

Workers, soldiers, and gynes – morphometric characterization and description of the female castes of *Camponotus singularis* (Smith, 1858) (Hymenoptera, Formicidae)

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Abstract

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Species of *Camponotus* Mayr, 1861 show a high variation of worker caste numbers, from a monomorphic worker caste to strong polymorphism along a continuous range of worker sizes or true worker dimorphism. *Camponotus singularis* (Smith, 1858) is used as a model for a *Camponotus* species with two very distinct worker castes (minors and majors) which are chiefly defined by morphometric data. We investigated shifts in proportions of *C. singularis* female castes in order to identify major allometric patterns useful for characterizing caste differences in this species as well as in other Camponotini. We describe the main morphological traits which are characteristic for the respective morphs. The major worker, or “soldier”, shows many characteristics which deviate from the minor worker, but also from the alate gyne. Its traits are presumably modified for its function in nest defence. Morphometric data clearly set Bornean specimens of *Camponotus singularis* (described as var. *rufomaculatus* Donisthorpe, 1941) apart from specimens with other proveniences, suggesting that this island population is a distinct species.

Introduction

Within the eight recent genera of the tribe Camponotini (Blaimer et al. 2015, Ward et al. 2016), the worker caste is developed in a variety of forms, comprising species with monomorphic (e.g., *Polyrhachis* Smith, 1857; Dorow 1995), continuously polymorphic (e.g., some species of *Camponotus* Mayr, 1861; Wilson 1953, Busher et al. 1985) and dimorphic workers (e.g., *Colobopsis* Mayr, 1861). Even the most speciose genus, *Camponotus*, exhibits all known types of worker polymorphism: from species with monophasic allometry to those with true worker dimorphism (Wilson 1953).

During our ongoing revision of the *Colobopsis cylindrica* group, which includes a morphometric analysis of species, a review of previous publications revealed multiple mentions of poly- or dimorphism in workers of Cam-

ponotini (e.g., Wilson 1953, Baroni Urbani 1974, Busher et al. 1985), but a comparatively small number of more recent studies focusing on morphometry (e.g., Diniz-Filho et al. 1994, Rakotonirina et al. 2016).

We herein present morphometric data on the Asian species *Camponotus singularis* (Smith, 1858), a large-bodied species with a wide distribution from Nepal to Borneo and Java (e.g., Smith 1858, Chapman and Capco 1951, Thapa 2000, Jaitrong and Nabhitabata 2005, Guénard and Dunn 2012, Bharti et al. 2016). We have chosen this taxon, because it serves as an example of a species with a clear worker dimorphism, most apparently characterized by the size and shape of the head, and without the occurrence of intermediate phenotypes. We describe the differentiating characters of the two worker castes (minors, majors) and compare them to the corresponding characters of the gynes (see Figs 1–6). Molet



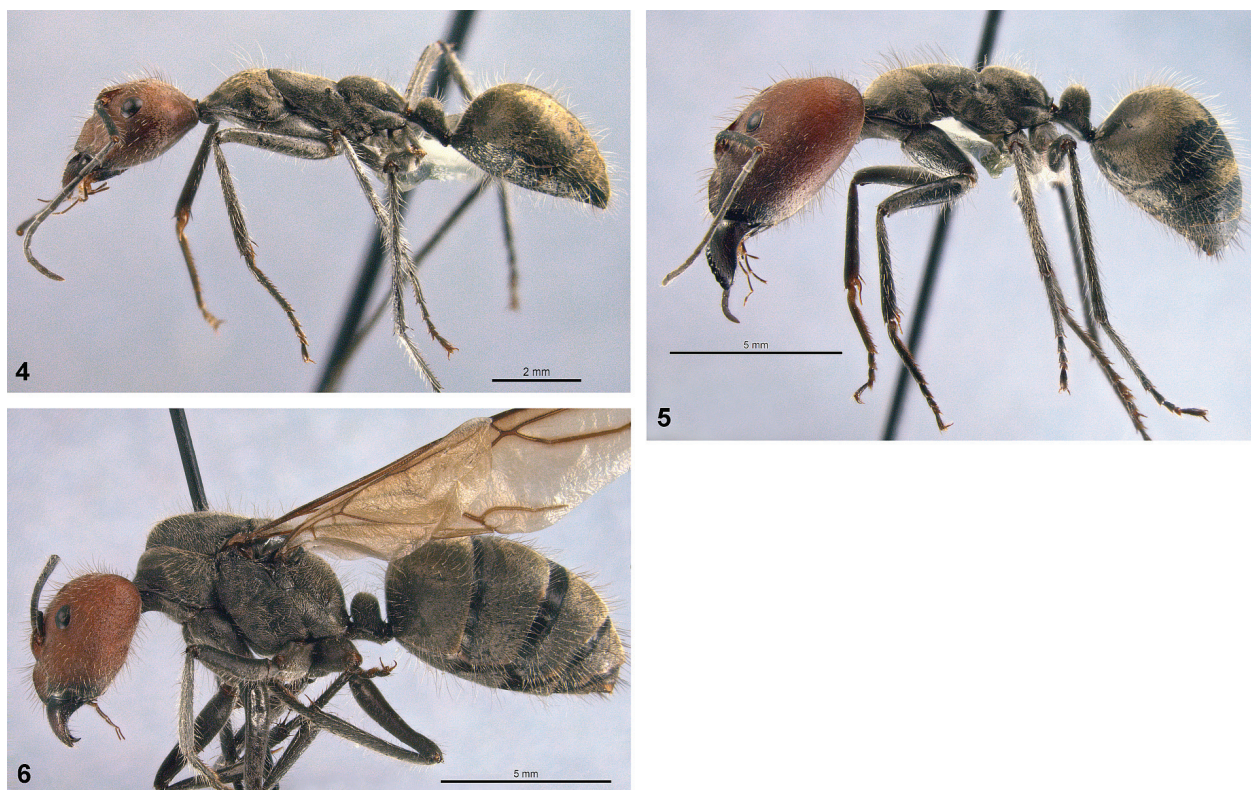
Figures 1–3. *Camponotus singularis*, head, frontal view, of (1) minor worker, (2) major worker, and (3) gyne. Notably different are head shape, development of posterior margin, and position of eyes. The minor has much longer scapes and maxillary palpi than the major.

et al. (2012, 2014) interpret specialized castes as mosaics of pre-existing phenotypes with novel or “recycled” developmental pathways. Building on this evolutionary model, we aim to characterize major and minor workers as two distinct subcastes based on their morphological proportions. Although morphometric differences in Camponotini may vary from clade to clade, within this study we attempt to identify representative caste-specific allometric patterns which may not only be applicable to the dimorphism of *C. singularis* but also serve to characterize caste-polymorphism in other camponotine ants.

Material and methods

Specimen depositories

BMNH	Natural History Museum, London, United Kingdom
CAS	California Academy of Sciences, San Francisco, USA
CZW	Coll. H. Zettel, Vienna, Austria
MCSN	Museo Civico di Storia Naturale Giacomo Doria (main collection and Carlo Emery’s collection), Genova, Italy



Figures 4–6. *Camponotus singularis*, lateral view, of (4) minor worker, (5) major worker, and (6) gyne. Notable are differences between the worker subcastes regarding head size, mesosoma height, and petiole shape. Mesosoma and gaster of the gyne are strongly enlarged for flight and reproduction.

NHMW	Natural History Museum Vienna, Austria
SKYC	Sk. Yamane Collection, Korimoto, Japan
THNHM	Thailand Natural History Museum, Phatumthani, Thailand
VNMN	Vietnam National Museum of Nature, Hanoi, Vietnam

Material examined

We measured specimens from most parts of the distribution area of *C. singularis*, except from Nepal and India. In total five gynes, ten major workers and 85 minor workers of *C. singularis*, as well as five minor workers and one gyne of *C. singularis* var. *rufomaculatus* Donisthorpe, 1941 were examined. During data processing we noticed that specimens from Borneo differed clearly from specimens collected in other localities. Consequently, we removed Bornean specimens from our in-depth analysis of morphs, but present some data on how to differentiate this population.

Camponotus singularis, typical form: **Myanmar:** 1 minor worker (BMNH), Mandalay Region, Pyin U Lwin, ca. 900 m a.s.l., V.1899, coll. Bingham [*Camponotus camelinus* Smith, Upper Burma Maymya, 3000 ft, 5.1899, Bingham coll.]; 1 major worker, 1 minor worker (MCSN), Kayin State, mountains east of Toungoo [Carin Cheba], 900–1100 m a.s.l., V.1888, leg. L. Fea; 1 minor worker (MCSN), Kayin State, Kawkaeret, I–II.1887, leg. L. Fea; 1 major worker, 2 minor workers (MCSN, NHMW), Kayin

State, [“Tenasserim”], Thagata, IV.1887, leg. L. Fea; 1 minor worker (MCSN), Tanintharyi Region, [“Tenasserim”], Malewoun, VII–VIII.1887, leg. L. Fea. – **Thailand:** 1 minor worker (BMNH), Chiang Mai [Chiengmai], 19.I.1936, Lot 317/94; 1 minor worker (NHMW), Thailand, Satun Province, Thale Ban National Park, 10–16. III.1993, leg. M. Madl; 1 minor worker (BMNH), Pattani Province, Bukit Besar near Amphoe Nong Chik (for interpretation see Woodley 2012), ca. 900 m a.s.l., 1903, leg. Annandale & Robinson [Bulsit [sic!] Besar, Siam: Malay States, No. 12, 3000’, Annandale & Robinson, Siamese Malay States 1903–127, *Camponotus camelinus* Sm. Donisthorpe det.]; 1 minor worker (THNHM), Chiang Rai Province, Mae Pha Laung District, 20.VI.2002, leg. W. Jaitrong; 1 minor worker (THNHM), Pattalung Province, Khao Pu – Khao Ya National Park, Reang Tong Waterfall, evergreen forest, 28.IX.2007, leg. P. Kosonpanyapiwat; 1 minor worker (THNHM), Ranong Province, Khlong Naka Wildlife Sanctuary, evergreen forest, 12.VIII.2009, leg. W. Jaitrong. – **Laos:** 6 minor workers (NHMW), Luang Nam Tha Province, 5–10 km SW of Muang Sing, 600 m a.s.l., 11.VI.1996, leg. H. Schillhammer (#23); 1 major worker (NHMW), Luang Nam Tha Province, ca. 20 km SE of Muang Sing, 950 m a.s.l., 12–13.VI.1996, leg. H. Schillhammer (#25); 1 major worker (NHMW), Luang Nam Tha Province, ca. 10 km E of Muang Sing, 600 m a.s.l., 19.VI.1996, leg. H. Schillhammer (#32); 1 major worker, 40 minor workers (CZW), Hua Phan Province, Ban Saleui, Phou Pan (Mt.), 1300–1900 m a.s.l., 20°12’N 104°01’E,

7–29.IV.2014 (various dates), leg. C. Holzschuh. – **Vietnam**: 1 minor worker (VNMN), Lao Cai Province, Van Ban, ca. 150 m a.s.l., 4.VI.2005, leg. B.T. Viet (#Code I). – **West Malaysia**: 1 minor worker (CZW), West Malaysia, Kelantan, 60 km NE Tanah Rata, Tanah Kerajaan, 1000 m a.s.l., 12–30.IV.2007, leg. P. Cechovsky; 3 minor workers (CZW), West Malaysia, Kelantan, 30 km NW Gua Musang, Ulu Lalat, Kpg. Sungai Om, 800–1000 m a.s.l., 21.VI.–14.VII.2010, leg. P. Cechovsky; 2 minor workers (CZW), West Malaysia, Perak, 25 km NE Ipoh, Banjaran Titi Wangsa mts., Korbu (Mt.), 1200 m a.s.l., 11.–16. I.1999, leg. P. Cechovsky; 1 major worker, 8 minor workers (CZW), West Malaysia, Perak, 30 km SE Ipoh, Cameron Highland, Ringlet, 900 m a.s.l., 25.IV.–5.VI.2001, leg. P. Cechovsky; 1 minor worker (CZW), West Malaysia, Perak, 40 km SE Ipoh, Banjaran Titi Wangsa mts., Ringlet, 900 m a.s.l., 25.III.–3.IV.2002, leg. P. Cechovsky. – **Indonesia**: 2 minor workers (NHMW), Sumatra (#877-2); 1 minor worker (NHMW), Sumatra, 1875, leg. Plason; holotype minor worker (BMNH), Java (# 55, 39), “*F. singularis* Sm., Type”, CASENT0903554; 5 alate gynes (NHMW), Java, leg. Adensamer; 1 major worker, 1 minor worker (NHMW), Java, leg. Vollenhov; 1 minor worker (NHMW), Java, 1874, leg. Plason; 2 minor workers (MCSN), Java, Kota Bogor [Buitenzorg], 1875, leg. G.B. Ferrari; 1 minor worker (MCSN), Java, Kota Bogor [Buitenzorg], IV.1876, leg. Beccari; 1 major worker (SKYC), Java, Kota Bogor, 3–5.XI.1985, leg. Sk. Yamane; 1 minor worker (SKYC), Java, G. Sarak, near Kota Bogor, 8.III.1997, leg. Sk. Yamane; 1 minor worker (CAS), Java, Kota Bogor, Botanical Gardens, 16.XII.1978, leg. E. S. Ross. – **Unknown localities**: 1 major worker, 1 minor worker (NHMW), coll. Felder; 1 major worker (NHMW), unknown collector.

Camponotus singularis var. *rufomaculatus*: **East Malaysia (Borneo)**: 2 minor workers (MCSN), Sarawak, 1865–1866, leg. G. Doria; 1 minor worker (SKYC), Sabah, Crocker Range, Inobong (forest), 500–600 m a.s.l., 26.II.2008, leg. Sk. Yamane; 1 dealate gyne (SKYC), Sabah, Sipitang, Muaya Forest Reserve, 700 m a.s.l., 28.VIII.2012, leg. Sk. Yamane; 1 minor worker (SKYC), Sarawak, Kubah National Park, 5.XII.1993, leg. Sk. Yamane; 1 minor worker (SKYC), Sarawak, Engkari, Ubah Ribu, 23.IV.1994, leg. K. Het.

Examined specimens were either pinned or dry mounted on card squares or triangles. Examination and measurements of specimens were carried out with a Nikon SMZ1500 binocular microscope at magnifications of up to 256 \times .

Measurements and indices

TL	Total length. The added lengths of head (including mandibles), mesosoma, petiole, and gaster.
HW	Head width. Maximum width of head in full-face view, excluding eyes if laterally protruding (few minor workers).
HL	Head length. Maximum length of head in full-face view, excluding mandibles, measured parallel to midline from anterior-most point of cly-

peus to midpoint of occipital margin (in minor workers) or to midpoint of an imaginary line connecting the apices of posterior projections (major workers and some gynes).

HS	Head size. $(HW+HL) / 2$.
EL	Eye length. Maximum diameter of compound eye.
SL	Scape length. Maximum length of antennal scape in dorsal view excluding basal neck and condyle.
ML	Mesosoma length. Measured laterally from anterior surface of pronotum proper (excluding collar) to posterior extension of propodeal lobes.
PH	Petiole height. Maximum height of the petiole in lateral view, measured from ventral-most point of petiolar sternum to dorsal apex.
PL	Petiole length. Maximum length of petiole in lateral view, measured from inflexion point of anterior constriction to posterior margin.
NH	Node height. Height of petiolar node, measured laterally, from the intersection point of the axes of maximum height and length to dorsal apex.
FeL	Femur length. Maximum length of hind femur, measured from base to apex.
PS5	Length of maxillary palp segment 5, measured from base to apex.
PS6	Length of maxillary palp segment 6, measured from base to apex.
CI	Cephalic index. $HW / HL \times 100$.
SI	Scape index. $SL / HW \times 100$.
EI	Eye Index. $EL / HW \times 100$
PI	Petiole Index. $PH / PL \times 100$
FeI	Femur Index. $FeL / HW \times 100$
PSI	Palp Segment Index. $(PS5+PS6) / HS \times 100$

All measurements are in millimetres and separated by caste. Due to the condition of some specimens, not all measurements were taken from all animals. Measurements of minor workers include the holotype (plotted separately in Figs 9, 12, 14). The total number of specimens measured is given for each morph (n), deviating numbers for individual characters are written in parentheses. The raw data set of all measurements is available as an electronic supplement (Suppl. material 1).

Digital photos were taken with a Leica DFC camera attached to a Leica MZ16 binocular microscope with the help of Leica Application Suite V3, and stacked with ZereStacker 64-bit. Processing of images was performed with Adobe Photoshop 7.0.

Results

Dimorphism of workers of *Camponotus singularis* (typical form):

Body size:

Measurements: alate gynes (n = 5): TL 18.42–20.48 (4); ML 6.52–6.78; major workers (n = 10): TL 16.76–19.57; ML 5.22–6.07; minor workers (n = 85): TL 9.26–15.39; ML 3.85–5.28 (84).

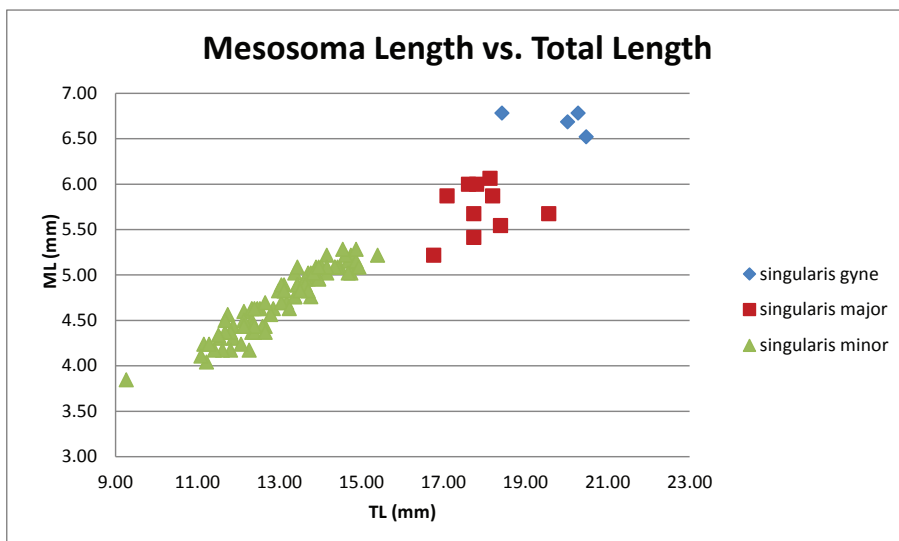


Figure 7. Distribution of mesosoma length (ML) in relation to total length (TL) in gynes, majors and minors of *Camponotus singularis*.

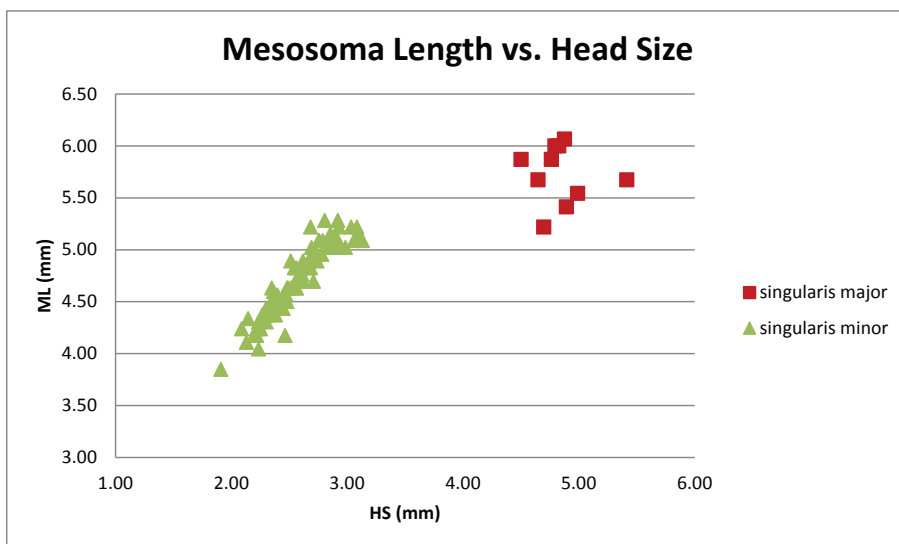


Figure 8. Distribution of mesosoma length (ML) in relation to head size (HS) in majors and minors of *Camponotus singularis*.

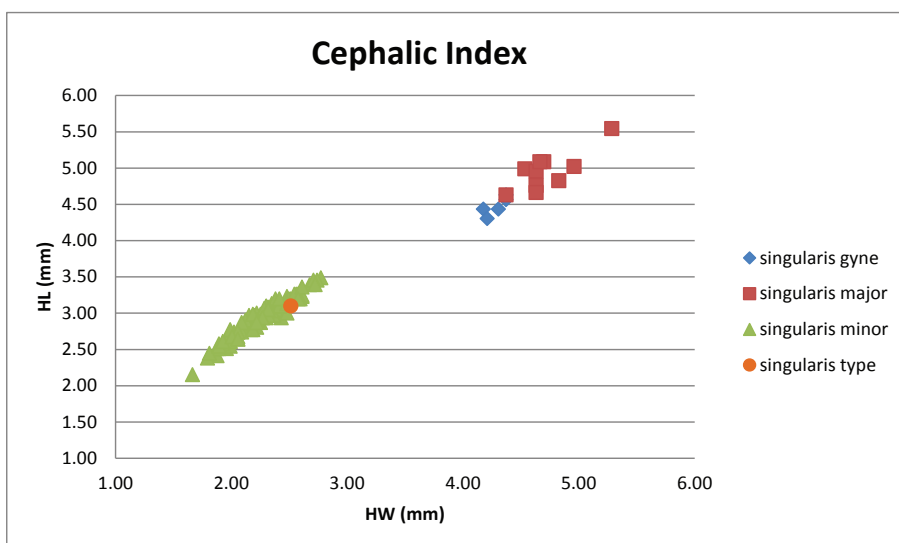


Figure 9. Distribution cephalic index (CI) in gynes, majors and minors of *Camponotus singularis*, holotype minor worker plotted separately.

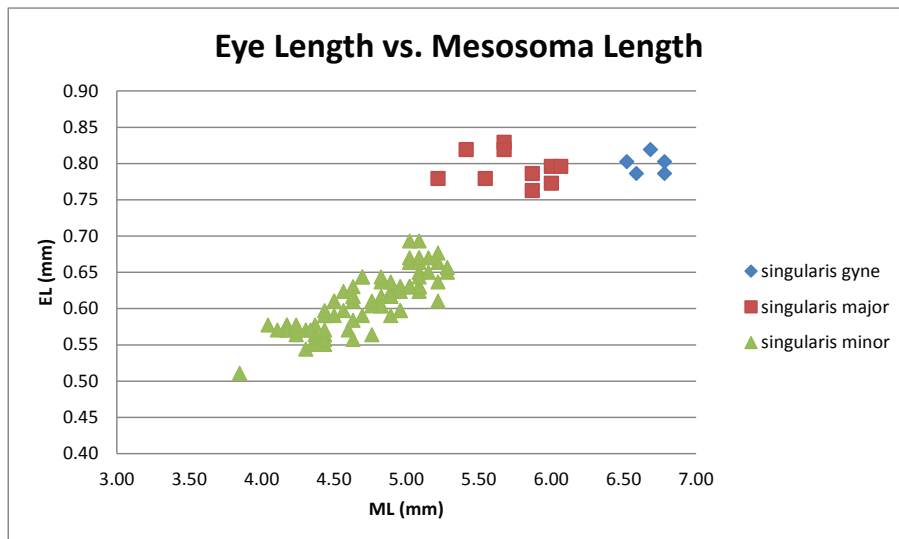


Figure 10. Distribution of eye length (EL) in relation to mesosoma length (ML) in gynes, majors and minors of *Camponotus singularis*.

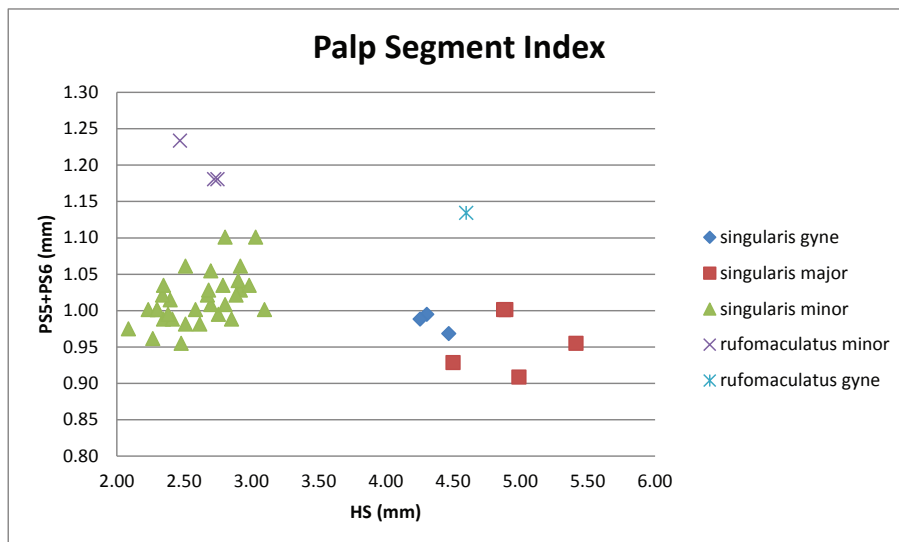


Figure 11. Distribution of maxillary palp segment index (PSI) in gynes, majors and minors of *Camponotus singularis*, as well as minors and gyne of var. *rufomaculatus*.

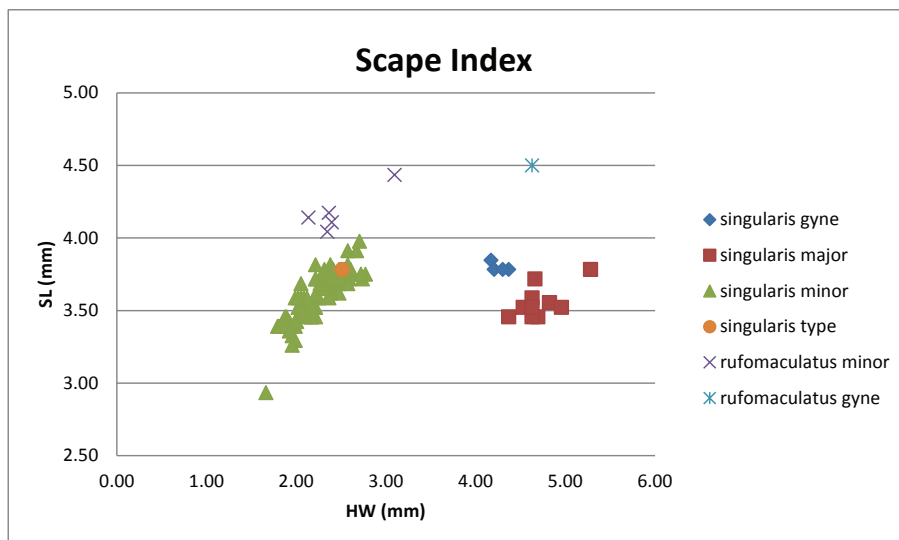


Figure 12. Distribution of scape index (SI) in gynes, majors and minors of *Camponotus singularis* (holotype minor worker plotted separately), as well as minors and gyne of var. *rufomaculatus*.

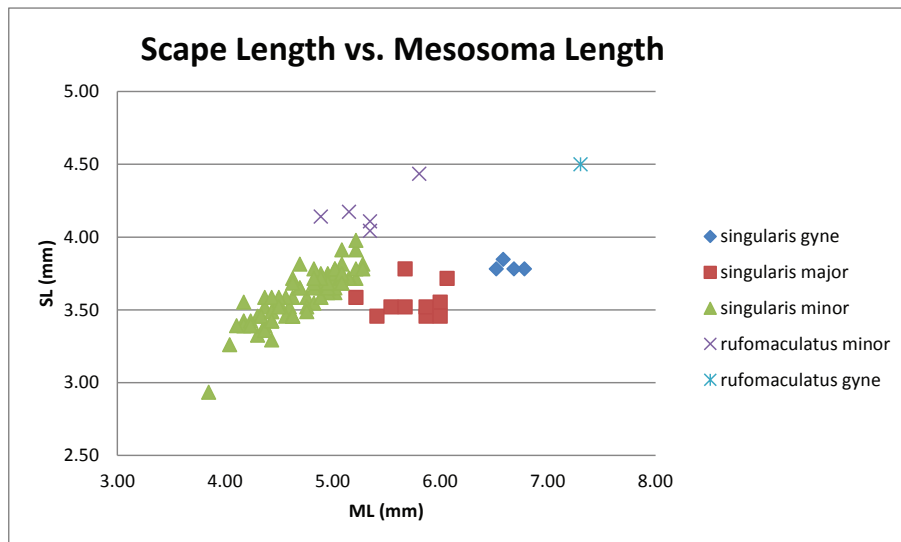


Figure 13. Distribution of scape length (SL) in relation to mesosoma length (ML) in gynes, majors and minors of *Camponotus singularis*, as well as minors and gyne of var. *rufomaculatus*.

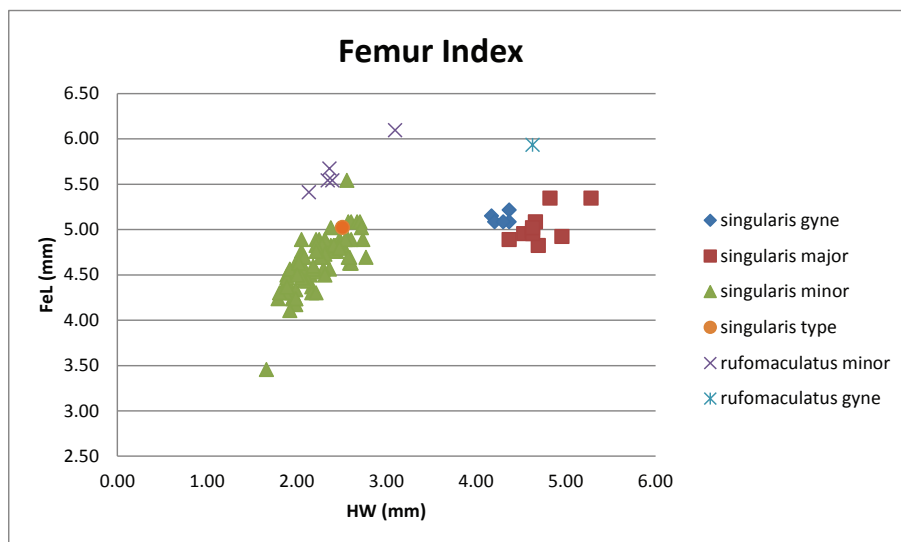


Figure 14. Distribution of femur index (FeL) in gynes, majors and minors of *Camponotus singularis* (holotype minor worker plotted separately), as well as minors and gyne of var. *rufomaculatus*.

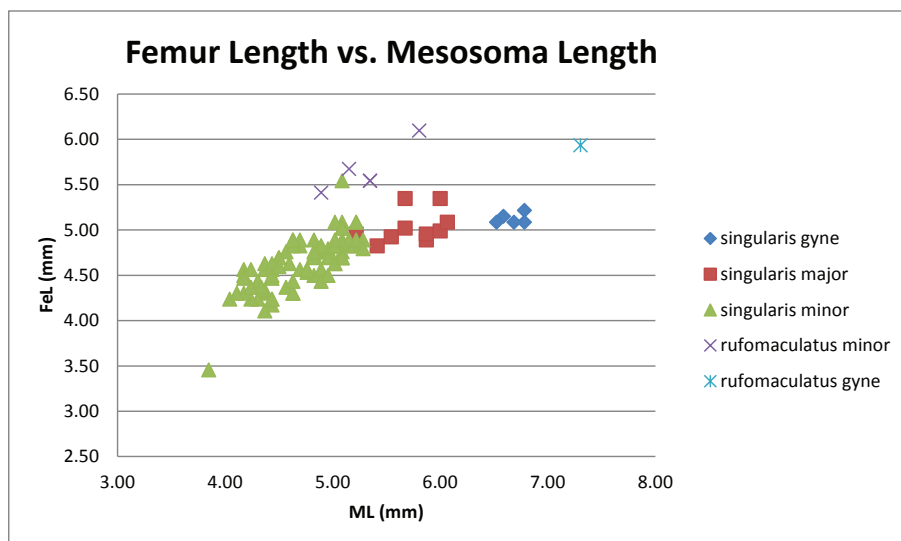


Figure 15. Distribution of femur length (FeL) in relation to mesosoma length (ML) in gynes, majors and minors of *Camponotus singularis*, as well as minors and gyne of var. *rufomaculatus*.

We used two measurements to describe body size, total length (TL) and mesosoma length (ML). Although traditionally used in myrmecology to facilitate rough comparisons of castes and species, total length strongly depends on the condition of the specimen (e.g., dilation or shrinking of the gaster from storage in alcohol or the drying process) so that TL can be relatively inaccurate. In *C. singularis* TL and ML are directly proportional in all female castes (Fig. 7). We therefore use ML as the main measurement for overall body size. There are two distinct subcastes of workers, minors and majors, which strongly differ in size range. Size variation is considerable in minors, whereas majors and gynes are more uniform in size (Fig. 7).

Head size and head shape:

Measurements: alate gynes (n = 5): HW 4.17–4.37; HL 4.30–4.63; HS 4.26–4.50; CI 94–98; major workers (n = 10): HW 4.37–5.28; HL 4.63–5.54; HS 4.50–5.41; CI 91–100; minor workers (n = 85): HW 1.66–2.77; HL 2.15–3.49; HS 1.91–3.13; CI 72–83.

HW and HL were measured. In relation to body size, head size (HS) is strongly disproportional in the two worker castes (Fig. 8). Major workers have a notably large head. The heads of gynes are also large, but on average less wide compared to major workers (Fig. 9).

The three castes differ considerably in head shape (Figs 1–3). In minor workers the ovate head is rounded posterior of the eyes, with a short, protruding collar; the narrow margin is dorsomedially depressed, and dorso-laterally slightly upcurved. In major workers the head is heart-shaped and posteriorly deeply concave. In gynes the head is slightly narrower than in majors and posteriorly almost straight. Furthermore, in both majors and gynes no collar or occipital margin is developed.

Eye size and eye position:

Measurements: alate gynes (n = 5): EL 0.79–0.82; EI 27–28; major workers (n = 10): EL 0.76–0.83; EI 23–27; minor workers (n = 85): EL 0.51–0.69; EI 36–46.

Eye size in minor workers is strongly correlated with body size (ML) (Fig. 10), and eyes appear smaller in majors since these workers have disproportionally large heads. In comparison to HW, the eyes of gynes are larger than those of major workers (EI 27–28 vs. 23–27).

In minor workers the eyes are dorsolaterally located, close to the lateral outline of the head in frontal view (Fig. 1). In contrast, the eyes of majors and gynes are shifted dorsally and placed approximately equidistant from the sides of the head and the frontal carinae (Figs 2, 3).

Ocelli:

Minor workers do not possess ocelli or other structures in their place. In one major worker from Myanmar we observed three reduced ocelli, whereas many other majors have small depressions or scars at these positions.

Clypeus shape:

The clypeus is similarly shaped in major and minor workers, whereas the medial protrusion is slightly longer in gynes (Figs 1–3). In major workers the lateral emarginations of the foremargin are wider than in minors to accommodate the thick bases of the mandibles.

Mandibles:

The mandibles of majors are much stouter than those of minors, especially in the basal half. The mandibles of gynes are of intermediate shape.

Maxillary palpi:

Measurements: alate gynes (n = 3): PS5 0.50–0.52; PS6 0.46–0.47; PSI 22–23; major workers (n = 5): PS5 0.49–0.54; PS6 0.42–0.48; PSI 18–21; minor workers (n = 32): PS5 0.52–0.60; PS6 0.42–0.50; PSI 32–47.

The maxillary palpi of minors are much longer in relation to HS than those of majors and gynes (PSI 18–23 in majors and gynes vs. 32–47 in minors; Fig. 11; see also Figs 1, 2). As palpi are very often obscured or damaged in mounted specimens, examination of this character was only possible in a small number of animals.

Antenna:

Measurements: alate gynes (n = 4): SL 3.78–3.85; SI 87–92; major workers (n = 10): SL 3.46–3.78; SI 71–80; minor workers (n = 83): SL 2.93–3.98; SI 135–189.

The antennae of majors and gynes are relatively shorter and thicker than those of minors. The scape index (SI) differs considerably (Fig. 12), but in relation to body size (ML), scape length is only slightly smaller in majors than in minors (Fig. 13).

Mesosoma shape:

The mesosoma of majors is slightly more robust (wider and higher) than that of minors, though no morphometric data were recorded except ML. Gynes always possess a well-developed flight apparatus, and their mesosoma morphology is strongly modified accordingly.

Leg length:

Measurements: alate gynes (n = 5): FeL 5.09–5.22; FeI 116–123; major workers (n = 10): FeL 4.83–5.35; FeI 101–114; minor workers (n = 85): FeL 4.46–5.45; FeI 169–238.

We measured the length of the hind femur (FeL) as an indicator for leg length. Whereas the femur index (FeI) is highly dissimilar in minors and majors (Fig. 14), majors have only slightly shortened legs compared to mesosoma length (Fig. 15). Gynes also possess shortened femora in comparison to minor workers, though the difference is not as pronounced as in majors (Fig. 14).

Petiole shape and petiole index:

Measurements: alate gynes (n = 5): PH 1.48–1.63; PL 1.04–1.17; NH 1.00–1.17; PI 134–144; major workers (n = 5): PH 1.13–1.48; PL 1.04–1.09 (4); NH 0.76–0.89 (4); PI 104–136 (4); minor workers (n = 49): PH 0.59–0.87 (38); PL 0.67–1.02 (35); NH 0.30–0.61 (46); PI 66–95 (31).

PI is highest in gynes, intermediate in majors and lowest in minors, reflecting the differences in dorsoventral height of the petiole and development of the petiolar node. While gynes and majors possess a petiole that is higher than long (PI > 100), with a well-developed node, the petiole of minors is dorsally rounded and longer than high (PI < 100). Due to the mounting method applied in some specimens, petiolar characters were partially obscured and therefore could not be measured in part of the material.

Gaster:

No evident differences were observed when comparing the gasters of minor and major workers. Due to the presence of reproductive organs, gynes possess a larger gaster relative to the rest of the body, but without apparent structural differences compared to the other castes.

Deviating characters of *Camponotus singularis* var. *rufomaculatus* from Borneo

The specimens from Borneo consistently differ from the rest of the examined material by the length of their appendages (maxillary palpi, antennae, and legs; Figs 11–15), as well as reddish colour of the dorsal mesosoma in some specimens, and darker setae on the head. Examination of photographs of the types of var. *rufomaculatus* (AntWeb: syntype major worker CASENT0903555, BMNH; syntype minor worker CASENT0903556, BMNH) suggests that this name is applicable to the Bornean population.

Maxillary palpi:

The examined gyne and minors of *C. s.* var. *rufomaculatus* possess relatively longer palpi than all the other examined specimens (PSI 43–50 in minors, 25 in gyne, see Fig. 11).

Antenna:

All examined *C. s.* var. *rufomaculatus* specimens differ from the rest of the material by considerably longer scapes relative to HW and ML (SI 143–194 in minors, 97 in gyne, see Figs 12, 13).

Leg length:

Camponotus singularis var. *rufomaculatus* differs from the typical form by relatively longer legs (FeI 197–253 in minors, 128 in gyne, see Figs 14, 15).

Discussion

Worker dimorphism and evolution of the major subcaste

The results of our morphometric analyses show that *C. singularis* possesses a true worker dimorphism sensu Wilson (1953) with distinct major and minor worker subcastes and without expression of intermediate morphology. As per the material represented in collections, majors have been observed to be much rarer compared to minors (85 minors and 10 majors examined). Although no complete nest series were available for analysis, the observed relatively low number of majors compared to minors agrees well with the results of previous studies on other Camponotini: Walker and Stamps (1986) as well as Hasegawa (1997) examined two species of *Colobopsis* and found optimal caste ratios of soldiers to lie at around 20% of the total nest-population.

Perhaps the most striking difference between the two worker subcastes is in the shape of the head, which is narrow and ovate with a well-developed collar in minors, but greatly enlarged, heart-shaped and without collar or margin in majors (Figs 1, 2). Though differing in the depth of the posterior concavity, the head-shape of majors is

strongly reminiscent of that of conspecific gynes (Fig. 3) with several major workers also possessing small ocelli or remnants thereof.

When comparing mesosomal architecture between castes, both major and minor workers possess a well-developed prothorax which is slightly enlarged in majors, whereas the mesothorax is greatly hypertrophied in gynes (Fig. 2). Keller et al. (2014) observed this morphological trade-off in multiple subfamilies of ants. They interpret a large prothorax as optimization for foraging and defence in workers, additionally providing attachments for muscles in large-headed majors, whereas the first mesosomal tergite is reduced in gynes to allow for the development of the flight apparatus. Additionally, majors and minors differ by the relative lengths of their appendages with major workers having consistently shortened legs, antennae and maxillary palpi when compared to conspecific minors (Figs 11–15). We could not find comparable data on Camponotini in the literature, but similar results were recently obtained in a study on *Colobopsis* sp. (Laciny et al., in prep., see below for details). In their study on leafcutter ants (*Atta colombica* Guérin-Méneville, 1844) and army ants (*Eciton hamatum* (Fabricius, 1782)), Feener et al. (1988) also found that legs became shorter with increasing body mass in workers of *Atta* and soldiers of *Eciton*. The authors attributed this result to the mechanics of foraging in the examined species. Shortened appendages relative to HS as well as to ML were also observed in the examined gynes of *C. singularis*, though to a slightly lesser extent than in majors. These observations of morphological similarities between majors and gynes may indicate the evolution of the developmental programme for major workers in this species by partial “recycling” of growth parameters for gyne-development (Molet et al. 2014). As elaborated in their 2014 study on *Cataglyphis bombycina* (Roger, 1859), Molet et al. propose that the evolution of specialized castes may be facilitated by reusing and recombining parts of developmental programmes already established in pre-existing castes. The resulting phenotypes are therefore often characterized by a mosaic of novel and recycled traits that set them apart as a distinct caste. Our results clearly show that major workers of *C. singularis* are not simply isometrically scaled-up versions of minor workers, but differ from all other castes by shifts in morphological proportions resulting from differing growth rules; they may therefore be more accurately termed “soldiers” sensu Molet et al. (2012, 2014).

Comparison to other Camponotini

A recent study focusing on morphological variation in a species of the *Colobopsis cylindrica* (COCY) group (Laciny et al., in prep.) found considerable size-variation within the examined minor workers and relatively uniform sizes of major workers (phragmotic in *Colobopsis*) and gynes. This trend is in accordance with studies on other camponotines (e.g., Lee 1938, Busher et al. 1985, Espadaler et al. 1990) reporting wide size ranges in work-

ers that are often correlated with size-specific division of labour. A similar result was obtained in the present study: In *C. singularis* the largest minors surpass their smallest conspecifics by up to 50% regarding head width as well as mesosoma length, while majors and gynes show far less variability (Figs 7–9). Another parallel between the observations in COCY ants and *C. singularis* is the shortening of appendages relative to body size in the major worker subcaste: Majors of both groups possess shorter legs, antennae and maxillary palpi than conspecific minors. However, while in *C. singularis* this holds true for majors as well as gynes, in the COCY group only major workers have shortened appendages, whereas the proportions of gynes were more similar to those of minor workers. The caste-specific architecture of the mesosoma, with a prothorax that is enlarged in workers – particularly in large-headed majors – and reduced relative to the mesothorax in alate gynes, as observed in *C. singularis* and in species of the COCY group, conforms to the morphology of other studied ant species (Keller et al. 2014).

Polyethism and the role of soldiers

The results of this study show a clear worker dimorphism and a conspicuously broad size range of minors, which is apparent in intraspecific as well as intracolony comparison. It is therefore a valid assumption that *C. singularis* colonies have evolved some form of polyethism or division of labour amongst their members. However, nothing is known about colony composition and task allocation in this species as of now. Studies on other formicine ants have yielded results that suggest a tendency towards division of labour even within the (minor) worker caste: Lee (1938) described such a trend in *Camponotus japonicus* var. *aterimus* Emery, 1895, Busher et al. (1985) observed division of labour in *Camponotus sericeiventris* (Guérin-Méneville, 1838), and Higashi (1974) reported similar results for *Formica yessensis* Wheeler, 1913. In contrast, in the moderately polymorphic dolichoderine ant *Liometopum microcephalum* (Panzer, 1798) differences in task performance could not be detected (Petráková and Schläghamerský 2014).

The high nutritional investment necessary for producing a distinct soldier subcaste suggests that these animals must serve a function greatly beneficial to colony survival and fitness (Tian and Zhou 2014). In many of the previously studied ant species the tasks of major workers or specialized soldiers do not only include nest defence, but also storage of food and liquid within their bodies: This was found to be true for the phragmotic major workers of *Colobopsis nipponica* (Wheeler, 1928) (Hasegawa 1993), large workers of the polymorphic *Camponotus foreli* Emery, 1881 (Espadaler et al. 1990) and the highly specialized soldiers of *Cataglyphis bombycina* (Molet et al. 2014). Whether this is also the case in *C. singularis* still remains to be studied. In majors of *C. singularis* the greatly enlarged, heart-shaped head is correlated with the presence of strongly developed mandibular adductor muscles, most probably linked to a function in colony defence. The defensive be-

haviour of soldiers may also contribute to the development of shortened cephalic appendages (antennae, maxillary palpi), so as to reduce the danger of injury in combat. Mysore et al. (2009, 2010) reported major workers of *Camponotus compressus* (Fabricius, 1787) and *Camponotus sericeus* (Fabricius, 1798) to have shorter antennae with reduced sensilla and corresponding neural structures in comparison to conspecific minors. The authors link this to the majors' specialization in nest defence, which makes differentiation of chemical cues less essential than for foraging minor workers. Corresponding to the observed shortened antennae of majors, the situation may be similar in *C. singularis*. However, this can only be a tentative assumption at this point and requires further investigation.

Altogether the results obtained within this study and their comparison to trends observed in the COCY clade (Laciny et al., in prep.) and other previously studied species (e.g., Lee 1938, Wilson 1953, Espadaler et al. 1990, Mysore et al. 2009, 2010, Molet et al. 2012) lead us to propose *C. singularis* as a useful model to characterize major morphometric trends in camponotine caste dimorphism: a wide size range of minor workers, a major worker or soldier subcaste specialized for defence and characterized by an enlarged head and shortened appendages, and a mosaic of novel, gyne-like, and worker-like traits expressed in such specialized phenotypes.

Differing characters of var. *rufomaculatus*

Examined specimens from Borneo clearly differ from specimens from other localities by proportions of appendages, colour pattern and setae. Donisthorpe (1941) originally described var. *rufomaculatus* as a colour variation of *Camponotus singularis*. New data suggest that this name might be applied to a distinct species. Taxonomic implications and details on this issue will be the subject of a separate publication after having examined the types of var. *rufomaculatus* (Zettel et al. in prep.). Faunistic data suggest that this form may be endemic to the island of Borneo, as no matching specimens from other proveniences have been reported so far.

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Supplementary material 1

Table S1: Measurements (mm) of all examined specimens of *Camponotus singularis* (n = 100) and *C. s.* var. *rufomaculatus* (n = 6).

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Data type: specimens data

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