Ito et al. 2017), but colonies of *A. glabfemoralis* Zhou & Zheng, 1997 often contain several undetermined kinds of seeds (Yamada et al. unpublished). *Acanthomyrmex* workers have ovaries but lack spermatheca, and exhibit a distinct dimorphism, i.e., major workers (hereafter referred to as majors) and minor workers (minors) that are morphologically different. Majors are considered to serve in colony defense, seed milling and food storage (Moffett 1985; Buschinger & Maschwitz 1998; Terayama et al. 1998; Gobin & Ito 2000, 2003; Eguchi et al. 2008). All female castes were shown to lay trophic eggs in *A. ferox* Emery, 1893 and nutrient redistribution via trophic eggs among colony members was confirmed (Gobin & Ito 2000).

Queens in the genus *Acanthomyrmex* have so far been described for seven species: two species (*A. ferox* Emery, 1893 and *A. thailandensis* Terayama, 1995) are characterized by the presence of alate queens, four species (*A. humilis* Eguchi et al., 2008, *A. padanensis* Terayama et al., 1998, *A. minus* Terayama et al., 1998, and *A. sulawesiensis* Terayama et al., 1998) are characterized by the complete replacement of alate queens with ergatoid queens (see Moffett 1986 and the original descriptions); and a single species (*A. glabfemoralis*) exhibits intraspecific polymorphism of queen phenotype (Eguchi et al. 2008). Eguchi et al. (2008) reported that queenright colonies of *A. glabfemoralis* at four sites in northern Vietnam (Chua Yen Tu (Quang Ninh Province), Ky Thuong Nature Reserve (Quang Ninh), Cuc Phuong National Park (Ninh Binh) and Pu Mat National Park (Nghe An)) had a single dealate queen, whereas those

at Van Ban (Lao Cai) had a single or multiple ergatoid queens. Both queen types were found in separate colonies at Tay Yen Tu Nature Reserve (Bac Giang), though intracolony polymorphism (i.e., production of both queen types in a single colony) has so far not been documented in this species (Eguchi et al., 2008).

Moffett (1986) mentioned remarkable "variations" of the minor of *A. basispinosus* Moffett, 1986 and *A. mindanao* Moffett, 1986. These "variations" are likely misrecognition of ergatoid queens, because the abnormal "minor" individuals show morphological traits similar to those of ergatoid queens in *A. humilis*, *A. padanensis*, *A. minus* and *A. sulawesiensis* (Yamada et al. unpublished). According to our morphological examinations of specimens obtained through colony sampling (Yamada et al. unpublished), *A. concavus* Moffett, 1986 and *A. dusun* Wheeler, 1919 also have ergatoid queens instead of alate queens (images of an ergatoid *A. concavus* queen given at AntWeb: <https://www.antweb.org/specimen/CASENT0101061>), while *A. crassispinus* Wheeler, 1930 in Taiwan exclusively had ergatoid queens, with similar morphological traits to those of *A. glabfemoralis* in Vietnam. These observations suggest that reproduction by ergatoid queens is more prevalent in the genus *Acanthomyrmex* than previously recognized.

In the present paper, another case of queen polymorphism in this genus is reported. Buschinger & Maschwitz (1998) mentioned an undetermined species found in Ulu Gombak, Selangor, Peninsular Malaysia, with notes on the habitat and role of the majors. With colonies newly collected in 1988 – 2013 by F. Ito in Ulu Gombak, we confirmed that the undetermined species interestingly exhibits intracolony queen polymorphism. The specimens were identified as *A. careoscrobis* Moffett, 1986 which is previously known only from the holotype minor collected from Gunung Mulu National Park (Sarawak, Malaysia), however future collection and examination of colony series from the type locality is necessary to confirm the taxonomic identity.

Here we present biological observations on the colony composition, new queen production, and egg-laying behavior of *A. careoscrobis* in Ulu Gombak. In addition, DNA barcodes,

redescription of the minor, and descriptions of the other female castes and the males are also given in the appendix for future comparison.

MATERIALS AND METHODS

Caste terminology

In the present paper, we use the term “ergatoid queen” to refer to permanently wingless reproductive females that differ morphologically from workers, following Peeters (2012).

Colony sampling and biological observation

A total of nine *Acanthomyrmex* colonies were collected from a lowland rainforest near the Ulu Gombak Field Station of the University of Malaya in Selangor, Peninsular Malaysia, in July 1998, August 1999, August – September 2009, March 2011, and March 2013. Each colony was given a unique colony code such as “FI98-77”. As many individuals as possible were collected alive from each colony. Adult members of each caste were counted for each colony, and some adult females were dissected by F. Ito soon after collection in order to observe ovariole numbers and the presence/absence of spermathecae. The presence of spermatheca filled with sperm indicates that mating has already occurred. Colonies were then transferred to artificial plaster nests and reared in a laboratory at Kagawa University (Kagawa Pref., Japan), fed with small pieces of mealworm and with sugar water, and used for the following observations.

Egg-laying behavior of colony FI99-418 (1 ergatoid queen, 1 major, 20 minors, and several larvae and eggs) was observed directly under a binocular microscope for a total of 96 hours from December 1999 to January 2000. Egg types (reproductive or trophic) and the number of eggs laid by each female caste were observed and the fate of the eggs traced as far as possible.

An orphaned colony fragment (15 minors, 7 larvae, and 20 eggs) was artificially isolated from the colony FI99-418 in March 2000, and another orphaned colony fragment (ca. 20 minors, several larvae and eggs) isolated from FI09-103 in December 2010. The new queens produced in the fragments within the three months after isolation were dissected to assess their reproductive condition.

After rearing observations, several adult females from each colony were dissected. Finally, a detailed morphological examinations of all castes and DNA barcoding were conducted. The voucher specimens are deposited in the following collections: AKYC, ACEG, and ACFI Ant collection of A. Yamada, K. Eguchi and F. Ito, respectively (see the contact address of the corresponding author); FRIM, Forest Research Institute Malaysia, Kepong, Selangor, Malaysia; MCZC, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MHNG, Muséum d’Histoire Naturelle, Geneva, Switzerland.

Morphological examination and imaging

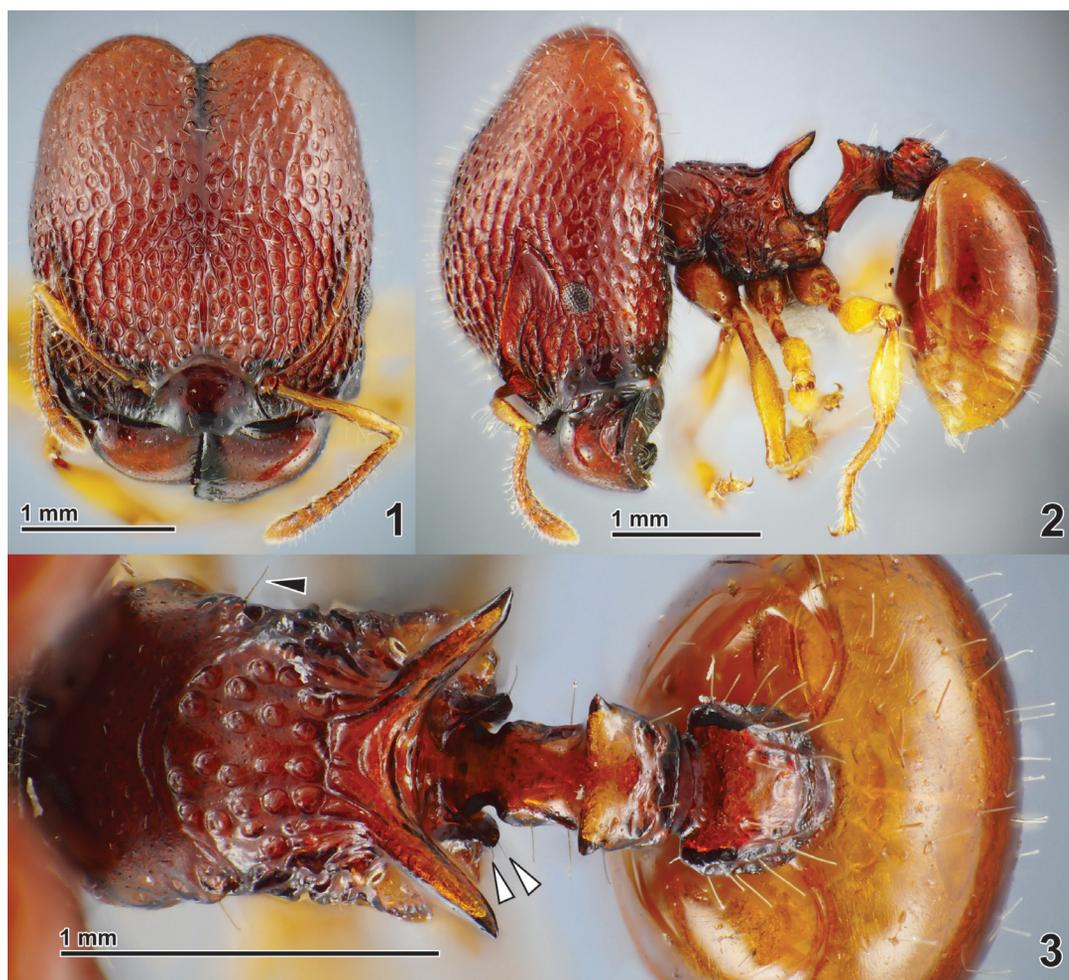
Point-mounted specimens of the adult individuals were examined with a Nikon SMZ1270 stereomicroscope. Male genitalia were cleaned by Chelex-TE protocol (for details see Satria et al. 2015), and then dehydrated in 99% ethanol, dissected into several main components in a small amount of Euparal on a slide glass, and covered with a cover slip. The morphological terminology follows Boudinot (2013). These slide-mounted specimens were examined with a Nikon Eclipse E600 microscope.

Source images for focus stacking and measurements were taken using a Lumix DMC GX8 digital camera attached to a Nikon AZ100 stereomicroscope (for the body excluding male genitalia) and Nikon Eclipse E600 microscope (for male genitalia). Focus stacked images were produced with Helicon Focus Pro 6.7.1, and then improved using the retouching function of Helicon Focus. Finally, the color balance and contrast were adjusted using GIMP 2.8 (available at <http://www.gimp.org>). Line drawing of male genitalia were prepared by tracing the multi-focused images.

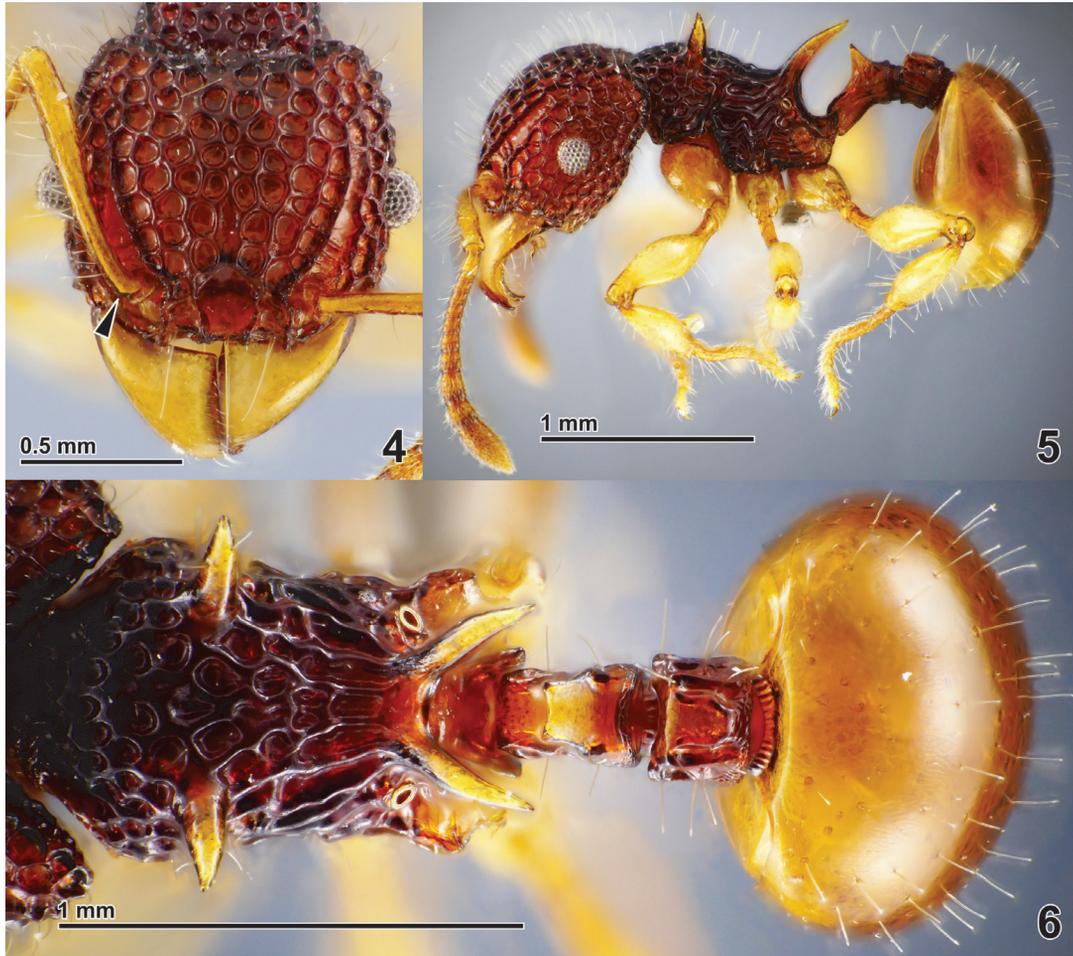
The abbreviations used for the measurements and indices are as follow.

HL Head length: maximal length of cranium (head capsule) in full-face view, measured from transverse line spanning the anteriormost points of clypeus to that of posteriormost points of cranium.

- HW Head width: maximal width of cranium in full-face view (excluding eyes).
- EL Eye length: diameter of major axis of eye in lateral view.
- OL Ocellus length: diameter of major axis of median ocellus in frontal view (for alate queen and male).
- SL Scape length: maximum length of antennal scape excluding basal condylar bulb.
- ML Mesosomal length: minimum length between posteroventral corner of pronotum and posterodorsal margin of propodeal spiracle in lateral view.
- PnSL Pronotal spine length: length of pronotal spine, measured from posterobasalmost point to apex of spine in lateral view (minor).
- PdSL Propodeal spine length: minimum length between posterodorsal margin of propodeal spiracle and apex of spine (for female).



Figs. 1 – 3. Major worker of *Acanthomyrmex careoscorbis*, FI09-121. (1) Head in full-face view. (2) Body in lateral view. (3) Mesosoma and metasoma in dorsal view.



Figs. 4 – 6. Minor worker of *Acanthomyrmex careoscrobis*, FI09-121. (4) Head in full-face view. (5) Body in lateral view. (6) Mesosoma and metasoma in dorsal view.

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|-----|--|------|---|
| PL | Petiole length: length of petiole measured from the anteroventral corner of petiolar peduncle to the posterodorsal corner of petiole in lateral view. | PPH | Postpetiolar height: maximum height of postpetiole in lateral view. |
| PH | Petiole height: height of petiole measured from the highest point of petiolar node to posteroventralmost points of petiole in lateral view (for female), or length of vertical line from anterodorsal corner of petiolar node to ventral margin of petiole in lateral view (for male). | CI | Cephalic index: $HW/HL \times 100$. |
| PPL | Postpetiolar length: maximum length of postpetiole in lateral view (excluding helcium). | EI | Eye index: $EL/HW \times 100$. |
| | | OI | Ocellus index: $OL/HW \times 100$ (for alate queen and male). |
| | | SI | Scape index: $SL/HW \times 100$. |
| | | PnSI | Pronotal spine index: $PnSL/ML \times 100$ (for minor). |

PdSI Propodeal spine index: $PdSL/ML \times 100$
(for female).

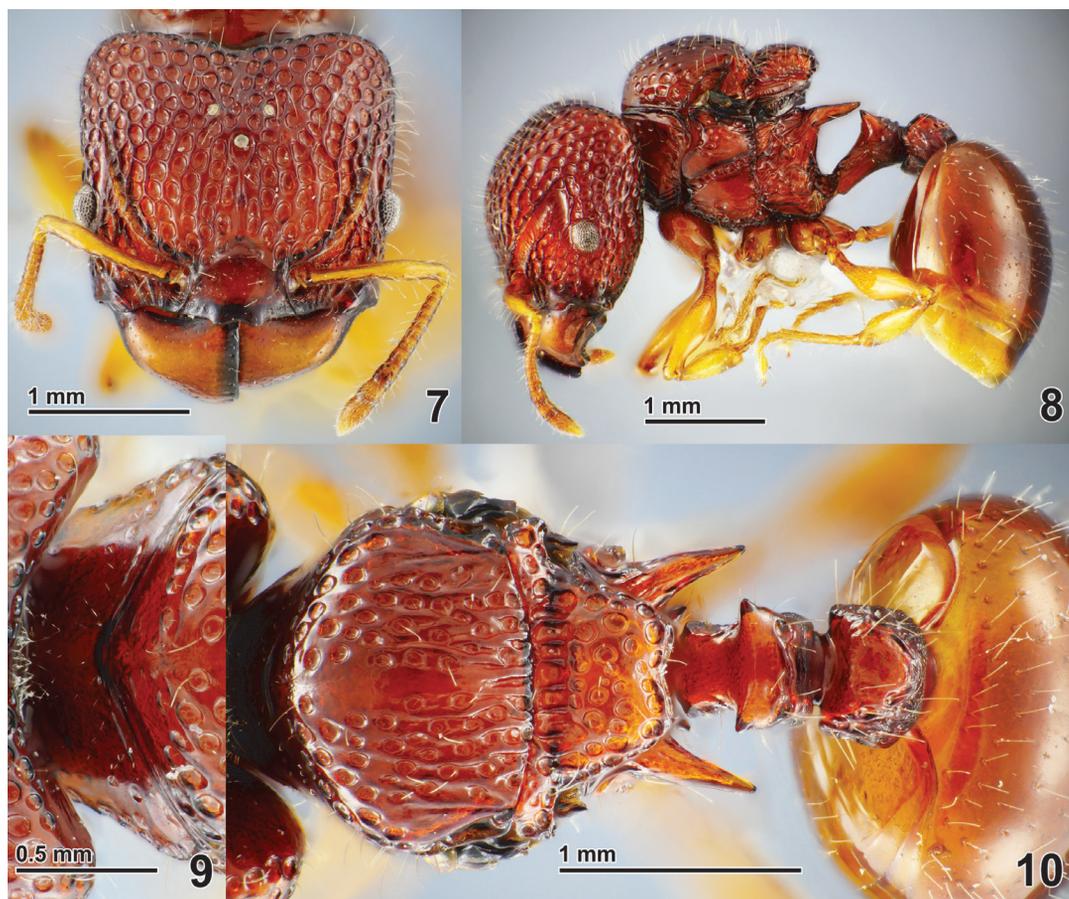
PI Petiolar index: $PL/PH \times 100$.

PPI Postpetiolar index: $PPL/PPH \times 100$.

DNA barcoding

A 658 bp region (the Folmer region) of the mitochondrial cytochrome c oxidase subunit I (COI) gene and complete ITS1 region of nuclear ribosomal DNA (ca. 1000 bp) were sequenced. A minor or male (male was used only for FI11-88) from six of nine colonies examined (i.e., excluding FI99-77, -167, -418) were used for DNA extraction by Chelex-TE protocol (for details see Satria et al. 2015); incubation time was 24 – 48 hours. The primers LCO-EG and

HCO-EG (modified from Folmer et al. 1994: 5'-TTTCAACAAATCACAAAGAYATYGG-3' and 5'-TAAACTTCAGGRTGACCRAAAAA TCA-3') were used for COI, and CAS18Fs1 and CAS5p8s1Bd (Ji et al. 2003; Smith & Fisher 2009: 5'-TACACACCGCCCGTCGCTACTA-3' and 5'-ATGTGCGTTCRAAATGTCGATGTTCA-3') were used for ITS1. PCR amplifications, cycle sequencing reactions, sequencing using ABI PRISM 3130xl (Applied Biosystems) and sequence assembly using ChromasPro 1.7.6 (Technelysium Pty Ltd., Australia) were conducted by following the protocols presented in Satria et al. (2015). The PCR thermal regime consisted of one cycle of 2 min at 94 °C; five cycles of 10 sec at 98 °C, 30 sec at 45 °C and 45 sec at 68 °C; 40 cycles (COI) or 45 cycles (ITS1) of 10 sec at 98 °C, 30 sec at 48.5 °C (COI) or 51



Figs. 7 – 10. Dealate queen of *Acanthomyrmex careosrobis*, FI09-121. (7) Head in full-face view. (8) Body in lateral view. (9) Pronotum in anterodorsal view. (10) Mesosoma and metasoma in dorsal view.



Figs. 11 – 19. Three representatives of the ergatoid queens of *Acanthomyrmex careoscrobis*. (11–13) A virgin ergatoid queen that was produced in FI09-103 under orphaned condition. (14–16) A mated ergatoid queen that was originally contained in FI11-88. (17–19) A virgin ergatoid queen that was produced in FI99-418 under orphan condition. (11, 14, 17) Head in full-face view. (12, 15, 18) Body in lateral view. (13, 16, 19) Mesosoma in dorsal view.

°C (ITS1) and 45 sec at 68 °C; and a final cycle of 7 min at 68 °C. Successful assembly of each COI sequence was confirmed by translating it to the amino acid sequence and checking the absence of frame shifts caused by erroneous indels. A total of ten sequences were submitted to the International Nucleotide Sequence Database (INSD) via DNA Data Bank of Japan (DDBJ).

RESULTS

Nesting site, colony composition, and ovariole number

Excluding FI98-77, which was a small colony fragment collected by litter sifting, eight colonies of *Acanthomyrmex careoscrobis* were found nesting in rotten branches under accumulated leaf

litter on the forest floor. The colonies contained 7 – 250 fig seeds inside their nests ($n = 5$) and 22.2 ± 12.5 workers in total; 1.8 ± 0.9 majors (Figs. 1 – 3), and 22.6 ± 11.1 minors (Figs. 4 – 6) ($n = 8$, average \pm SD) (Table 1). Six colonies contained a single dealate queen (Figs. 7 – 10), whereas two colonies, FI11-88 and FI99-418, contained a mated ergatoid queen (i.e., a worker-like queen with a sperm-filled spermatheca), instead of a dealate queen. External morphology of these ergatoid queens was clearly distinct from workers (for details, see “External morphology of ergatoid queens” below). FI13-83 contained four alate queens in addition to a dealate queen. FI98-77 contained a queen that was morphologically similar to the mated ergatoid queen from FI11-88, but fertilization could not be confirmed by dissection; the individual was therefore regarded as a virgin ergatoid queen. Two

colonies, FI09-121 and FI11-79 contained three and six males, respectively.

The orphaned colony fragment isolated from FI99-418, that originally contained a mated ergatoid queen, produced an alate queen and two ergatoid queens, while the orphaned colony fragment isolated from FI09-103, that originally contained a dealate queen, produced four ergatoid queens. Consistent with the fact that production of males was never observed in these colony fragments during our observations, all of these newly produced ergatoid queens were virgin when dissected.

Alate queens ($n = 4$), ergatoid queens ($n = 8$), and majors ($n = 7$) always had six ovarioles per individual (three ovarioles per ovary). Minors ($n = 23$) always had two ovarioles per individual (one ovariole per ovary).

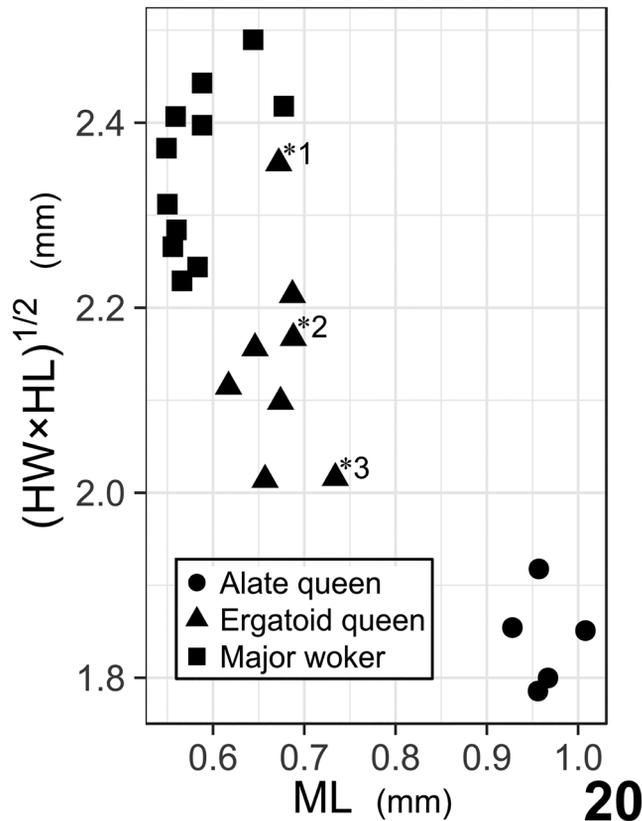


Table 1. Colony compositions and the number of fig seeds inside the nests of *Acanthomyrmex careoscribis* collected in Ulu Gombak. The numbers of queens produced under rearing condition are given in round brackets. * a colony fragment. ** the fertilization could not be confirmed during dissection. n/a data not available.

Colony code	Dealate queen	Alate queen	Ergatoid queen	Major	Minor	Male	Fig seed
FI98-77*	0	0	1**	1	4	0	n/a
FI98-167	1	0	0	1	23	0	>20, <40
FI99-418	0	0 (1)	1 (2)	1	20	0	n/a
FI09-103	1	0	0 (4)	2	19	0	150
FI09-121	1	0	0	3	19	3	250
FI11-78	1	0	0	1	13	0	50
FI11-79	1	0	0	3	28	6	7
FI11-88	0	0	1	1	12	0	13
FI13-83	1	4	0	2	47	0	n/a

External morphology of ergatoid queens

External morphology of a total of eight ergatoid queens was examined. Ergatoid queens resembled majors in general appearance due to their enlarged head and reduced mesosoma, but exhibited variable characteristics intermediate between majors and alate queens (Figs. 11 – 19). In comparison to majors, ergatoid queens had smaller head size [$HW \times HL = 4.60 \pm 0.48$ in ergatoid queens ($n = 8$), 5.53 ± 0.41 in majors ($n = 11$), average \pm SD; Welch's t-test, $t = 4.41$, $df = 13.6$, $P < 0.001$] and larger mesosomal length [$ML = 0.67 \pm 0.03$ mm in ergatoid queens ($n = 8$), 0.58 ± 0.04 mm in majors ($n = 11$), average \pm SD; Welch's t-test, $t = 5.07$, $df = 16.6$, $P < 0.001$], although there was overlap (Fig. 20). All ergatoid queens had ocelli (at least median ocellus) except for a single individual from FI09-103. The individual lacking ocelli also resembled majors most closely, with a comparable head size (Figs. 11 – 13; plot *1 in Fig. 20), but was distinguished from majors by the structure of the mesoscutellum, which was vestigial but recognizable as a small process in lateral view (a black arrow in Fig. 12). Six of the other ergatoid queens from FI11-88, FI98-77, FI99-418, and FI09-103 (one representative is shown in Figs. 14 – 16, plot *2 in Fig. 20) were distinguished from majors by the combinations of the following characteristics: i) head size almost comparable with majors or reduced to intermediate values

between majors and alate queens; ii) presence of at least a median ocellus (black arrows in Fig. 14); and iii) mesoscutellum vestigial or conspicuously raised (a black arrow in Fig. 15). One ergatoid queen from FI99-418 (Figs. 17 – 19, plot *3 in Fig. 20) was particularly distinct from majors and rather close to alate queens in morphology in having the following characteristics: head greatly reduced in size, with broadly concave posterior margin in full-face view; both median and lateral ocelli present (black arrows in Fig. 17); ML largest among all ergatoid queens measured; pronotum larger than in other ergatoid queens; forewing rudiments present (black arrows in Fig. 19); and mesopleuron separated from metapleuron.

Egg-laying behavior

Observations of egg-laying behavior in FI99-418 (which contained three adult female castes: 1 ergatoid queen, 1 major, and 20 minors) are shown in Table 2. A total of three ovipositions by the ergatoid queen, four by the major and 21 by the minors were recorded during 96 hours of observation. There were two morphologically distinguishable types of eggs (constant-sized and bean-shaped reproductive eggs vs. variable-sized and round trophic eggs), as also reported for *A. ferox* (Gobin & Ito 2000). In total, egg-laying of two reproductive and 26 trophic eggs was observed. Reproductive eggs were laid by the ergatoid queen only, whereas trophic eggs were

Table 2. The number of trophic and reproductive eggs laid and the fate of the former eaten in F199-418. Number of individuals of each castes is shown in round bracket.

Castes	Number of eggs laid		Trophic eggs eaten by			
	Reproductive eggs	Trophic eggs	Ergatoid queen	Major	Larvae	Unknown
Ergatoid queen (1)	2	1	0	0	0	1
Major (1)	0	4	0	0	4	0
Minor (20)	0	21	5	3	12	1

Table 3. Current data on the queen types in all known *Acanthomyrmex* species. **AQ** alate queen. **EQ** ergatoid queen; ? the EQ was recognized based on morphologically ergatoid-like individuals which were described as variations of "minor" by Moffett (1986); * the EQ was recognized based on the colony composition and the differentiation on the external morphology, i.e., the presence of spermatheca have not yet confirmed by dissection. **AQ + EQ** intracolony polymorphism. **AQ/EQ** intraspecific polymorphism without evidence of intracolony polymorphism. **n/a** data not available.

Species	Queen type	EQ morphology	Data source
<i>A. basispinosus</i>	EQ?	minor-like	Moffett (1986)
<i>A. careoscrobis</i>	AQ+EQ	variable intermediate between major and AQ	the present paper
<i>A. concavus</i>	EQ*	intermediate between major and minor	AntWeb (CASENT0101061); Yamada et al. unpublished
<i>A. crassispinus</i>	EQ	AQ-like	Yamada et al. unpublished
<i>A. dusun</i>	EQ*	minor-like	Yamada et al. unpublished
<i>A. ferox</i>	AQ	n/a	Moffett (1986); Gobin & Ito (2000, 2003)
<i>A. foveolatus</i>	n/a	n/a	n/a
<i>A. glabfemoralis</i>	AQ/EQ	AQ-like	Eguchi et al. (2008)
<i>A. humilis</i>	EQ*	intermediate between major and minor	Eguchi et al. (2008)
<i>A. laevis</i>	n/a	n/a	n/a
<i>A. lucirolae</i>	n/a	n/a	n/a
<i>A. mindanao</i>	EQ?	intermediate between major and minor	Moffett (1986)
<i>A. minus</i>	EQ	intermediate between major and minor	Terayama et al. (1998)
<i>A. notabilis</i>	n/a	n/a	n/a
<i>A. padanensis</i>	EQ	minor-like	Terayama et al. (1998)
<i>A. sulawesiensis</i>	EQ	minor-like	Terayama et al. (1998)
<i>A. thailandensis</i>	AQ	n/a	Terayama (1995)

laid by the ergatoid queen, major and minors. The majority of the trophic eggs were given to larvae, but the ergatoid queen and major also fed on trophic eggs laid by minors.

DISCUSSION

Prevalence and diversity of the ergatoid queen in the genus *Acanthomyrmex*

Colonies of *A. careoscrobis* in Ulu Gombak (Selangor, Malaysia) were monogynous, with either a single dealate queen or ergatoid queen (except for incomplete data from FI98-77 which was a tiny colony fragment and contained a virgin ergatoid queen). Furthermore, both alate and ergatoid queens were produced in an artificially orphaned colony fragment of an ergatoid-queen-right colony (FI99-418), and ergatoid queens were produced in that of a dealate-queen-right colony (FI09-103). This indicates that colonies have the ability to produce both types of queens, and that ergatoid queens may function as cheaper secondary reproductive females to extend colony life span after the death of the founding queen. Ergatoid queens might also potentially engage in dependent colony foundation (DCF; Cronin et al. 2013) though we have no direct evidence of this.

Ergatoid queens have so far been documented in six *Acanthomyrmex* species (including *A. careoscrobis*). Furthermore, we have unpublished data showing the presence of ergatoid queens in the other three species, and the abnormal “minor” individuals recognized in *A. basispinosus* and *A. mindanao* by Moffett (1986) are morphologically ergatoid-like (Table 3). The extent to which the morphology of the thorax and head in ergatoid queens differs from that of workers and alate queens is highly variable among species. In *A. dusun*, *A. padanensis* and *A. sulawesiensis*, ergatoid queens closely resemble minors, and lack any ocelli. In *A. minus*, *A. humilis* and *A. concavus*, ergatoid queens exhibit characteristics rather intermediate between majors and minors, i.e., head intermediate in size and structure; ocelli absent; and mesosoma intermediate, or somewhat major-like, in its size and structure. In *A. glabfemoralis* and *A. crassispinus*, ergatoid queens are similar to alate queen, i.e., both median and lateral ocelli

present; main mesosomal sclerites unfused (but reduced in volume); and wing rudiments present (Terayama et al. 1998; Eguchi et al. 2008; Yamada et al. unpublished). In *A. careoscrobis* ergatoid queens have variable characteristics intermediate between majors and alate queens. To our knowledge, major-like ergatoid queens characterized by an extremely enlarged head have never been reported in any ant species. Large intraspecific/intrapopulation/intracolony variation in morphology of ergatoid queens as observed in *A. careoscrobis* has not been reported in the other congeners. However, this is consistent with the general tendency in ants that ergatoid queens coexisting in a population with alate queens show variable morphology, while ergatoid queens exhibit less variation when alate queens have been completely replaced by ergatoid queens, as shown in the genus *Myrmecina* (Ito 1996; Buschinger and Schreiber 2002; Miyazaki et al. 2005, 2010) which putatively belongs to a clade together with *Acanthomyrmex* (Ogata & Okido 2007; Ward et al. 2014).

When ergatoid queens engage in colony foundation, they are generally considered to be specialized for DCF (Peeters 2012). In this sense, the morphology of the ergatoid queens in *Acanthomyrmex* may be associated with the resource allocation for DCF. Seed milling is an important task for colony survival in *Acanthomyrmex*, and a main role of the majors (Moffett 1985; Buschinger & Maschwitz 1998; Ito et al. 2017); the enlarged head and robust mandibles with nearly completely edentate masticatory margins appear well adapted to this task. Under independent colony foundation (ICF), the foundress queen has to do all necessary tasks including seed milling during the founding stage. This is likely the reason why alate queens in *Acanthomyrmex* have a moderately enlarged head and major-like mandibles. Indeed, in *A. ferox*, the dealate queen mills seeds in the absence of the major, whereas minors never do so (Ito, unpublished). The distinct morphology of the ergatoid queen, especially in head, is likely determined with different capabilities for such tasks, and different production costs. Therefore, the presence of ergatoid queens instead of alate queens may affect the optimal allocation of colony members for DCF. It is hence worth

comparing the resource allocation in DCF from the point of view of the morphological diversification of the ergatoid queen, although direct observations of DCF are difficult (but see Chéron et al. 2011). These arguments cannot explain, however, why ergatoid queens are found in *Acanthomyrmex*. About three-fifths of all the known species of *Acanthomyrmex* have ergatoid queens (Table 3) although unpublished/unconfirmed data are included, and this contrasts with other speciose myrmicine genera such as *Pheidole*, *Crematogaster*, and *Carebara* in which no ergatoid queens are known (Peeters 2012). Future comparative evolutionary studies under a comprehensive phylogenetic framework are required to answer the questions.

Trophic ecology of *Acanthomyrmex careoscribis* in Ulu Gombak

Consistent with knowledge on the only sympatric congener *A. ferox* in Ulu Gombak (Gobin & Ito 2000), the number of fig seeds stored inside nests was highly variable, and nutrient redistribution via trophic eggs was observed in *A. careoscribis*. All female castes are probably able to produce trophic eggs, as known in *A. ferox*, although colonies with dealate queens were not studied here. Use of trophic eggs may be a common characteristic in *Acanthomyrmex* and associated with the unpredictable availability of seeds which are their principal food source.

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APPENDIX

Taxonomic accounts

Acanthomyrmex careoscrobis Moffett, 1986

Acanthomyrmex careoscrobis Moffett, 1986: 78, figs. 39A, 40 – 43, type: holotype (minor); type loc.: Malaysia, Sarawak, Gunung Mulu National Park (Collins N.M. col.; 14/iii/1978).

Type materials examined: Images of the holotype given in AntWeb (<https://www.antweb.org/specimen/CASENT0901703>) were examined.

Non-type materials examined: Nine colony series from Ulu Gombak (Selangor, Malaysia) were examined, i.e., 5 dealate queens, 8 ergatoid queens, 11 majors, 33 minors and 18 males (16 for male genitalia) in total. **Colony FI98-77**, 1 ergatoid queen, 3 minors, F. Ito col., 17/vii/1998, ACFI; **FI98-167**, 1 dealate queen, 1 major, 7 minors, F. Ito col., 24/vii/1998, ACFI; **FI99-418**, 1 dealate queen, 2 ergatoid queens, 1 major, 1 minor, 1 male, F. Ito col., 21/viii/1999, MCZC; **FI09-103**, 4 ergatoid queens, 1 major, 7 minors, 3 males, F. Ito col., 31/viii/2009, MHNG, AKYC; **FI09-121**, 2 majors, 9 minors, 1 dealate queen, 5 males, F. Ito col., 16/iii/2009, FRIM, AKYC; **FI11-78**, 1 dealate queen, 1 major, 2 minors, Y. Kitagawa col., 15/iii/2011, AKYC; **FI11-79**, 2 major, 3 minor, 1 males, F. Ito col., 15/iii/2011, FRIM; **FI11-88**, 1 ergatoid queen, 1 major, 3 males, F. Ito col., 17/iii/2011, AKYC; **FI13-83**, 1 dealate queen, 2 major, 5 minors, 5 males, S. Miyazaki col., iii/2013, MCZC.

DNA barcode: Barcode sequences are opened at INSD (LC312371 – LC312376 for CO1, LC312377 – LC312380 for ITS1). Maximal pairwise divergences (proportion of different sites) among the six COI sequences are 0.068 (based on 555bp). All of the four ITS1 sequences were completely identical when the sites with indels and ambiguous data were completely excluded (1004bp after the exclusion).

Description

Major: Figs. 1 – 3. *Structure.* Cranium in full-face view with posterior margin strongly and narrowly concave medially; dorsal margin in lateral view strongly raised dorsad in frons and faintly impressed in vertex. Frons and vertex medially with an inconspicuous narrow longitudinal sulcus accompanied with a shallow depression on vertex. Funicular scrobe conspicuous but short. Antennal scape when folded back not reaching midlength of cranium in full-face view. Median part of clypeus produced anteriorly, with anterior margin concave medially. Promesonotal suture present dorsally as a weak groove. Propodeal spine in lateral view broad, weakly downcurved at basal part, faintly upcurved near apex. Anterior peduncle of petiole in lateral view approximately a little longer than half length of entire petiole. Petiolar node in lateral view inverted V-shaped; in posterior view dorsal margin between dorsolateral angles concave; apical width measured between the angles approximately as large as or a little larger than basal width of the node. Postpetiolar tergite in lateral view just slightly convex without forming prominent dorsal uplift.

Sculpture. Dorsal and lateral faces of cranium foveolate-reticulate; foveae shallower and sparser on vertex and ventrolateral face than on frons where virtually reticulated; gena below antennal scrobe roughly reticulate. Pronotum smooth. Mesonotum with sparse large foveae. Mesopleuron, metapleuron, and lateral face of propodeum coarsely rugose. Petiole largely smooth. Postpetiolar tergite smooth on anterodorsal face and with two longitudinal rugae on lateral face (but often coarse and ambiguous).

Pilosity. Dorsal and lateral faces of cranium with relatively dense standing hairs. Clypeus with sparse standing hairs among short appressed hairs. Antennal scape with sparse standing hairs on leading edge and dorsoapical part. Pronotum with sparse, short appressed hairs, and just 1 – 2 standing hairs (a black arrow in Fig. 3) near dorsoposterolateral corner. Mesonotum with sparse standing hairs. Propodeal spine only with a few very short appressed hairs. Propodeal lobe with some standing hairs (white arrows in Fig. 3) on outer face. Outer faces of femur and tibia of each leg with sparse vertically standing hairs among short appressed hairs. Petiole with 1 – 3 standing hairs on lateral face, and 3 – 5 standing hairs on posterior slope of node. Postpetiolar tergite with 13 – 16 standing hairs. Abdominal tergite III with sparse standing hairs among short appressed hairs. Abdominal tergite IV with a sparse and transverse series of standing hairs near the posterior margin.

Measurement and indices. HW 2.03 – 2.27 mm; HL 2.43 – 2.73 mm; EL 0.21 – 0.27 mm; SL 0.97 – 1.05 mm; ML 0.55 – 0.68 mm; PdSL 0.49 – 0.62 mm; PL 0.60 – 0.69 mm; PH 0.44 – 0.52 mm; PPL 0.29 – 0.34 mm; PPH 0.39 – 0.47 mm; CI 82 – 88; EI 10 – 12; SI 44 – 50; PdSI 84 – 99; PI 131 – 141; PPI 72 – 77 (n = 11).

Minor (redescription based on specimens from Ulu Gombak; see also “Taxonomic remarks” below): Figs. 4 – 6. *Structure.* Cranium in full-face view with posterior margin strongly and broadly concave medially; posteroventral margin in lateral view faintly concave. Funicular scrobe absent. Anterior margin of the median part of clypeus with just two weak submedian processes from which oblique-longitudinal submedian ridge run backward (the ridge occasionally coarsely divergent or distorted). Antennal scape when folded back extending a little beyond posterolateral corner of cranium in full-face view; basal corner of leading edge of scape shaft (a black arrow in Fig. 4) not forming a conspicuous longitudinal lobe. Pronotal spine in lateral view short, faintly curved anteriorly. Propodeal spine in lateral view much longer than pronotal spine, entirely weakly downcurved. Anterior peduncle of petiole in lateral view approximately a little longer than half length of entire petiole. Petiolar node in lateral view inverted V-shaped; in posterior view dorsal margin between dorsolateral angles concave; apical width measured between the angles narrower than basal width of the node. Postpetiolar tergite in lateral view just slightly convex without forming prominent dorsal uplift.

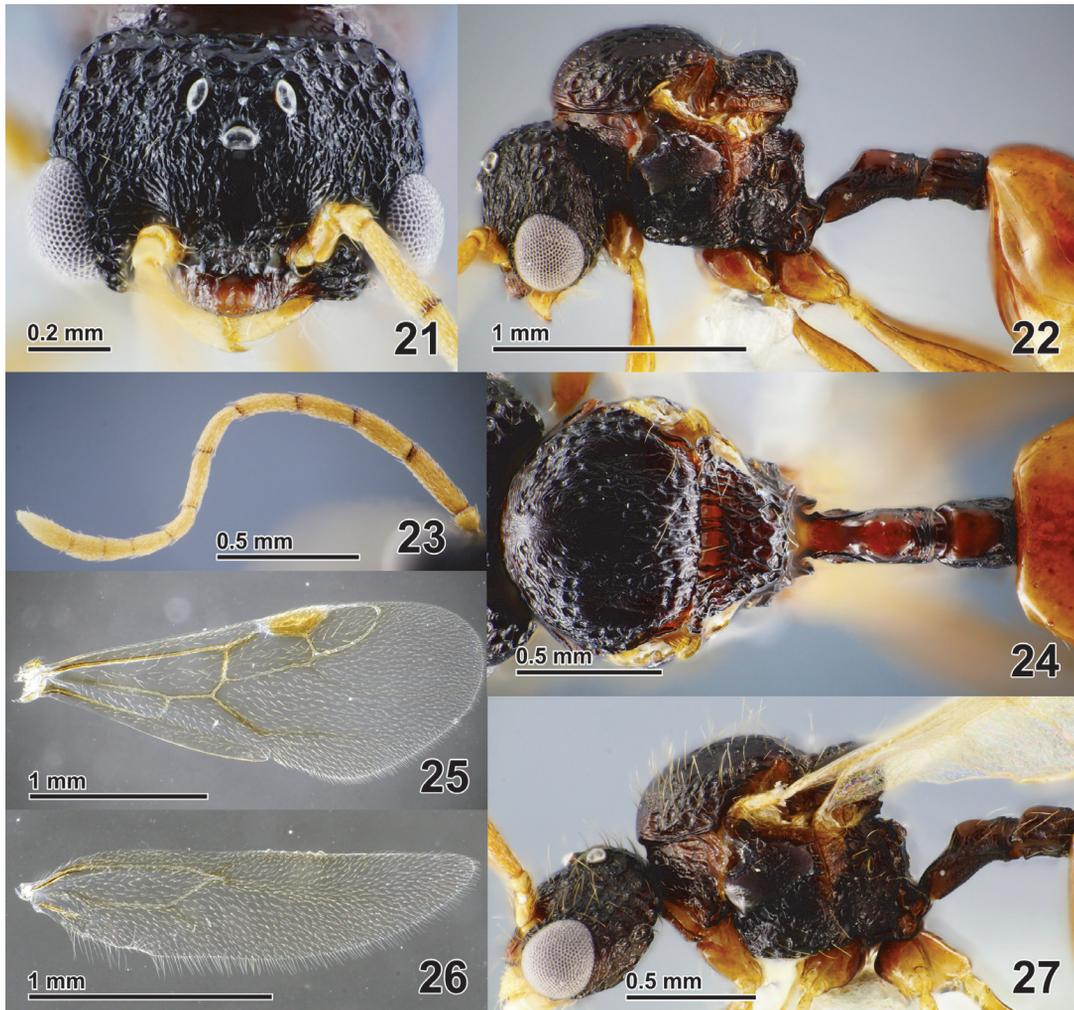
Sculpture. Dorsal and lateral faces of cranium, anterodorsal and lateral faces of promesonotum foveolate-reticulate; remaining face of mesosoma (except for posterior face of propodeum) with rugae which run longitudinally in dorsal part but become irregularly in ventral part of lateral face. Petiole largely smooth. Postpetiolar tergite smooth on anterodorsal face, and with two longitudinal rugae on lateral face.

Pilosity. Dorsal and lateral faces of cranium with relatively dense standing hairs. Area between two submedian ridges of clypeus without standing hairs except for a long and thick median seta on the anterior margin. Antennal scape with sparse standing hairs among short appressed hairs on leading edge and dorsoapical part. Dorsolateral face of pronotum and dorsum of promesonotum with sparse standing hairs. Pronotal spine with a few short appressed hairs and 2 – 3 standing hairs. Propodeal spine without standing hairs but with a few short appressed hairs. Propodeal lobe with a few standing hairs on outer face. Outer faces of femur and tibia of each leg with sparse vertically standing hairs among short appressed hairs. Petiole with 1 – 2 standing hairs on lateral face and two standing hairs on posterior base of node. Postpetiolar tergite with 7 – 10 standing hairs. Abdominal tergite III with sparse standing hairs among short appressed hairs. Abdominal tergite IV with a sparse and transverse series of standing hairs near the posterior margin.

Measurement and indices. HW 1.03 – 1.14 mm; HL 0.95 – 1.01 mm; EL 0.17 – 0.20 mm; SL 0.89 – 0.94 mm; ML 0.41 – 0.47 mm; PnSL 0.22 – 0.25 mm; PdSL 0.43 – 0.48 mm; PL 0.42 – 0.46 mm; PH 0.33 – 0.37 mm; PPL 0.20 – 0.23 mm; PPH 0.24 – 0.27 mm; CI 108 – 114; EI 17 – 18; SI 83 – 88; PnSI 51 – 60; PdSI 99 – 113; PI 120 – 133; PPI 77 – 90 (n = 8).

Alate queen: Figs. 7 – 10 (wings not examined). *Structure.* Cranium in full-face view with posterior margin weakly and broadly concave medially. Frons with a weak narrow median longitudinal sulcus running backward from posterior clypeal margin and ending at the fovea encircled median ocellus. Vertex medially with shallow depression. Funicular scrobe conspicuous but short. Mesoscutellum in lateral view roundly raised posterodorsad without prominent tapering posteriorly; its dorsal outline not exceeding imaginary line tangent to dorsal outline of mesoscutum. Mesoscutellum in dorsal view subtrapezoidal, with posteromedian margin weakly concave. Propodeal spine in lateral view, almost straight, faintly upcurved at apex. Petiole and postpetiole mostly as in the major.

Sculpture. Dorsal and lateral faces of cranium entirely foveolate-reticulate. Pronotum smooth with a few foveae. Mesoscutum with submedially rugose-foveolate. Mesoscutellum with sparse large foveae. Mesopleuron largely smooth just with some large foveae. Metapleuron and lateral face of propodeum coarsely rugose. Petiole and postpetiole as in the major.



Figs. 21 – 27. Male body of *Acanthomyrmex careoscrobis*. (21–26) FI09-121. (21) Head in full-face view. (22) Body in lateral view. (23) Antennal funiculus in dorsal view. (24) Mesosoma and metasoma in dorsal view. (25) Forewing. (26) Hindwing. (27) A example of variation on the pilosity, FI09-103, body in lateral view: this variation also occurs in the FI09-121.

Pilosity. Cranium, antenna, clypeus, and pronotum as in the major. Mesoscutum, mesoscutellum with sparse standing hairs. Katepisternum, metapleuron, and lateral face of propodeum with a few standing hairs respectively. Propodeal spine with 1 – 3 standing hairs and a few very short appressed hairs. Propodeal lobe and legs as in the major. Petiole with 2 – 5 standing hairs on lateral face, and 2 – 7 standing hairs on posterior slope of the node. Postpetiolar tergite with 19 – 21 standing hairs. Abdominal tergite III and IV as in the major.

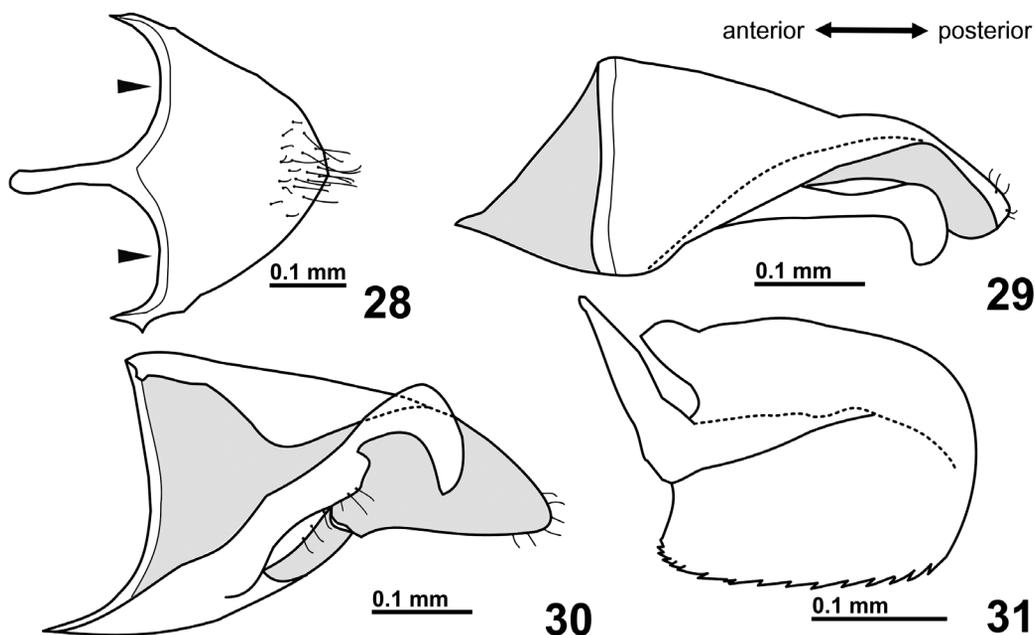
Measurement and indices. HW 1.86 – 2.00 mm; HL 1.72 – 1.84 mm; EL 0.27 – 0.31 mm; OL 0.08 – 0.10 mm; SL 0.93 – 1.03 mm; ML 0.93 – 1.00 mm; PdSL 0.63 – 0.67 mm; PL 0.70 – 0.77 mm; PH 0.46 – 0.54 mm; PPL 0.33 – 0.37 mm; PPH 0.47 – 0.54 mm; CI 108 – 111; EI 14 – 15; OI 4 – 5; SI 49 – 56; PdSI 66 – 72; PI 140 – 153; PPI 66 – 70 (n = 5).

Ergatoid queen: Figs. 11 – 19. See “External morphology of ergatoid queens” above.

Measurement and indices. HW 1.94 – 2.18 mm; HL 2.08 – 2.54 mm; EL 0.23 – 0.28 mm; OL 0.06 – 0.08 mm; SL 0.94 – 0.99 mm; ML 0.62 – 0.73 mm; PdSL 0.50 – 0.64 mm; PL 0.64 – 0.72 mm; PH 0.45 – 0.51 mm; PPL 0.26 – 0.33 mm; PPH 0.40 – 0.55 mm; CI 84 – 94; EI 12 – 14; OI 2 – 4; SI 47 – 51; PdSI 74 – 98; PI 132 – 145; PPI 46 – 81 (n = 7 for OL and OI, n = 8 for the others).

Male: Figs. 21 – 31. *Color.* Body dark brown to black; antennae, mandibles, legs and gaster yellowish.

Structure. Cranium in full-face view subrectangular, wider than long, with posterior margin slightly and broadly concave. Frontal carina virtually absent or present just as rugulae. Antennal scrobe present as a short, broad and shallow depression. Median part of clypeus produced anteriorly, with anterior margin weakly convex. Antennal scape very short, when folded back, not reaching transverse line spanning the posteriormost points of compound eyes. Antennal segment II almost as long as broad, much shorter than antennal scape; III – VIII much longer than broad; III longest, slightly flattened dorsoventrally, in dorsal view with almost straight lateral outline; IV – VIII almost same



Figs. 28 – 31. Male genitalia of *Acanthomyrmex careoscrobis*. (28) Abdominal sternite IX, in ventral view. (29) Paramere, right side, in dorsal view. (30) Paramere, right side, in inner view. (31) Penisvalva, left side, in outer view.

length; each of them longer than IX; each of IV – VII slightly to weakly bent; VIII almost straight or slightly bent; IX – XII almost same length; IX relatively strongly bent; XIII a little longer than IX, almost as long as VIII. Masticatory margin of mandible with 3 – 4 distinct teeth between a relatively large apical tooth and basal angle. Mesoscutellum in lateral view roundly raised posterodorsad, in dorsal view subtrapezoidal with posteromedian margin almost straight. Posterodorsolateral part of propodeum with a short lobate process directed posteroventrad. Venation of wings as in Figs. 25 – 26. Petiolar node in lateral view very low and weakly roundly raised, in posterior view with its dorsal margin almost straight; posterior slope behind the apex of node very gently descend. Dorsal margin of postpetiolar tergite in lateral view almost straight.

Sculpture. Cranium weakly and coarsely foveolate-reticulate. Pronotum largely smooth. Mesoscutum coarsely microrugose, and overlaid with relatively shallow and irregular foveae on the submedian face. Mesoscutellum coarsely reticulate. Anepisternum relatively smooth, but weakly microreticulate on posterior part. Katepisternum coarsely and irregularly reticulate. Metapleuron and lateral face of propodeum coarsely and irregularly rugose-reticulate. Petiole and postpetiolar tergite largely smooth, but weakly and coarsely rugose on a part of lateral face.

Pilosity. Highly variable among individuals even in a single colony: cranium, dorsum of mesosoma, abdominal tergite III with few standing hairs (Fig. 22), or with standing and/or decumbent hairs relatively dense (Fig. 27); femur and tibia of each leg with sparse decumbent hairs but with few standing hairs, or with sparse decumbent to standing hairs; petiole and postpetiole with few hairs (Fig. 22), or with several decumbent to standing hairs (Fig. 27).

Genitalia. Pygostyle digitiform with long hairs on the apical half. Abdominal sternite IX (Fig. 28) a little wider than long to a little longer than wide (including spiculum); spiculum long, 0.37 – 0.51 times as long as entire length of the sternite IX when spiculum length measured from transverse line spanning the posteriormost points of each anterolateral margin (black arrows in Fig. 28); posterior part gently tapering posteriad, forming lobe subparabolic in outline, with several short to long hairs on outer face of apical part of the lobe. Cupula wider than long. Paramere with acute gonostipital arm, in lateral view with distinctly concave ventral outline around the articulation between basimere and telomere (Fig. 29 – 30). Telomere in lateral view longer than high. Cuspis virtually absent or present just as small lobe in inner lateral view. Digitus in lateral view long, with round apex, entirely downcurved and necked basally. Valviceps in lateral view almost as long as wide and gently tapering posteriad, forming a broadly rounded apex; anteroventral corner weakly produced anteriad; ventral margin with 11 – 18 denticles (Fig. 31).

Measurement and indices. HW 0.94 – 1.02 mm; HL 0.66 – 0.70 mm; EL 0.32 – 0.34 mm; OL 0.07 – 0.09 mm; SL 0.13 – 0.16 mm; ML 0.55 – 0.64 mm; PL 0.42 – 0.48 mm; PH 0.19 – 0.23 mm; PPL 0.20 – 0.26 mm; PPH 0.20 – 0.24 mm; PPW 0.20 – 0.22; CI 137 – 145; EI 33 – 35; OI 8 – 9; SI 14 – 16; PI 204 – 224; PPI 96 – 117 (n = 5).

Taxonomic remarks: The minor from Ulu Gombak was differentiated from the holotype (minor) from Gunung Mulu National Park (given in AntWeb: <https://www.antweb.org/specimen/CASENT0901703>) as follows: the former has normal standing hairs on the abdominal tergite III (gastral tergite I) and IV, but the latter lacks these; the former has a little shorter pronotal spine (PnSI 51 – 60) and more elongate petiole (PI 120 – 133) than the latter (PnSI 65; PI 110).

