

## **New mimetic ants from Southeast Asia – the *Camponotus (Myrmamblys) inquilinus* group (Hymenoptera: Formicidae: Camponotini)**

Herbert ZETTEL, Pia BALÁKA, Seiki YAMANE,  
Alice LACINY, Linda LIM & Irina S. DRUZHININA

### **Abstract**

The *Camponotus (Myrmamblys) inquilinus* group is established. It presently includes *Camponotus (Myrmamblys) kutteri* FOREL, 1915 from Simeulue, Indonesia, *Camponotus (Myrmamblys) trietericus* MENOZZI, 1926 from the Philippines, and nine species new to science: *Camponotus (Myrmamblys) inquilinus* ZETTEL & LACINY sp.n., *C. (M.) paracolobopsis* ZETTEL & YAMANE sp.n., and *C. (M.) syaukanii* ZETTEL & YAMANE sp.n. from Borneo; *C. (M.) concurrens* ZETTEL & LACINY sp.n. from Borneo, Peninsular Malaysia, and Thailand; *C. (M.) benguetensis* ZETTEL & BALÁKA sp.n. from the Philippines; *C. (M.) sophiae* ZETTEL & BALÁKA sp.n., *C. (M.) schulzianus* ZETTEL & BALÁKA sp.n., and *C. (M.) weiserti* ZETTEL & LACINY sp.n. from Thailand; *C. (M.) paraleonardi* ZETTEL & YAMANE sp.n. from Thailand and Myanmar. Species of the *C. (M.) inquilinus* group differ from other Asian *Myrmamblys* species by an unmodified propodeum. Their overall great similarity to species of the *Colobopsis cylindrica* group (“exploding ants”) is interpreted as a type of mimicry, as species of these two groups are often found in close proximity.

**Key words:** *Camponotus*, mimicry, *Myrmamblys*, new species group, new species, taxonomy, classification, species diversity, Brunei, Indonesia, Malaysia, Philippines, Thailand, xenobiotic.

### **Zusammenfassung**

Die *Camponotus (Myrmamblys) inquilinus*-Gruppe wird vorgestellt. Sie umfasst derzeit *Camponotus (Myrmamblys) kutteri* FOREL, 1915 von Simeulue, Indonesien, *Camponotus (Myrmamblys) trietericus* MENOZZI, 1926 von den Philippinen und neun für die Wissenschaft neue Arten: *Camponotus (Myrmamblys) inquilinus* ZETTEL & LACINY sp.n., *C. (M.) paracolobopsis* ZETTEL & YAMANE sp.n. und *C. (M.) syaukanii* ZETTEL & YAMANE sp.n. von Borneo; *C. (M.) concurrens* ZETTEL & LACINY sp.n. von Borneo, Westmalaysien und Thailand; *C. (M.) benguetensis* ZETTEL & BALÁKA sp.n. von den Philippinen; *C. (M.) sophiae* ZETTEL & BALÁKA sp.n., *C. (M.) schulzianus* ZETTEL & BALÁKA sp.n. und *C. (M.) weiserti* ZETTEL & LACINY sp.n. von Thailand; sowie *C. (M.) paraleonardi* ZETTEL & YAMANE sp.n. von Thailand und Myanmar. Die Arten der *C. (M.) inquilinus*-Gruppe unterscheiden sich von anderen asiatischen *Myrmamblys*-Arten durch ein unmodifiziertes Propodeum. Ihre insgesamt sehr starke Ähnlichkeit mit Arten der *Colobopsis cylindrica*-Gruppe, den „explodierenden Ameisen“, wird als eine Form der Mimikry interpretiert, da Arten dieser beiden Gruppen oft in nächster Nähe gefunden wurden.

## Introduction

In the course of a multidisciplinary project investigating the Southeast-Asian “exploding ants” of the *Colobopsis cylindrica* (COCY) group, multiple samples from nests and foraging trails were found to contain aberrant worker specimens (see also DAVIDSON et al. 2016, LACINY et al. 2017). These closely resembled the workers of the respective COCY species in size and colouration, but were determined as hitherto undescribed members of *Camponotus* subgenus *Myrmamblys* FOREL, 1912. Intrigued by the conspicuous similarity in outer morphology and lack of observed aggression between the species, the present authors establish and define this group of presumably COCY-associated, mimetic ants and describe nine of its members as new to science.

The number of species placed in the subgenus *Myrmamblys* has changed considerably in history, reaching its largest extent in the work of EMERY (1925), who included 57 Old World species in seven species groups. Only one year later, SANTSCHI (1926) transferred all African species (Emery’s groups 4–7) and the Southeast Asian species of the *C. moeschi* group (Emery’s group 3) to other (partly new) subgenera. Subsequently, only two groups remained: Emery’s group 2 (*greeni*) containing three species from the Indian subcontinent, and Emery’s group 1 (*reticulatus*) with around 30 species, subspecies, and variations covering a wide distributional area from Sri Lanka to New Caledonia. This group also contains a few more recently described species, like *C. aruensis* KARAWAIEW, 1933, *C. anezkae* KLIMES & McARTHUR, 2014, and *C. wanangus* KLIMES & McARTHUR, 2014 (see descriptions by KLIMES & McARTHUR 2014).

Previously described species, *C. kutteri* and *C. trietericus*, were placed in *Camponotus* subgenus *Myrmamblys* in the respective original descriptions (FOREL 1915, MENOZZI 1926). EMERY (1925: p. 138) accepted the position of *C. kutteri* in *Myrmamblys* and placed this species in his “1<sup>er</sup> Groupe *reticulatus*”. McARTHUR (2012) transferred both species to *Camponotus* subgenus *Colobopsis* along with a good number of other *Myrmamblys* species. WARD et al. (2016), however, kept both taxa in *Camponotus* after giving *Colobopsis* the rank of a genus. Without access to the type of *C. trietericus* and solely based on McArthur’s photographs, LACINY et al. (2018) regarded *C. trietericus* as a synonym of *Colobopsis corallina* ROGER, 1863 in the *C. cylindrica* group. With new information on the type, this is revised in the present study.

## Material and methods

**Specimens** are dry mounted on card squares or triangles. Examination of specimens was carried out with a Leica Wild M10 binocular microscope; measurements were taken at magnifications of up to 256×. Stacked digital images were taken with a Leica DFC490 camera attached to either a Leica MZ16 binocular microscope or a Leica Z16 APO zoom macroscope, using Leica Application Suite V3. Images were stacked with ZereneStacker 64-bit, and processed with Adobe Photoshop 7.0.

### Depositories of specimens:

BRM	Brunei Museum, Kota Batu, Brunei Darussalam
CDF	Coll. W. Dorow, Frankfurt am Main, Germany
CZW	Coll. Herbert Zettel, Vienna, Austria
IEB	Instituto di Entomologia “Guido Grandi”, University of Bologna, Italy

- MZB Bogor Zoology Museum, Bogor City, Indonesia  
 NHMW Natural History Museum Vienna, Austria  
 NMNH Philippine National Museum of Natural History, Manila, Philippines  
 SKYC Seiki Yamane Collection, Kagoshima-shi, Japan  
 THNHM Thailand Natural History Museum, Technopolis, Thailand

Measurements and indices (\* = only gynes):

- HW Head width. Maximum width of head in full-face view (including eyes if protruding).  
 HL Head length. Maximum length of head in full-face view, excluding mandibles, measured from anterior clypeal margin to posterior-most point of head vertex.  
 SL Scape length. Maximum length of antennal scape in dorsal view excluding basal neck and condyle.  
 SW Scape width. Maximum width of antennal scape in dorsal view.  
 EL Eye length. Maximum diameter of compound eye, measured in lateral view.  
 ML Mesosoma length. Measured laterally from anterior surface of pronotum (where the pronotum meets the cervical shield) diagonally to posterior extension of propodeal lobes.  
 HaL Hair length. Length of the longest standing hair on first gastral tergite, measured from base to apex.  
 FeL Femur length. Maximum length of metafemur, measured from base to apex.  
 OeW\* Ocellus width. Maximum diameter of median ocellus.  
 FWL\* Forewing length. Maximum length of forewing, measured from tegula to distal tip.  
 CI Cephalic index.  $HW / HL \times 100$   
 SI Scape index.  $SL / HW \times 100$   
 EI Eye index.  $EL / HW \times 100$   
 FeI Femur index.  $FeL / HW \times 100$

Additional measurements and indices sensu WARD et al. (2016):

- HW<sub>ex</sub> Head width. Maximum width of head, excluding the eyes.  
 ASM Antennal sclerite minimum. Minimum distance between the antennal sclerites (inter-torular distance).  
 CLW Clypeus width. Width of clypeus at the anterior tentorial pits.  
 CLL Clypeus length. Maximum length of clypeus along the midline (medial indentations on either margin do not decrease length).  
 ASM/HW<sub>ex</sub>, ASM/CLW, CLW/CLL

## Taxonomy

**The *Camponotus* (*Myrmamblys*) *inquilinus* species group**

**Diagnosis:** Small species, HW (minor) 1.11–1.55, HW (major) 1.67–1.96, with a strongly dimorphic worker caste, including a phragmotic major worker. – Minor worker: Microsculpture relatively uniform, consisting of fine isodiametric meshes. With numerous stiff, erect or suberect, acuminate setae all over dorsum (except with short setae on pronotum in two species). Head roundish or domed on vertex, always longer than wide. Distance of antennal insertions in the range of *Camponotus* ( $ASM/HW_{ex} = 0.26–0.36$ ,  $ASM/CLW = 0.55–0.73$ ). Clypeus distinctly wider than long ( $CLW/CLL = 1.12–1.61$ ) with anterolateral extremities neither extended nor set off from rest of clypeus by a sulcus or impression; base often emarginate. In most species frontal carinae relatively short and antennal insertion approximately at their midlength. Mandible punctate, with five teeth. Scape long and slender. Mesosoma elongated, narrow, and low, not strongly constricted; propodeum unmodified, without elevations of outline in lateral aspect. Gaster variably coloured, but never with strongly contrasting yellow marks or broad translucent hind margins of tergites. – Major worker (not known in all species): Head phragmotic, obliquely truncated; anterior part (clypeus and genae) often with coarse punctures. All appendages much shorter than in minor worker. Setae often reduced. – Gyne (only known in few species): Head shape intermediate. Sculpture of head similar to major worker.

**Systematic position:** Minor workers of this group strongly resemble species of *Colobopsis*, specifically of the *Colobopsis cylindrica* group (sensu EMERY 1925, modified and discussed by LACINY et al. 2018). However, the minor workers of the *C. inquilinus* group differ from the *Colobopsis cylindrica* group by long, stiff setae on mesosoma and petiole, a shallowly convex dorsal outline of the petiole (not medially flat or shallowly concave), and smaller mesothoracic and propodeal spiracles. In addition, the measurements of *C. inquilinus* group species largely fit the discrimination characters of *Camponotus* presented by WARD et al. (2016) (compare Table 1). Moreover, in some species pupae are confirmed to be not naked as in *Colobopsis*, but with cocoons as in *Camponotus* (comp. WHEELER 1904).

We place the *C. inquilinus* group within *Myrmamblys* and thereby follow a system used by most of the previous authors (EMERY 1925, SANTSCHI 1926). Deviating from EMERY (1925), who placed *C. kutteri* in the *C. reticulatus* group, we preliminarily include this species in our new species group. Species of the *C. reticulatus* group have various modifications of the propodeum, which is either saddle-shaped anteriorly or with long posterior convexity. Species of the *C. inquilinus* group, on the other hand, are lacking peculiar modifications of the dorsal mesosomal outline. In addition, the species included in the *C. inquilinus*

Tab. 1: Morphometric characters in minor workers of *C. inquilinus* group (this study) compared to discriminating data presented for *Camponotus* and *Colobopsis* by WARD et al. (2016).

Character	<i>Camponotus</i>	<i>Colobopsis</i>	<i>Camponotus inquilinus</i> species group
HW <sub>ex</sub>	0.70–3.00	0.65–1.70	1.09–1.55
ASM/HW <sub>ex</sub>	0.22–0.35	0.36–0.47	0.26–0.36
ASM/CLW	0.35–0.68	0.66–0.98	0.55–0.73
or			
CLW/CLL	1.25–1.62 (exceptions occur)	0.96–1.32	1.12–1.61



group lack yellow patches and broad translucent hind margins of tergites as commonly seen in species of the *C. reticulatus* group. The common character of the *C. inquilinus* group is a strong similarity to species of the *Colobopsis cylindrica* group, a fact that is interpreted as a form of mimicry.

**Biology:** We have evidence that at least some of the treated species are associated with species of *Colobopsis*, which closely resemble the respective species in colouration. Although their biology is still poorly studied, this fact suggests some form of mimicry, probably linked to a parabiotic lifestyle in the *C. inquilinus* group. See biological notes for *C. inquilinus* sp.n., *C. trietericus*, and *C. paracolobopsis* sp.n.

**Distribution:** As far as known, this group is distributed from Myanmar eastwards to Borneo and the Philippines. This area largely overlaps with the distribution of the *Colobopsis cylindrica* group, which, however, reaches Sulawesi in the east.

#### Key to species (worker castes)

- 1 Head (and mesosoma and gaster) very dark brown or black, at most somewhat reddish anteriorly. .... 2
- Head yellowish, brownish, orange, or red. .... 5
- 2 Gaster tergites and dorsal parts of mesosoma with dense yellow to golden pubescence (Figs. 64, 65). Myanmar, Thailand. .... *C. paraleonardi* sp.n.
- Gaster and mesosoma with much less conspicuous, whitish pubescence. .... 3
- 3 Both minor and major with narrow but distinct pale hind margins of gaster tergites 1–4 (Figs. 70, 71). Head of major without microsculpture, strongly shiny (Fig. 69). Simeulue Island near Sumatra. .... *C. kutteri*
- Minor and major without or with very inconspicuous pale hind margins of gaster tergites. Head of major with reticulated microsculpture over large parts of head dorsum, partly matt (Figs. 53, 61). .... 4
- 4 Posterior margin of clypeus in both minor and major triangularly incised (Figs. 49, 53). Major worker with about 12–16 groove-like punctures on clypeus, and genae with some comparatively large punctures (both sometimes indistinct). Scape chiefly blackish brown; funicular segments 1 and 2 of similar colour, with orange base (minor) or entirely orange-brown (major), rarely entire funiculus strongly infuscated. Borneo. .... *C. paracolobopsis* sp.n.
- Posterior margin of clypeus in minor almost straight (Fig. 59), in major with a deep medial furrow (Fig. 61). Major worker with about 6–8 large groove-like punctures on clypeus, no such punctures on genae. Scape chiefly orange coloured; in minor orange-brown funicular segment 1 strongly contrasting with black segment 2. Philippines (Luzon). .... *C. benguetensis* sp.n.
- 5 Gaster dorsally with yellowish brown or orange areas; if with small marks only (Figs. 20, 21), then mesosoma entirely orange. .... 6
- Gaster entirely black or dark brown. Mesosoma laterally at least slightly infuscated. .... 9
- 6 Pronotum with reduced microsculpture, strongly shiny at least at sides (Figs. 22, 32). Minor coloured orange or yellowish brown except part of gaster infuscated. .... 7
- Pronotum densely reticulated, matt (Figs. 20, 36). Colour variable, often infuscated. .... 8
- 7 Minor: dorsal outline of mesosoma very characteristic (Fig. 22), with a strongly convex pronotum and almost straight at mesonotum and propodeum. Pronotum only with

- very short, inconspicuous standing setae. Major: only infuscated on gaster; head shiny (Figs. 28, 29); pronotum with short setae. Thailand, Peninsular Malaysia, Borneo. ... *C. concurrens* sp.n.
- Minor: dorsal outline of mesosoma with slightly convex pronotum, mesonotum and propodeum, and a low depression between mesonotum and propodeum (Fig. 32). Pronotum with several long, standing setae. Major unknown. Thailand. .... *C. weiserti* sp.n.
  - 8 Minor: gaster black, except tergite 1(–2) with orange-brown mark (Figs. 16, 21). Propodeum with slightly convex dorsal outline (Fig. 20). Antennomere 7 about twice as long as wide. Philippines. .... *C. trietericus*
  - Minor: gaster dorsally chiefly pale brown, at most diffusely infuscated, ventrally black (Fig. 36). Propodeum with straight dorsal outline (Fig. 36). Antennomere 7 almost three times as long as wide. Thailand. .... *C. sophiae* sp.n.
  - 9 Minor with short standing setae on dorsum of head, pronotum, and mesonotum (Fig. 40). Major with strongly shiny head (Fig. 46). Borneo. .... *C. syaukanii* sp.n.
  - Minor with long standing setae on dorsum of head, pronotum, and mesonotum (Figs. 1, 11). Major (unknown in *C. schulzianus* sp.n.) with reticulated microsculpture on head (Fig. 7). .... 10
  - 10 Pronotum with traces of microreticulation. Dorsal outline of mesonotum and propodeum straight (Fig. 1). Head vertex weakly domed (Fig. 3). Borneo. .... *C. inquilinus* sp.n.
  - Pronotum smooth. Dorsal outline of both mesonotum and propodeum slightly convex, more or less separated by a weak depression (Fig. 11). Vertex distinctly domed (Fig. 13). Thailand. .... *C. schulzianus* sp.n.

### Treatment of species

#### *Camponotus (Myrmamblys) inquilinus* ZETTEL & LACINY sp.n. (Figs. 1–10)

Type material: Holotype (minor worker #1122; BRM) from Brunei, Temburong, Kuala Belalong Field Studies Centre, artificial nest 29, 5.IV.2015, leg. A. Kopchinskiy, #346/347. Paratypes (BRM, NHMW): 8 minor workers (#1114–1121), 3 major workers (#1111–1113), and 1 dealate gyne (#1110), same nest series; 1 minor worker (#1173), same locality, artificial nest 27, 16.IV.2015, leg. A. Kopchinskiy, #362.

Diagnosis for worker castes: Minor worker: Bicoloured species; head and mesosoma reddish brown, the latter in some specimens with infuscated areas; gaster black. Entire dorsum with long standing setae. Vertex hardly domed. Clypeus basally slightly emarginated, with median carina in basal half. Flagellum of normal length. Pronotum reticulated, on shiny sides sculpture slightly reduced but still visible; with long standing setae. Dorsal outline of pronotum moderately convex, of mesonotum and anterior propodeum straight. – Major worker: Colour similar as in minor, but head rather yellowish clay-coloured. Setae on head very short, on mesosoma, petiole and gaster moderately long. Head squared, sculpture consisting of large punctures and very fine reticulation on frons, vertex and sides where the punctures are spaced. Eyes small. Frontal carinae high. Clypeus and genae with confluent punctures, giving the head a rugose appearance. Sculpture of mesosoma, petiole, and gaster as in minor.

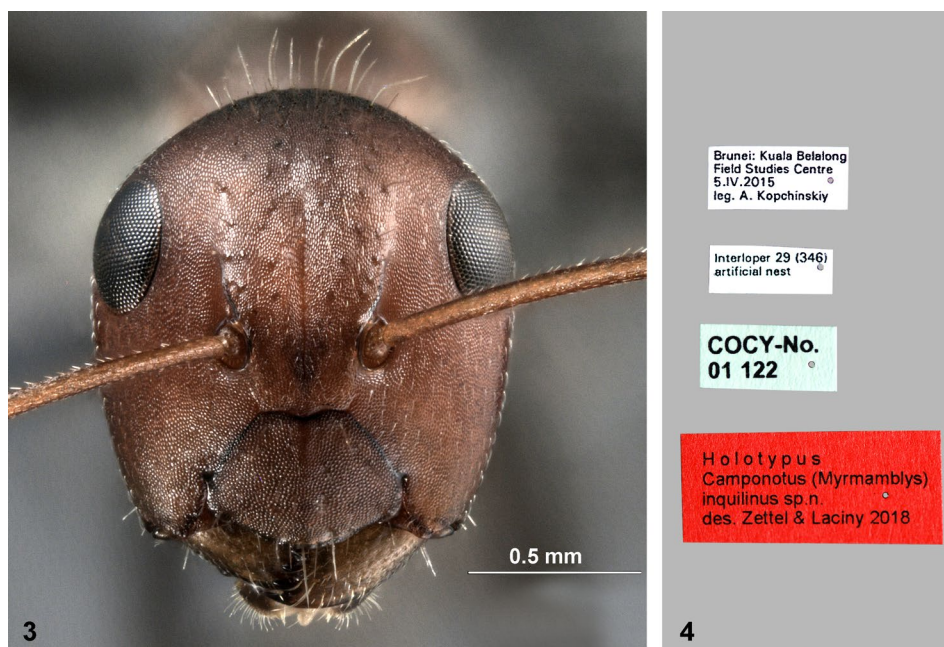
Description of minor worker: Measurements of holotype: HW 1.30; HL 1.41; SL 1.46; SW 0.13; EL 0.45; ML 2.02; HaL 0.29; FeL 1.66; CI 92; SI 112; EI 35; FeI 128. – Ward's Indices: ASM/HW<sub>ex</sub> 0.28; ASM/CLW 0.59; CLW/CLL 1.40.



Figs. 1–2: *Camponotus (Myrmamblys) inquilinus* ZETTEL & LACINY sp.n., holotype, minor worker, (1) lateral and (2) dorsal view. © P. Baláka.

Measurements of paratypes (n = 9): HW 1.32–1.52; HL 1.39–1.63; SL 1.41–1.50; SW 0.14–0.16; EL 0.45–0.50; ML 2.02–2.28; HaL 0.29–0.34; FeL 1.45–1.76; CI 90–95; SI 96–111; EI 33–35; FeI 107–129. – Ward's Indices:  $ASM/HW_{ex}$  0.28–0.31;  $ASM/CLW$  0.59–0.70;  $CLW/CLL$  1.21–1.53.

Structures: Head roundish, dorsally reticulated and matt; laterally, ventrally, and on vertex with reduced microsculpture and shiny. Lateral outline of eye and head contiguous.



Figs. 3–4: *Camponotus (Myrmamblys) inquilinus* ZETTEL & LACINY sp.n., holotype, minor worker, (3) frontal view and (4) labels. © P. Baláka.

Vertex evenly rounded. Frons with shiny midline. Clypeus with very small emargination at middle of basal margin, distal margin protruded in middle, in basal half with shiny median impression. Mandible strongly punctate, with five teeth. – Mesosoma slender and low, reticulated and matt, except for shiny sides of pronotum where the microsculpture is reduced to traces; dorsal outline of pronotum and posterior slope of propodeum moderately convex, of mesonotum and anterior part of propodeum straight. – Petiole with stocky node, its anterior and posterior face almost parallel, apex strongly obliquely truncated. – Gastral tergites with dense reticulation, absent only on very narrow marginal stripes of tergites 3 and 4 (ca. 0.01 mm).

Pilosity: Entire dorsum with long whitish standing setae, longest on propodeum and apex of gaster. Subdecumbent pubescence short, thin, whitish; very sparse on head.

Colour: Head dark reddish brown. Mandibles yellowish. Mesosoma of same colour, but with some variable infuscated areas, in most specimens a large part of propodeum blackish. Petiole dark brown to black. Gaster black. Scape and first funicular segment orange yellow, the following segments black. Legs black, foretibia and -tarsus often paler, brown.

Description of major worker: Measurements of paratypes (n = 3): HW 1.83–1.91; HL 2.04–2.11; SL 1.22–1.28; SW 0.14–0.19; EL 0.52–0.56; ML 2.35–2.41; HaL 0.24–0.30; FeL 1.57–1.61; CI 89–91; SI 65–68; EI 28–29; FeI 84–86.

Structures: Head squared, slightly longer than wide. Eyes small, laterally not reaching sides of head. Frontal carinae prominent, curved. Vertex and frons with large, widely spaced punctures; interspaces with weak reticulation. Genae and clypeus with very coarse





Figs. 5–6: *Camponotus (Myrmamblys) inquilinus* ZETTEL & LACINY sp.n., paratype, major worker, (5) lateral and (6) dorsal view. © P. Balàka.

sculpture consisting of confluent large punctures. Clypeus narrow, about twice as long as wide; median carina indistinct; basal margin medially incised, appearing bilobed; anterior margin strongly convex, but not surpassing genae. Mandibles with large punctures and minute micropunctures on interspaces. Mesosoma stouter than in minor worker, but otherwise of similar structure and sculpture. Node of petiole narrow, anterior and posterior faces almost parallel. Gaster similar as in minor.

Pilosity: White standing setae on head very short, on mesosoma, petiole, and gaster distinctly shorter than in minor worker. Subdecumbent pubescence absent from head.

**Colour:** Differs from minor chiefly by a yellowish clay-coloured anterior portion of the head. In one specimen also the colour of mesosoma tending to yellowish.

**Description of gyne:** Measurements paratype (n = 1): HW 1.72; HL 1.80; SL 1.28; SW 0.17; EL 0.62; ML 3.20; HaL 0.16; FeL 1.71; OcW 0.11; FWL n.a.; CI 95; SI 75; EI 36; FeI 100.

**Structures:** Head more similar to major than to minor, but slightly more rounded. Eyes large, surpassing sides of head capsule. Ocelli present. Sculpture similar to major. Mesosoma with gyne-specific features. Pronotum anteriorly and laterally shiny. Wings broken off. Node of petiole narrow, anterior and posterior faces converging, apex rounded. Gaster larger than in workers, otherwise similar.

**Pilosity:** Similar as in major worker.

**Colour:** Head colour intermediate between minor and major worker.

**Comparative notes:** The minor worker of *C. inquilinus* sp.n. can be recognized by colour (Figs. 1, 2) in combination with a normally shaped vertex (Fig. 3) and long white standing setae on entire dorsum. The major is similarly coloured, except for the yellow head. Its head (Fig. 7) is very stout, dorsally with short setae and very dense, confluent puncturation, very similar to some species of *Colobopsis*. In gynes, the head resembles that of the major worker, but with less pronounced features.

**Distribution and biological notes:** Currently, no records of *C. inquilinus* sp.n. exist outside of Brunei. All examined specimens were found in artificial nests (#27 and #29) placed in the vicinity of the Kuala Belalong Field Studies Centre (KBFS) in May 2014. The nests were constructed out of wooden stakes with holes drilled into them to create an internal cavity (for illustrations and details of construction, see LACINY et al. 2017, 2018). Nest #29 contained a colony consisting only of *C. inquilinus* sp.n., which allowed the sampling of minor workers, major workers, gynes and brood. The pupae exhibited cocoons, which is consistent with the current definition of the genus *Camponotus* (WARD et al. 2016). Nest #27 was occupied by a colony of the undescribed COCY (= *Colobopsis cylindrica* group) species *Colobopsis* sp. “nrSA” of the *Colobopsis saundersi* clade. Within this nest sample, a single minor worker specimen of *C. inquilinus* was found among minor workers of *C. sp. “nrSA”* (LACINY et al. 2017). It was presumably mistaken for a conspecific COCY worker during sampling, due to its close resemblance in size and coloration. This finding further strengthens the hypothesis of an inquiline lifestyle closely connected to the exploding ants of the COCY group.

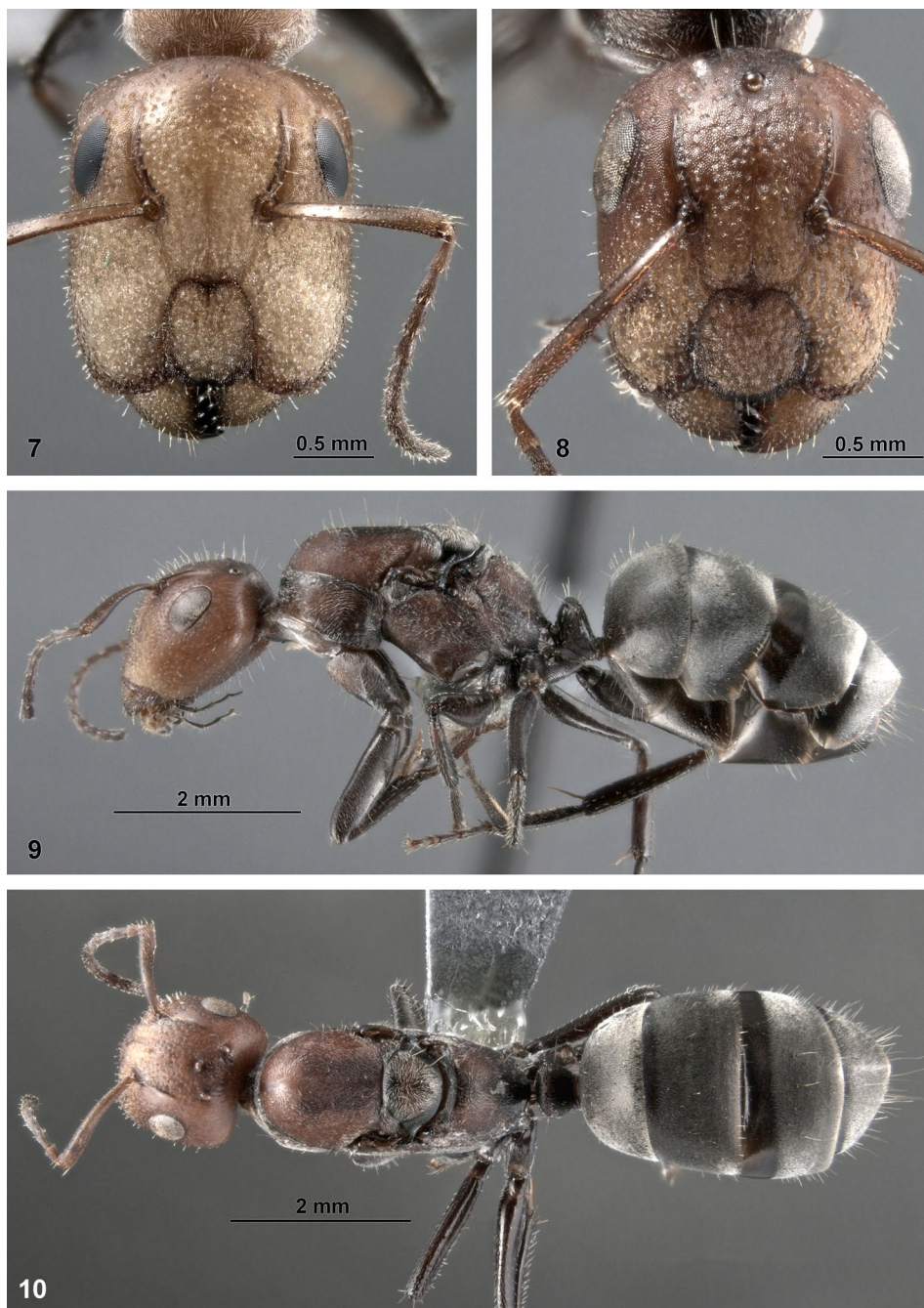
**Etymology:** Named after the suspected inquiline lifestyle in nests of COCY ants.

### ***Camponotus (Myrmamblys) schulzianus* ZETTEL & BALÁKA sp.n. (Figs. 11–14)**

**Type material:** Holotype (minor worker #515; NHMW) from Thailand, Phang-nga Province, Khao Lak N.P., Thone Chong Fa Falls, N8°40', E98°18', 100–300 m a.s.l., leg. A. Schulz & K. Vock, #T13. Paratypes (NHMW): 1 minor worker (#388), same label data; 2 minor workers (#401, 402), same label data except T14.

**Diagnosis for worker castes:** Minor worker: Head and scape orange; mesosoma orange brown with variable light or medium brown areas dorsally, especially on propodeum. Vertex domed. Clypeus basally shallowly emarginated, with a hardly traceable median carina. Flagellum of normal length. Pronotum with reduced sculpture, somewhat





Figs. 7–10: *Camponotus (Myrmamblys) inquilineus* ZETTEL & LACINY sp.n., paratype, major worker, (7) frontal view, and paratype, dealate gyne, (8) frontal, (9) lateral and (10) dorsal view. © P. Balàka.

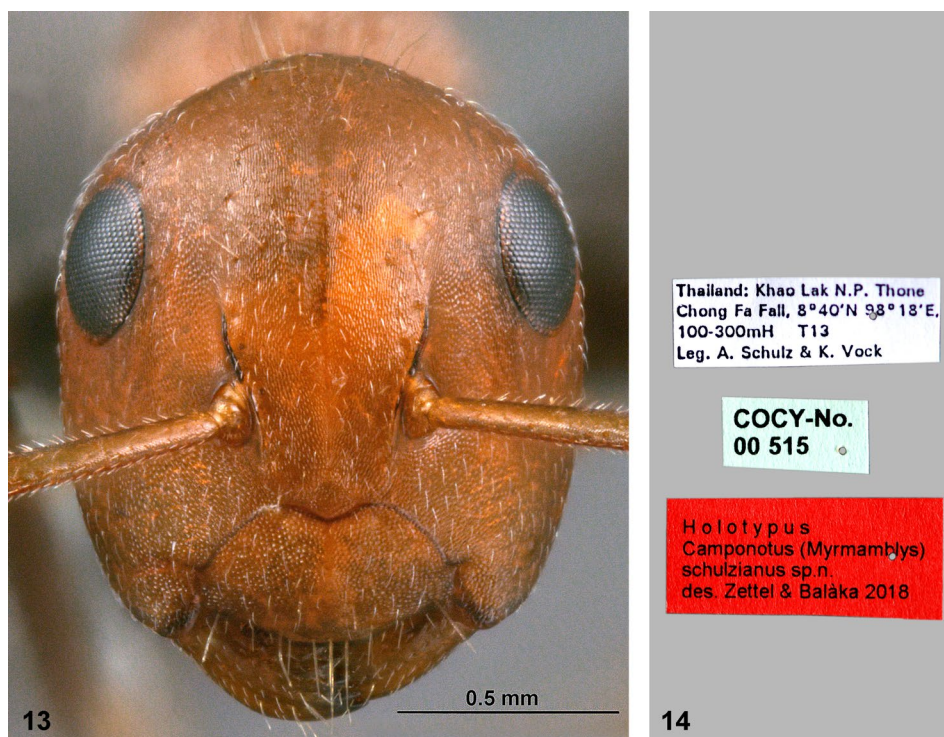


Figs. 11–12: *Camponotus (Myrmamblys) schulzianus* ZETTEL & BALÁKA sp.n., holotype, minor worker, (11) lateral and (12) dorsal view. © P. Baláka.

shiny, with long standing setae. Dorsal outline of mesonotum and propodeum slightly convex, in some specimens separated by a weak depression. – Major worker unknown.

Description of minor worker: Measurements of holotype: HW 1.26; HL 1.41; SL 1.30; SW 0.11; EL 0.39; ML 1.86; HaL 0.21; FeL 1.47; CI 89; SI 103; EI 31; FeI 116. – Ward's Indices:  $ASM/HW_{ex}$  0.31;  $ASM/CLW$  0.62;  $CLW/CLL$  1.45.



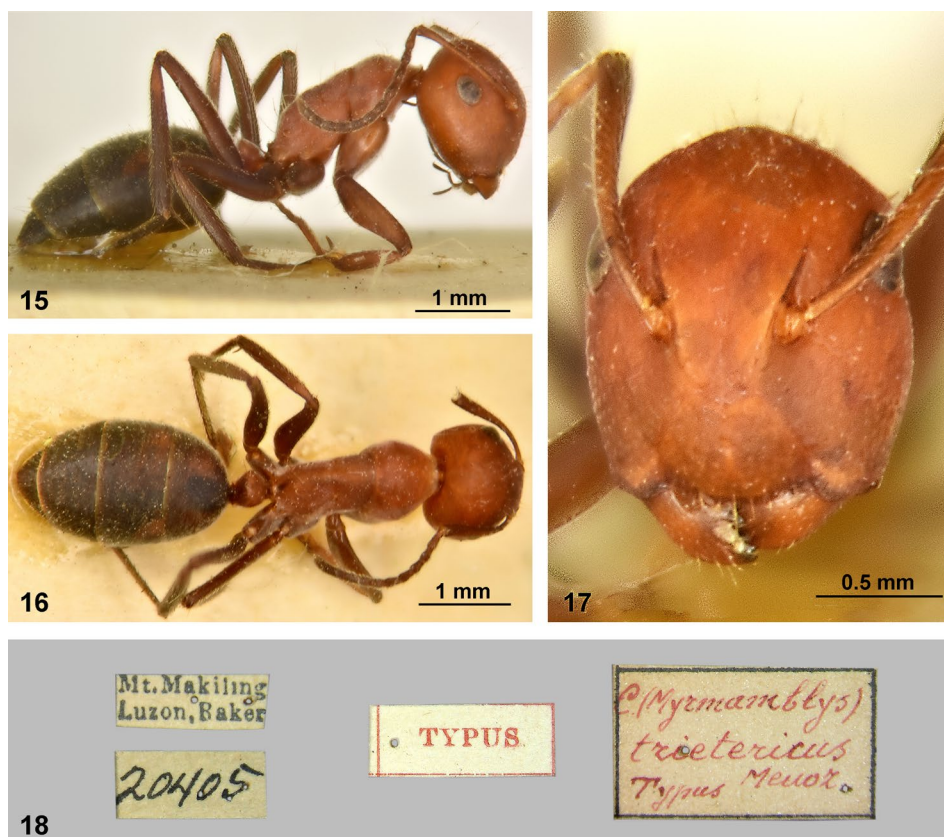


Figs. 13–14: *Camponotus* (*Myrmamblys*) *schulzianus* ZETTEL & BALÁKA sp.n., holotype, minor worker, (13) frontal view and (14) labels. © P. Balàka.

Measurements of paratypes (n = 3): HW 1.17–1.24; HL 1.26–1.35; SL 1.20–1.24; SW 0.14–0.15; EL 0.38–0.39; ML 1.83–1.89; HaL 0.21–0.30; FeL 1.34–1.43; CI 91–93; SI 96–104; EI 31–32; FeI 113–119. – Ward's Indices:  $ASM/HW_{ex}$  0.30–0.31;  $ASM/CLW$  0.62–0.63;  $CLW/CLL$  1.44–1.54.

Structures: Head roundish, dorsally reticulated and matt; laterally, ventrally, and on vertex with reduced microsculpture and shiny. Lateral outline of eye and head contiguous, or eye just not reaching head sides. Vertex moderately raised. Shiny midline of frons reduced. Clypeus with broad, but shallow emargination of basal margin; distal margin protruded in middle, laterally slightly concave; median impression in basal half indistinct. Mandible strongly punctate, with five teeth. – Mesosoma moderately slender and low, reticulated and matt, except for shiny, unsculptured pronotum (except minute depressions of setae); dorsal outline of pronotum and posterior slope of propodeum moderately convex, with a weak indentation between pro- and mesonotum, and with a shallow depression in front of propodeum. – Petiole with stocky node, its anterior and posterior face almost parallel, apex strongly obliquely truncated. – Gaster tergites with dense reticulation, absent only on very narrow marginal stripes (ca. 0.02 mm on tergites 1 and 2, slightly broader on tergites 3 and 4).

Pilosity: Entire dorsum with long whitish standing setae, longest on propodeum, petiole, and apex of gaster. Subdecumbent pubescence short, thin, whitish; very sparse on head.



Figs. 15–18: *Camponotus (Myrmamblys) trietericus* MENOZZI, 1926, holotype, minor worker, (15) lateral, (16) dorsal, and (17) frontal view; (18) labels. © P. Rosa.

Colour: Head reddish brown. Mandibles yellowish. Mesosoma of similar colour as head, but with some variable infuscated areas; part of propodeum blackish. Petiole dark brown to black. Gaster black. Scape orange yellow; funicular segment chiefly orange, increasingly infuscated towards apex. Legs black, tibia dark brown, tarsi apically reddish brown.

Major worker and gyne: unknown.

Comparative notes: The minor worker of *C. schulzianus* sp.n. is similar to *C. inquilinus* sp.n. by colour and sculpture, but differs by a more highly raised vertex, a slightly different outline of the clypeus, a slightly stouter mesosoma, a more structured dorsal outline of the mesosoma including a slight depression in front of the propodeum, reddish brown antennomeres that are increasingly infuscated towards apex, and reddish distal tarsomeres. The eyes are slightly smaller than in *C. inquilinus* sp.n. (EI 31–32 vs. 33–35); in full-face view, they are laterally not fully reaching the head sides in two of four specimens.

Distribution: Only known from the type locality in Phang-nga Province, Thailand.

Etymology: Named in honour of Andreas Schulz, who collected the type specimens.

***Camponotus (Myrmamblys) trietericus* MENOZZI, 1926 (Figs. 15–21)**

*Camponotus (Myrmamblys) trietericus*: MENOZZI 1926: 95. Holotype (?) minor worker, Philippines.

*Camponotus (Myrmamblys) trietericus* MENOZZI, 1926: BOLTON 1995: 127.

*Camponotus trietericus*, subgenus *Colobopsis*: McARTHUR 2012: 56.

*Colobopsis corallina* ROGER, 1863: LACINY et al. 2018: 29 (erroneous synonymy).

Illustrations of type material examined: Holotype (?) minor worker (IEB) from Philippines, “Luzon / Mt. Makiling / Baker” // “20405” // “TYPUS” // “C. (Myrmamblys) / trietericus / Typus / Menoz”.

Non-type material examined (CZ W): 1 minor worker (#681) from Philippines, Luzon, Quezon Province, Atimonan, Old Zigzag Road, 24–30.III.1998, leg. H. Zettel; 1 minor worker (#674), same locality and collector, 27–28.I.2002.

Diagnosis for worker castes: Minor worker: Bicoloured, the black gaster strongly contrasting with the orange forebody; gaster tergites 1 (–2) with variably large orange (–brown) spots. Entire body densely microreticulated and matt. Vertex domed. Clypeus basally very shallowly emarginated in middle. Flagellum of normal length. Dorsal outline of mesosoma slightly convex. Node of petiole stout. – Major worker unknown.

Description of minor worker: Measurements of holotype, taken from illustration: Ward’s Indices: ASM/HW<sub>ex</sub> 0.31; ASM/CLW 0.70; CLW/CLL 1.36.

Measurements of non-type specimens (n = 2): HW 1.20, 1.30; HL 1.35, 1.37; SL 1.37, 1.57; SW 0.14, 0.15; EL 0.35, 0.38; ML 1.83, 2.02; HaL 0.24, 0.32; FeL 1.48, 1.55; CI 87, 97; SI 115, 120; EI 29; FeI 114, 130. – Ward’s Indices: ASM/HW<sub>ex</sub> 0.28, 0.29; ASM/CLW 0.59, 0.62; CLW/CLL 1.32, 1.37.

Structures: Entire body with dense microreticulation, matt. Head roundish, vertex domed, sometimes strongly. Lateral outline of eye minimally surpassing outline of head. Shiny midline of frons weakly developed. Clypeus with very shallow medial emargination of basal margin; distal margin almost evenly rounded; median impression very short, at base. Mandible strongly punctate, with five teeth. – Mesosoma slender and low; dorsal outline with weak indentions between pro- and mesonotum and between mesonotum and propodeum. – Petiole with stocky node, its anterior and posterior face almost parallel, apex obliquely truncated. – Gaster tergites with dense reticulation, absent only on very narrow marginal stripes (ca. 0.01 mm) on tergites 3 and 4.

Pilosity: Entire dorsum with long whitish standing setae, longest on vertex, propodeum, petiole, and apex of gaster. Subdecumbent pubescence short, thin, whitish; very sparse on head.

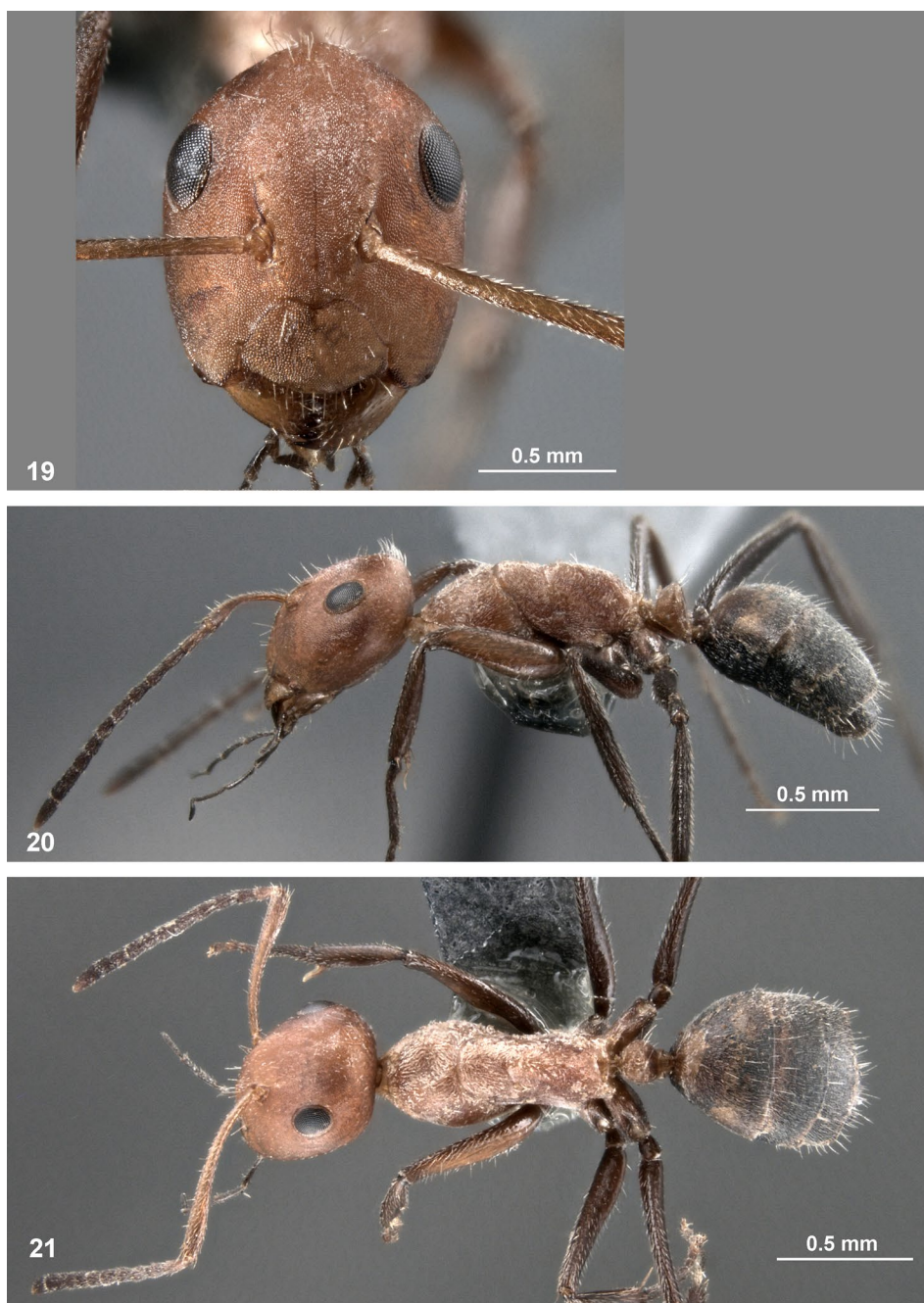
Colour: Head, mandibles, scape, antennal segment 2, mesosoma, and petiole orange. Gaster black; tergite 1 (sometimes also tergite 2) with orange brown patches. Antennal segments 3–12 blackish brown. Legs dark brown.

Major and gyne: Unknown.

Comparative notes: *Camponotus trietericus* has a unique colour pattern, being the only species with orange patches on a black gaster. It is the only bicoloured species of the Philippines, where it is probably endemic. The black tergites strongly contrast with the orange petiole. The entire surface is densely reticulated and matt. The vertex of the disproportionally large head is raised in a dome-like shape, sometimes strongly.

Further notes: *Camponotus trietericus* and *Colobopsis corallina* have a very similar colour pattern, notably the orange patches on gaster tergites 1 and 2. A mixed sample from Luzon indicates that these two species forage together.





Figs. 19–21: *Camponotus (Myrmamblys) trietericus* MENOZZI, 1926, minor worker from Luzon, Quezon Province, (19) frontal, (20) lateral and (21) dorsal view. © P. Balàka.



**Distribution:** Described from Mt. Makiling in Laguna Province and newly recorded from nearby Quezon Province, both on Luzon Island. Probably restricted to the Philippines.

***Camponotus (Myrmamblys) concurrens* ZETTEL & LACINY sp.n. (Figs. 22–31)**

**Type material:** Holotype (minor worker #1787; NHMW) from Brunei, Temburong, Kuala Belalong Field Studies Centre, N04°33', E 115°09', 60 m a.s.l., 6.IV.1994, leg. D.W. Davidson, #KB05-36. Paratypes (NHMW, THNMH, CDF): 3 major workers (#1788–1790) and 2 alate gynes (#1791, 1792), same nest series as holotype; 2 minor workers (#1656, 1657), 2 major workers (#1654, 1655), Thailand, Chanthaburi Province, Pheao N.P., Troknong Waterfall, tropical rainforest, 24.XI.2003, leg. W. Jaitrong, #TH03-WJT502; 1 minor worker (#1658), Thailand, Loei Province, Phu Luang W.S., 13.V.2007, leg. S. Hasin, #SH07-TH; 1 minor worker, Thailand, Khao Yai N.P., 900–1000 m a.s.l., 20.V.2000, leg. Sk. Yamane; 1 minor worker (#1160), 1 major worker (#1161), Malaysia, Selangor, Kuala Lumpur, Ulu Gombak FSC, N 3.32466°, E 101.752717°, 240–270 m a.s.l., 21.I.1987, leg. W. H. O. Dorow, #SEA-0742.

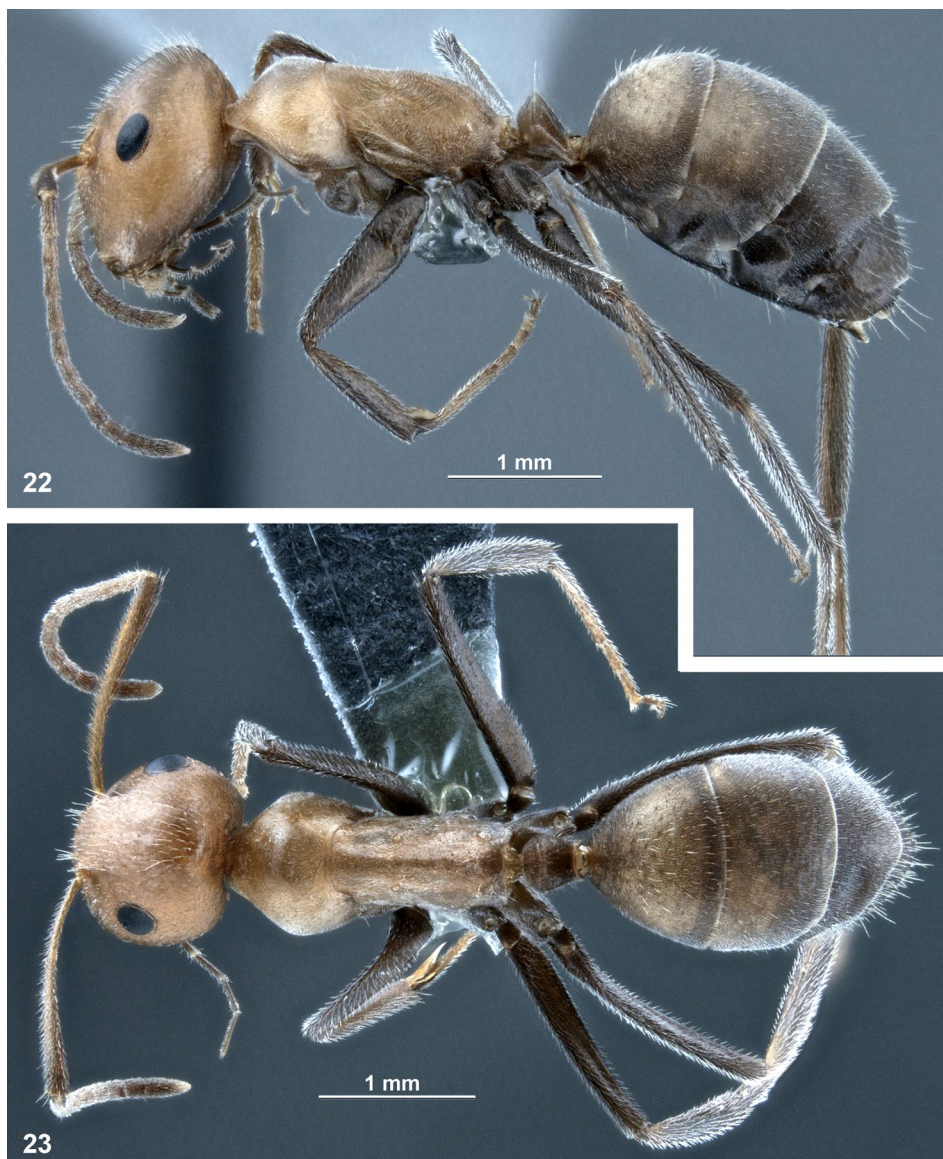
**Diagnosis for worker castes:** Minor worker: Trunk chiefly yellowish or pale orange; distal segments of antenna and parts of gaster brownish infuscated. Vertex highly domed. Clypeus at base broadly and shallowly emarginated and with a short, deep median impression; anterior margin straight. Flagellum slender. Mesosoma with reduced sculpture, shiny. Pronotum with short standing setae. Dorsal outline of pronotum strongly convex, of mesonotum and propodeum almost straight. – Major worker: Colour similar as in minor, head slightly darker. Head squared, shiny, with coarse puncturation; microsculpture evanescent except for area between high frontal carinae and eye. Eyes small. Clypeus with concave basal margin, a pair of large setiferous punctures near base, and a large shallowly depressed area apically. Reticulated sculpture of mesosoma more distinct than in minor, reduced only on pronotum. Petiole and gaster reticulated as in minor. Petiolar node more slender than in minor.

**Description of minor worker:** Measurements of holotype: HW 1.28; HL 1.47; SL 1.50; SW 0.16; EL 0.40; ML 1.96; HaL 0.18; FeL 1.79; CI 87; SI 117; EI 32; FeI 140. – Ward's Indices:  $ASM/HW_{ex}$  0.33;  $ASM/CLW$  0.64;  $CLW/CLL$  1.48.

Measurements of paratypes (n = 5): HW 1.20–1.35; HL 1.37–1.54; SL 1.35–1.45; SW 0.13–0.15; EL 0.36–0.42; ML 1.70–2.15; HaL 0.21–0.26; FeL 1.60–1.86; CI 82–87; SI 107–116; EI 30–35; FeI 136–147. – Ward's Indices:  $ASM/HW_{ex}$  0.29–0.31;  $ASM/CLW$  0.59–0.63;  $CLW/CLL$  1.30–1.51.

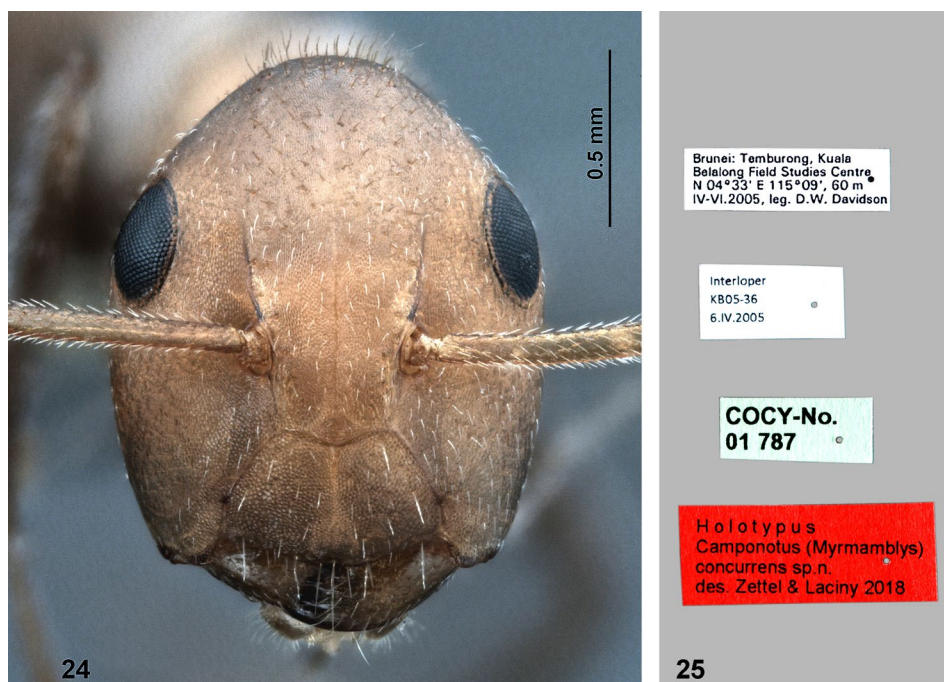
**Structures:** Head elongated, dorsally finely reticulated and matt; ventrally with reduced microsculpture and shiny. Lateral outline of eye and head contiguous. Vertex strongly domed. Shiny midline of frons very fine. Clypeus with broad, but shallow emargination of basal margin; distal margin not protruded in middle; median impression reduced, very short, although deep. Mandible finely punctured, with five teeth. – Mesosoma moderately slender and low, shiny; reticulated microstructure reduced, especially on pronotum; dorsal outline of pronotum strongly, posterior slope of propodeum weakly convex; indentation between pro- and mesonotum and mesonotum and propodeum indistinct. – Petiole with stocky, comparatively low node, its anterior and posterior face almost parallel, apex obliquely truncated. – Gaster tergites with dense reticulation, also on the very narrow, weakly delimited, translucent marginal stripes.

**Pilosity:** Whitish standing setae on dorsum comparatively short, moderately long on vertex (only few), propodeum, petiole, and apex of gaster. Subdecumbent pubescence short, thin, inconspicuous; very sparse on head.



Figs. 22–23: *Camponotus (Myrmamblys) concurrens* ZETTEL & LACINY sp.n., holotype, minor worker, (22) lateral and (23) dorsal view. © P. Balàka.

Colour: Head, mesosoma, and petiole pale yellowish or orange, tending to light brown. Gaster brownish infuscated, ventrally stronger than dorsally; tergites 1–2 light yellowish brown. Antennae yellow, distally brownish. Legs proximally dark brown, distally paler, tending to yellow.



Figs. 24–25: *Camponotus (Myrmamblys) concurrens* ZETTEL & LACINÝ sp.n., holotype, minor worker, (24) frontal view and (25) labels. © P. Balàka.

Description of major worker: Measurements of paratypes (n=6): HW 1.67–1.91; HL 1.98–2.27; SL 1.17–1.35; SW 0.15–0.21; EL 0.46–0.50; ML 2.22–2.67; HaL 0.13–0.21; FeL 1.47–1.70; CI 84–88; SI 67–73; EI 26–30; FeI 87–95.

Structures: Head squared, clearly longer than wide. Eyes small, laterally not reaching sides of head. Ocellar scars absent or present. Frontal carinae prominent, curved. Dorsal surface with strong, widely spaced punctures; interspaces with reduced, hardly visible microsculpture, except area between high frontal carinae and eye clearly reticulated. Clypeus moderately narrowed, about 1.5 times as long as wide, with relatively fine, widely spaced punctures and with a pair of deep setiferous grooves near basal corners (a few larger punctures may occur at sides); basal margin medially with wide and shallow emargination; no median carina; anterior margin strongly protruded, but not surpassing genae; a large distal area shallowly depressed. Mandibles with fine, widely spaced punctures only. – Mesosoma with finely reticulated microsculpture and matt, except for the shiny pronotum. Dorsal outline of pronotum moderately convex, dorsal indentions behind pronotum and mesonotum weak. – Node of petiole narrow, apex narrowly rounded. – Gaster similar as in minor.

Pilosity: Standing setae similar as in minor; with a pair of short setae in basal corners of clypeus. Short pubescence absent from head.

Colour: Similar as in minor, but slightly darker on head and posterior parts of tergites 1 and 2. Ventral parts of mesosoma variably infuscated.



**Description of gynes:** Measurements of paratypes (n = 2): HW 1.51–1.52; HL 1.70–1.72; SL 1.33–1.36; SW 0.17–0.18; EL 0.52–0.53; ML 2.93; HaL 0.17–0.21; FeL 1.92; OcW 0.11; FWL 8.54–8.67; CI 88–90; SI 88–89; EI 35; FeI 126–127.

**Structures:** Intermediate between minor and major in many characters. Head roundish. Eyes large, slightly surpassing outline of head. Ocelli present. Sculpture of head similar as in major, but punctures generally larger and denser. Posterior part of head (from middle of frons to vertex) with variable large reticulated area (large in the illustrated specimen). Clypeus with emarginated base and medially protruded anterior margin, without distal depressed area. – Entire mesosoma, including pronotum with reticulated microsculpture, slightly shiny. – Petiole similar as in major, the node slightly lower. – Gaster large, but otherwise similar as in worker castes, the translucent margins slightly wider.

**Pilosity:** As in major worker, including absence of short pubescence on head.

**Colour:** As in major worker. Wings with strong grayish-yellow tinge. Veins yellow.

**Comparative notes:** The minor of *C. concurrens* sp.n. can be easily recognized by colour and the shiny, strongly convex pronotum. The major has a similar colour, but appears very different by a very shiny head (matt in minor), a reticulated microstructure of the mesosoma (except pronotum) and a moderately convex pronotum. Both castes can be distinguished from most other species (except *C. syaukanii* sp.n.) by short pronotal setae. These two species are very similar in structures and sculpture, although very different in colour, with *C. syaukanii* sp.n. having a strongly infuscated mesosoma and petiole, and black gaster. Two clear differences are found in minor workers: Firstly, in *C. concurrens* sp.n., the anterior clypeal margin is straight, whereas in *C. syaukanii* sp.n. it is distinctly protruded in the middle. Secondly, the strongly convex, “humped” pronotum of *C. concurrens* sp.n. is evenly and moderately convex in *C. syaukanii* sp.n.

Specimens of *C. concurrens* sp.n. from the Asian mainland differ from the type series from Borneo by a ground colour that is rather orange than yellowish, darker and slightly stouter funicular segments of antenna, and by a slightly lower, more stocky petiolar node. We consider these variations as intraspecific.

**Further notes:** One male collected with the type series is possibly conspecific, but not described because it differs considerably in colour.

**Distribution:** Thailand, West Malaysia, Brunei.

**Etymology:** Participle of the Latin verb concurrere, meaning “running together”. The name refers to the supposed foraging on COCY ant trails.

### ***Camponotus (Myrmamblys) weiserti* ZETTEL & LACINY sp.n. (Figs. 32–35)**

**Type material:** Holotype (minor worker #417; NHMW) from Thailand, Phang-nga Province, Khao Lak N.P., Thone Chong Fa Falls, N8°40', E98°18', 100–300 m a.s.l., leg. A. Schulz & K. Vock, #T11. Paratypes (NHMW): 3 minor workers (#414–416), same label data.

**Diagnosis for minor worker caste:** Minor worker: Body chiefly light reddish-brown; head somewhat darker; gaster ventrally infuscated. Pronotum with long standing setae. Trunk with dense microreticulation, matt; only pronotum with weaker sculpture, shiny. Clypeus basally shallowly emarginated. Flagellum of normal length, antennomere 7 about twice as long as wide. Dorsal outline of entire mesosoma slightly convex, of pronotum moderately convex, in front of propodeum with shallow depression. – Major worker unknown.



Figs. 26–27: *Camponotus (Myrmamblys) concurrens* ZETTEL & LACINY sp.n., paratype, major worker, (26) lateral and (27) dorsal view. © P. Balàka.

Description of minor worker: Measurements of holotype: HW 1.22; HL 1.41; SL 1.28; SW 0.15; EL 0.38; ML 1.89; HaL 0.27; FeL 1.60; CI 86; SI 105; EI 31; FeL 131. – Ward's Indices:  $ASM/HW_{ex}$  0.29;  $ASM/CLW$  0.59;  $CLW/CLL$  1.47.

Measurements of paratypes (n = 3): HW 1.24–1.28; HL 1.37–1.43; SL 1.26–1.28; SW 0.14–0.15; EL 0.38–0.39; ML 1.83–1.92; HaL 0.20–0.25; FeL 1.57–1.70; CI 86–94;





Figs. 28–30: *Camponotus (Myrmamblys) concursus* ZETTEL & LACINY sp.n., paratype, major worker, (28) frontal view, and paratype, alate gyne, (29) frontal and (30) dorsal view. © P. Balàka.

SI 100–102; EI 31; FeI 122–137. – Ward's Indices:  $ASM/HW_{ex}$  0.27–0.28;  $ASM/CLW$  0.55–0.57;  $CLW/CLL$  1.40–1.56.

Structures: Head roundish, uniformly reticulated and matt dorsally and laterally, ventrally with slightly reduced microsculpture and somewhat shiny. Lateral outline of eye barely meeting outline of head. Vertex slightly domed. Frons with very narrow shiny midline. Clypeus with very small emargination at middle of basal margin, distal margin slightly protruded in middle, basally with a very short, deep, shiny median impression. Mandible punctate, with five teeth. Mesosoma slender, moderately low; mesonotum and propodeum densely reticulated and matt, pronotum with indistinct sculpture, shiny; dorsal outline of pronotum, anterior portion of mesonotum and posterior slope of propodeum distinctly





Fig. 31: *Camponotus (Myrmamblyus) concurrens* ZETTEL & LACINY sp.n., paratype, alate gyne, lateral view. © P. Balàka.

convex, outline of posterior mesonotum and anterior part of propodeum slightly concave, creating a low depression between mesonotum and propodeum. Petiole with moderately high node, its anterior and posterior face parallel, apex strongly obliquely truncated. Gaster tergites with dense reticulation until hind margin.

Pilosity: Pale, moderately long standing setae scattered all over dorsum, longest on propodeum and gaster tergite 1. Subdecumbent pubescence short, thin, whitish, rather inconspicuous.

Colour: Body reddish-brown, tending to orange on mesosoma, gaster and scapes; head somewhat darker; ventral side of gaster, antennal flagellum, maxillary palpi, and legs dark brown; gastral tergites 2–4 with very narrow translucent margins.

Major and gyne: Unknown.

Comparative notes: This species is similar to *C. sophiae* sp.n. from the same locality. It differs by a shinier, less reticulated pronotum, a normally long antennal flagellum,

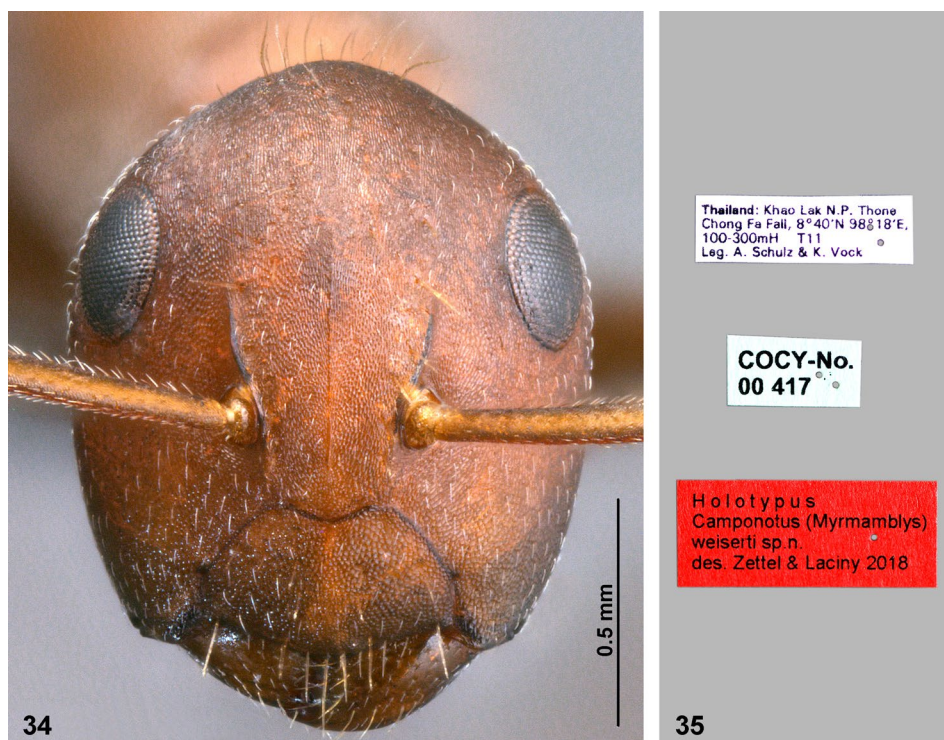


Figs. 32–33: *Camponotus (Myrmamblys) weiserti* ZETTEL & LACINY sp.n., holotype, minor worker, (32) lateral and (33) dorsal view. © P. Balàka.

a concave dorsal outline between mesonotum and propodeum, and slightly shorter and less abundant standing setae. It differs from *C. concurrens* sp.n. by the only moderately convex pronotum (humped in minors of *C. concurrens* sp.n.) and bearing long standing setae, and by the shallow depression in the anterior part of the propodeum.

**Distribution:** Only known from the type locality in Phang-nga Province, Thailand.





Figs. 34–35: *Camponotus (Myrmamblys) weiserti* ZETTEL & LACINY sp.n., holotype, minor worker, (34) frontal view and (35) labels. © P. Balàka.

**Etymology:** This species is named in memory of Fritz Weisert (1936–2018), amateur lepidopterist in Vienna and former editor of this journal.

***Camponotus (Myrmamblys) sophiae* ZETTEL & BALÀKA sp.n. (Figs. 36–39)**

**Type material:** Holotype (minor worker #413; NHMW) from Thailand, Phang-nga Province, Khao Lak N.P., Thone Chong Fa Falls, N8°40', E98°18', 100–300 m a.s.l., leg. A. Schulz & K. Vock, #T11. Paratypes (NHMW): 1 minor worker (#418), same label data.

**Diagnosis for minor worker caste:** Minor worker: Body chiefly light brown; head tending to orange red; gaster ventrally infuscated. Trunk, including pronotum with dense microreticulation, matt. Clypeus basally slightly emarginated and with distinct median impression of about one third of length. Flagellum long, antennomere 7 almost three times as long as wide. Propodeum with straight dorsal outline. Major worker and gyne unknown.

**Description of minor worker:** Measurements of holotype: HW 1.28; HL 1.37; SL 1.50; SW 0.15; EL 0.40; ML 2.02; HaL 0.33; FeL 1.65; CI 94; SI 117; EI 31; FeI 128. – Ward's Indices:  $ASM/HW_{ex}$  0.28;  $ASM/CLW$  0.59;  $CLW/CLL$  1.40.

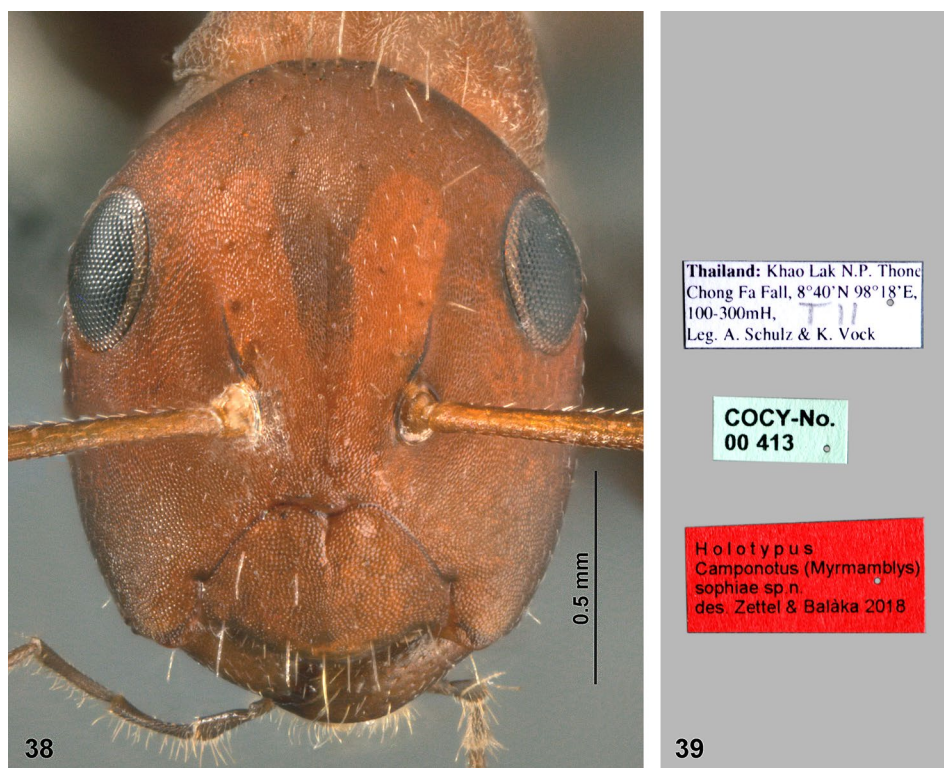
Measurements of paratype (n = 1): HW 1.24; HL 1.41; SL 1.46; SW 0.15; EL 0.40; ML 1.89; HaL 0.34; FeL 1.70; CI 88; SI 118; EI 32; FeI 137. – Ward's Indices:  $ASM/HW_{ex}$  0.27;  $ASM/CLW$  0.56;  $CLW/CLL$  1.42.



Figs. 36–37: *Camponotus (Myrmamblys) sophiae* ZETTEL & BALÁKA sp.n., holotype, minor worker, (36) lateral and (37) dorsal view. © P. Baláka.

Structures: Head roundish, uniformly reticulated and matt dorsally and laterally, ventrally with slightly reduced microsculpture and somewhat shiny. Lateral outline of eye and head contiguous. Vertex moderately raised. Frons with hardly discernable shiny midline.





Figs. 38–39: *Camponotus (Myrmamblys) sophiae* ZETTEL & BAL  KA sp.n., holotype, minor worker, (38) frontal view and (39) labels.   P. Bal  ka.

Clypeus with very small emargination at middle of basal margin, distal margin slightly protruded in middle, basally with a rather deep, shiny median impression. Mandible punctate, with five teeth. – Mesosoma slender and very low, densely reticulated and matt; dorsal outline of pronotum and posterior slope of propodeum moderately convex, outline of mesonotum and anterior part of propodeum straight. – Petiole with very high node, its anterior and posterior face parallel, apex strongly obliquely truncated. – Gaster tergites with dense reticulation.

Pilosity: Pale long standing setae abundant all over dorsum, longest on propodeum, petiole, gaster tergites 1 and 4. Subdecumbent pubescence short, thin, whitish, rather inconspicuous.

Colour: Trunk reddish, tending to orange on head and mesosoma, and to luteous on petiole and gaster; in the paratype the mesosoma also rather luteous, and gaster with posteriorly slightly infuscated tergites; ventral side of gaster black; tergites 2–4 with very narrow translucent margins. Antenna and legs dark brown; scape yellowish.

Major and gyne: Unknown.

Comparative notes: This species is similar in colour to *C. weiserti* sp.n. from the same locality. It differs by the matt, densely reticulated pronotum, a longer median impression at the base of the clypeus, and in a longer flagellum: antennomere 7 is about three times as long as wide, while hardly more than twice as long in *C. weiserti* sp.n.

**Distribution:** Only known from the type locality in Phang-nga Province, Thailand.

**Etymology:** This species is named after the first author's younger daughter, Sophie.

***Camponotus (Myrmamblys) syaukanii* ZETTEL & YAMANE sp.n. (Figs. 40–46)**

**Type material:** Holotype (minor worker #1785; MZB) from Indonesia, Kalimantan, Tanah Tidung, Gunung Rian, hard dead branch, 26.III.2016, leg. Sk. Yamane & Syaukani, KM16-SKY-134. Paratypes (MZB, SKYC, CZW, NHMW): 5 minor workers, 4 major workers, same nest series as holotype.

**Diagnosis for worker castes:** Minor worker: Head and dorsal parts of mesosoma reddish brown; ventral parts of mesosoma, petiole, and gaster black; antenna orange, distally infuscated. Vertex highly domed. Basal margin of clypeus triangularly emarginated; anterior margin medially convex and shiny. Flagellum of normal length. Mesosoma with reduced sculpture, shiny. Pronotum with short standing setae. Dorsal outline of pronotum moderately convex, of mesonotum and propodeum almost straight. – Major worker: Colour similar as in minor; head slightly darker. Head squared, shiny, with coarse puncturation; microsculpture evanescent except on area between high frontal carinae and eye. Eyes small. Clypeus with concave basal margin, a pair of large setiferous punctures near base, and a large, shallowly depressed area apically. Reticulated sculpture of mesosoma more distinct than in minor, reduced only on pronotum. Petiole and gaster reticulated as in minor. Petiolar node more slender than in minor.

**Description of minor worker:** Measurements of holotype: HW 1.50; HL 1.76; SL 1.50; SW 0.16; EL 0.46; ML 2.22; HaL 0.16; FeL 1.86; CI 85; SI 100; EI 31; FeI 124. – Ward's Indices:  $ASM/HW_{ex}$  0.32;  $ASM/CLW$  0.73;  $CLW/CLL$  1.15. Note that the holotype is extraordinarily large compared to other minor workers.

**Measurements of paratypes (n = 5):** HW 1.24–1.36; HL 1.52–1.58; SL 1.49–1.58; SW 0.13–0.16; EL 0.38–0.40; ML 1.96–2.04; HaL 0.13–0.21; FeL 1.90–1.98; CI 82–90; SI 113–120; EI 29–31; FeI 142–153. – Ward's Indices:  $ASM/HW_{ex}$  0.30–0.32;  $ASM/CLW$  0.65–0.70;  $CLW/CLL$  1.16–1.24.

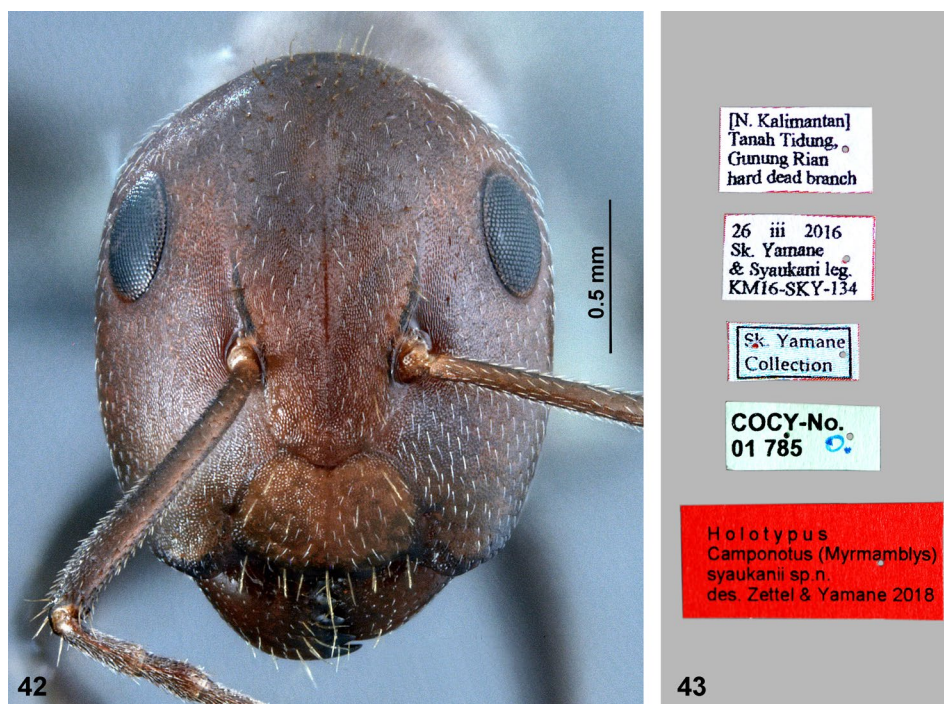
**Structures:** Head in full-face view longer than wide, with strongly convex vertex. Clypeus distinctly wider than long; posterior margin triangularly incised at middle; anteriorly produced, with extreme anterior margin truncate. Eye large, weakly convex, not breaking lateral outline of head. Mandible with five teeth, which decrease in size toward base. Dorsum of head extensively and densely micropunctate; temple and gena covered with dense longitudinal microstriae; ventral face of head superficially microsculptured; occiput almost smooth, shiny. Clypeus densely micropunctured but its anterior narrow strip more weakly sculptured with a few pits from which setae arise. Mandible with microstriae area close to inner basal portion. Antennal scape long, with head in full-face view surpassing posterior margin of head by more than two fifths of its length; first funicular segment (pedicel) longer than second, as long as apical segment. Mesosoma in dorsal view widest at pronotum; mesonotum as wide as propodeum. Suture between pronotum and mesonotum distinct; suture between mesonotum and propodeum less pronounced. Posterior half of mesonotum and propodeum together dorsally forming rather sharp longitudinal ridge. Mesosoma in profile weakly convex dorsally; posterior portion of pronotum and mesonotum forming almost flat dorsal outline; propodeum sloping posteriad with only weak differentiation of dorsal from posterior face; posterior face (declivity) of propodeum sometimes margined laterally by blunt carinae near base. Propodeal spiracle very small, almost of the size of the mesothoracic spiracle. Mesosoma extensively with dense micro-





Figs. 40–41: *Camponotus (Myrmamblys) syaukanii* ZETTEL & YAMANE sp.n., holotype, minor worker, (40) lateral and (41) dorsal view. © P. Balàka.

sculpture that is slightly larger than on head; lateral and posterior portions of pronotum and propodeal declivity more weakly sculptured and shiny. Petiole in frontal view apically shallowly but distinctly convex (in smaller minors) or almost flat (larger minors), in dorsal view short, its node shorter than wide, with transversely ridged summit; in profile node narrowed apically, as long as high, with short anterior face, anteriorly sloping dorsal face and rather steep posterior face. Gaster in dorsal view oviform, widest at second and third segments; first tergite with anterior margin evenly rounded; each tergite with very short (narrow) apical lamellate area. Gastral tergites 1–3 dorsally densely and finely sculptured,



Figs. 42–43: *Camponotus (Myrmamblys) syaukanii* ZETTEL & YAMANE sp.n., holotype, minor worker, (42) frontal view and (43) labels. © P. Balàka.

scattered with slightly larger pits from which setae arise. Dorsa of tergites 4–5, ventral sides of all tergites and entire sternites weakly sculptured and shiny.

**Pilosity:** Almost entire body covered with short, white, appressed pubescence. All standing setae on body straight and whitish. Dorsum of head between frontal carinae and on vertex with many standing setae, longer on vertex than on frons. Gena without standing setae; clypeus with sparse standing setae over disk; in frontal view its anterior margin bearing long median seta and several pairs of shorter ones. Mandible in frontal view with many standing setae along masticatory, anterior and lateral margins. Antennal scape with dense suberect to appressed short hairs mixed with very sparse longer setae (the latter more easily visible in lateral view). Mesosoma in profile with sparse standing setae that are roughly paired; those on propodeum much longer than others; lateral side of mesosoma without such setae. Petiole with two (rarely three) pairs of long standing setae and unpaired much shorter ones. Gastral tergites and sternites with many standing setae that are sometimes slanting or weakly curved. Legs covered with short suberect to appressed hairs; dorsal and ventral faces of forecoxa, and ventral face of forefemur (occasionally) with a few long standing setae.

**Colour:** Head and mesosoma reddish brown to orange, but mesosoma with dark areas. Petiole and gastral dorsum generally much darker than head and mesosoma. Area with lighter colour variable among individuals of the same colony. Gaster often with red tinge (fourth and fifth tergites always dark brown to black). Antenna reddish brown. Legs dark reddish brown to blackish brown.





Figs. 44–45: *Camponotus (Myrmamblys) syaukanii* ZETTEL & YAMANE sp.n., paratype, major worker, (44) lateral and (45) dorsal view. © P. Balàka.

Description of major worker: Measurements of paratypes (n=4): HW 1.91–1.96; HL 2.11–2.35; SL 1.30–1.37; SW 0.17–0.19; EL 0.47–0.50; ML 2.46–2.53; HaL 0.09–0.16; FeL 1.74–1.90; CI 82–91; SI 67–70; EI 25–26; FeI 90–98.





Figs.46: *Camponotus (Myrmamblys) syaukanii* ZETTEL & YAMANE sp.n., paratype, major worker, frontal view. © P. Balàka.

Structure: Head in full-face view almost rectangular, longer than wide, with weakly sinuated posterior margin and weakly roundly produced posterolateral corners. Frontal carina curved outwardly at midlength to form distinct frontal lobe; shallow median furrow present between frontal carinae. Clypeus much longer than wide; basal margin medially incised, laterally roundly convex; anterior two-thirds of clypeus with parallel lateral margins; anterior portion of clypeal disc lowered with short (narrow) apical strip that slightly extends forward; extreme anterior margin of the strip shallowly convex. Eye elongate, very shallowly convex, not reaching lateral margin of head. Antennal scape short, barely reaching posterolateral corner of head; first funicular segment as long as apical segment. Mesosoma similar to that of minor worker except in the following aspects: seen from above mesonotum not longitudinally ridged dorsally and ridge on propodeum more rounded than in minor worker; metanotum transversely rhombic, delimited from mesonotum and propodeum by distinct sutures. With petiole in frontal view dorsal outline of node almost flat. Gaster as in minor worker.

Pilosity: Similar to minor worker. Standing setae on frons and vertex relatively shorter than in the latter. Clypeus with one pair of stiff short standing setae near posterior margin; other parts of disc only occasionally with a few very short standing setae; anterior margin with median seta that is rather short but longer than lateral pairs. Mandible with several

standing setae around bases of teeth and along anterior margin. Antennal scape covered with very short decumbent pubescence and several standing setae on anterior face. Standing setae on pronotum and mesonotum very sparse and short; those on propodeum much longer. Petiole with two to three pairs of standing setae and some shorter softer hairs; venter of petiole with dense short soft hairs. Standing setae on gastral tergites 1–3 short; those on tergites 4–5 and posterior margins of sternites much longer.

Colour: Head and anterior half of mesosoma reddish brown; rest of mesosoma, petiole, gaster and legs much darker (often blackish) but occasionally with reddish tinge to varying extent. Antennal scape reddish brown.

Comparative notes: This species is rather dark in colouration compared with *C. weiserti* sp.n. and *C. concurrens* sp.n. The most closely related species is *C. weiserti*, but in the latter the mandible with a smaller striate area, in addition to colour difference. The minor worker of *C. concurrens* sp.n. is easily separable from *C. syaukanii* sp.n. by the strongly convex pronotum (see further notes under *C. concurrens* sp.n.).

Distribution: Only known from the type locality in Kalimantan, Indonesia.

Etymology: The specific epithet, *syaukanii*, is dedicated to our Indonesian friend, Dr. Syaukani of Syiah Kuala University, Aceh, Indonesia.

### ***Camponotus (Myrmamblys) paracolobopsis* ZETTEL & YAMANE sp.n. (Figs. 47–56)**

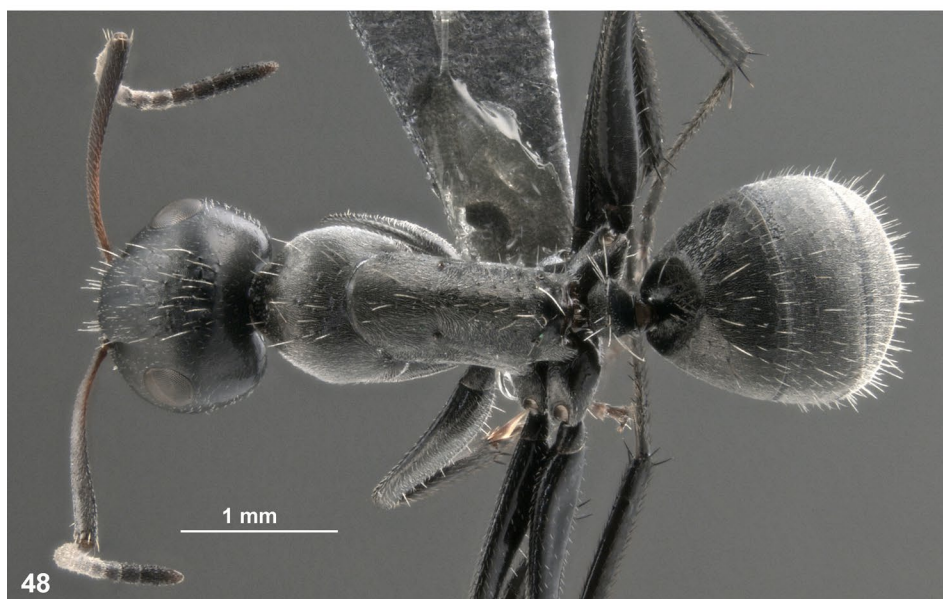
Type material: Holotype (minor worker #1132; BRM) from Brunei, Temburong, Kuala Belalong Field Studies Centre, visitor canopy walkway, 14.IV.2015, leg. A. Kopchinskiy, #VCW 322. Paratypes (BRM, SKYC, CZW, NHMW): 5 minor workers (#1128–1131, 1133), 3 major workers (#1125–1127), and 2 alate gynes (#1123, 1124), same nest series; 1 minor worker, same locality, sample 45; 1 major worker (#1807), 1 minor worker (#1808), Malaysia, Sarawak, Lambir N.P., Canopy 4 ha, 8.III.2004, leg. H.O. Tanaka, P(10) B(5), TY(04)-(637) (“sp. 65”); 5 minor workers (#1818), 7 major workers (#1821, 1822), Indonesia, Borneo, North Kalimantan, Tanah Tidung, Gunung Rian, in hard dead wood, 26.III.2016, leg. Sk. Yamane & Syaukani, KM16-SKY-111.

Diagnosis for worker castes: Minor worker: Black species with brown scape and base of funiculus; only on tergites 3–4 with very narrow, translucent hind margins. Long white standing setae abundant all over dorsum. Basal margin of clypeus with distinct concavity. Flagellum of normal length. Pronotum with distinct sculpture, but somewhat shiny. Dorsal outline of mesonotum and propodeum slightly convex, propodeum moderately downcurved. Petiolar node high and narrow in lateral aspect. – Major worker: Colour as in minor, except anterior margin of head medium to yellowish brown; anterior part of frons and mandibles reddish brown. Head with scattered medium-sized punctures, denser on genae and clypeus. Clypeus with about 14–16 groove-like punctures, base with narrow medial impression. Genae with some comparatively large punctures.

Description of minor worker: Measurements of holotype: HW 1.46; HL 1.54; SL 1.48; SW 0.13; EL 0.50; ML 2.09; HaL 0.33; FeL 1.86; CI 94; SI 101; EI 35; FeI 128. – Ward’s Indices: ASM/HW<sub>ex</sub> 0.28; ASM/CLW 0.58; CLW/CLL 1.43.

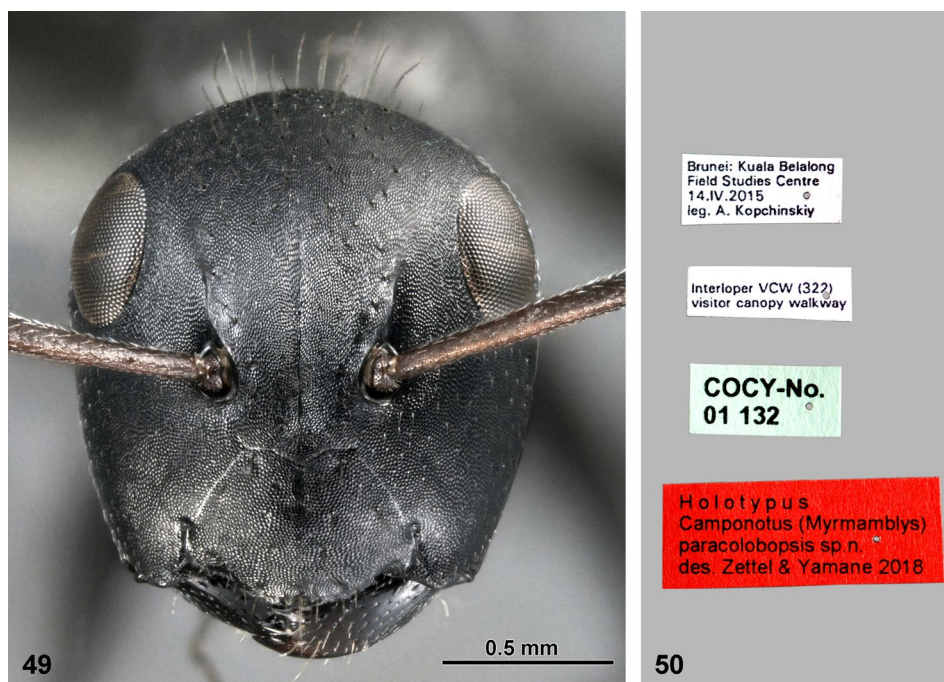
Measurements of paratypes (n = 7): HW 1.35–1.55; HL 1.43–1.63; SL 1.40–1.50; SW 0.15–0.16; EL 0.46–0.54; ML 2.02–2.22; HaL 0.27–0.44; FeL 1.76–1.86; CI 89–98; SI 94–107; EI 33–36; FeI 115–137. – Ward’s Indices: ASM/HW<sub>ex</sub> 0.26–0.28; ASM/CLW 0.55–0.65; CLW/CLL 1.15–1.38.

Structures: Head roundish, uniformly reticulated and matt dorsally and laterally, ventrally with slightly reduced microsculpture and somewhat shiny. Lateral outline of eye and head



Figs. 47–48: *Camponotus (Myrmamblys) paracolonopsis* ZETTEL & YAMANE sp.n., holotype, minor worker, (47) lateral and (48) dorsal view. © P. Balàka.





Figs. 49–50: *Camponotus (Myrmamblys) paracolobopsis* ZETTEL & YAMANE sp.n., holotype, minor worker, (49) frontal view and (50) labels. © P. Balàka.

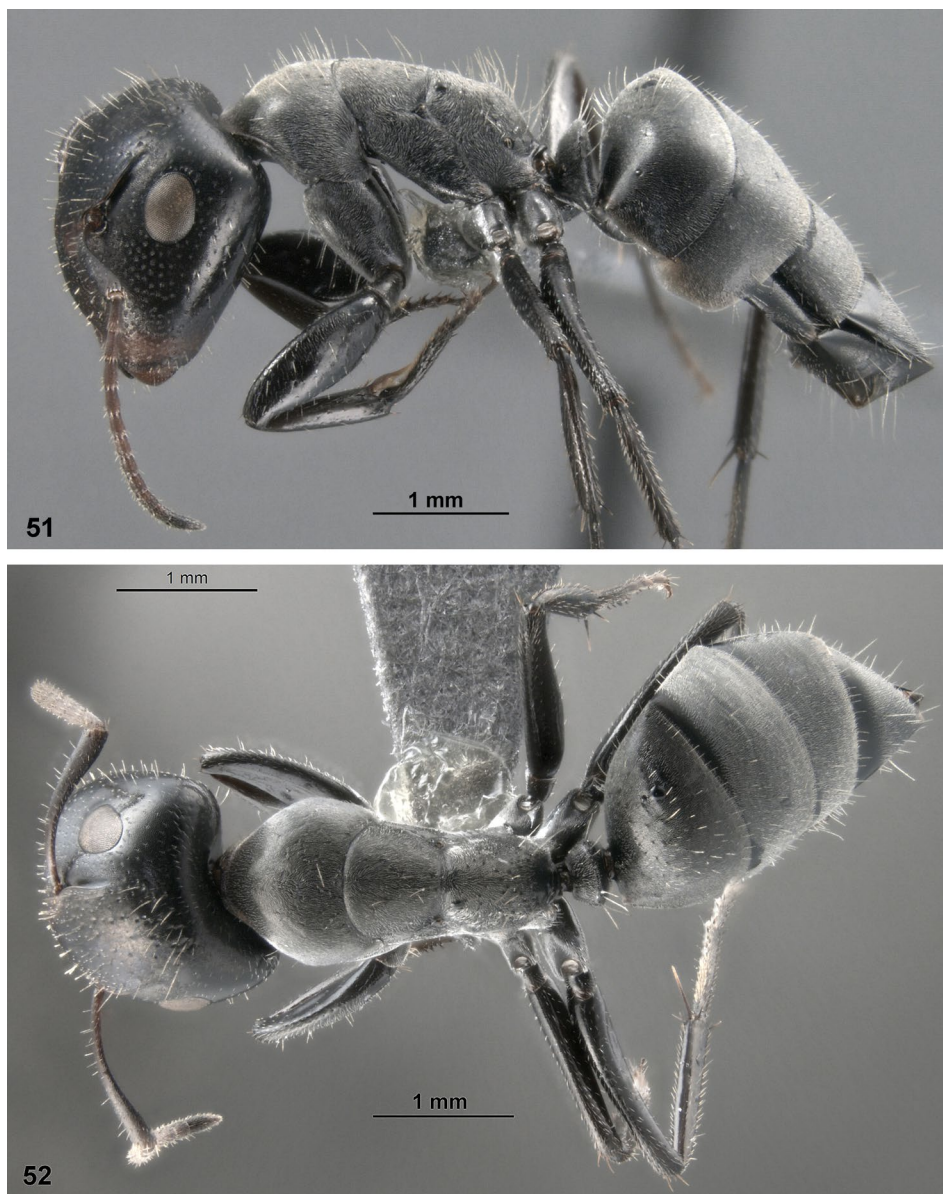
contiguous. Vertex moderately raised, not domed. Frons with hardly discernable shiny midline. Clypeus with distinct emargination at middle of basal margin, with distal margin slightly protruded in middle, with very narrow often reduced shiny midline. Mandible scarcely punctured, with five teeth. – Mesosoma slender and low, entirely reticulated, but with a silky shimmer; dorsal outline convex, on pronotum and propodeum moderately convex, without distinct indentions. – Petiolar node posteriorly very high, its anterior and posterior face parallel, apex strongly obliquely truncated. – Gaster tergites entirely with dense reticulation, including very narrow translucent margins on tergites 3–4.

Pilosity: White long standing setae abundant all over dorsum, longest on mesonotum, propodeum, gaster tergites 1 and 4. Subdecumbent pubescence short, thin, whitish, extremely sparse and inconspicuous on head, dense and distinct on mesosoma, petiole, and gaster.

Colour: Trunk, mandibles, palpi, and legs black. Antenna black, except larger part of scape and basis of funicular segments 1–4(5) brown or orange brown. Tergites 3–4 with very narrow translucent margins.

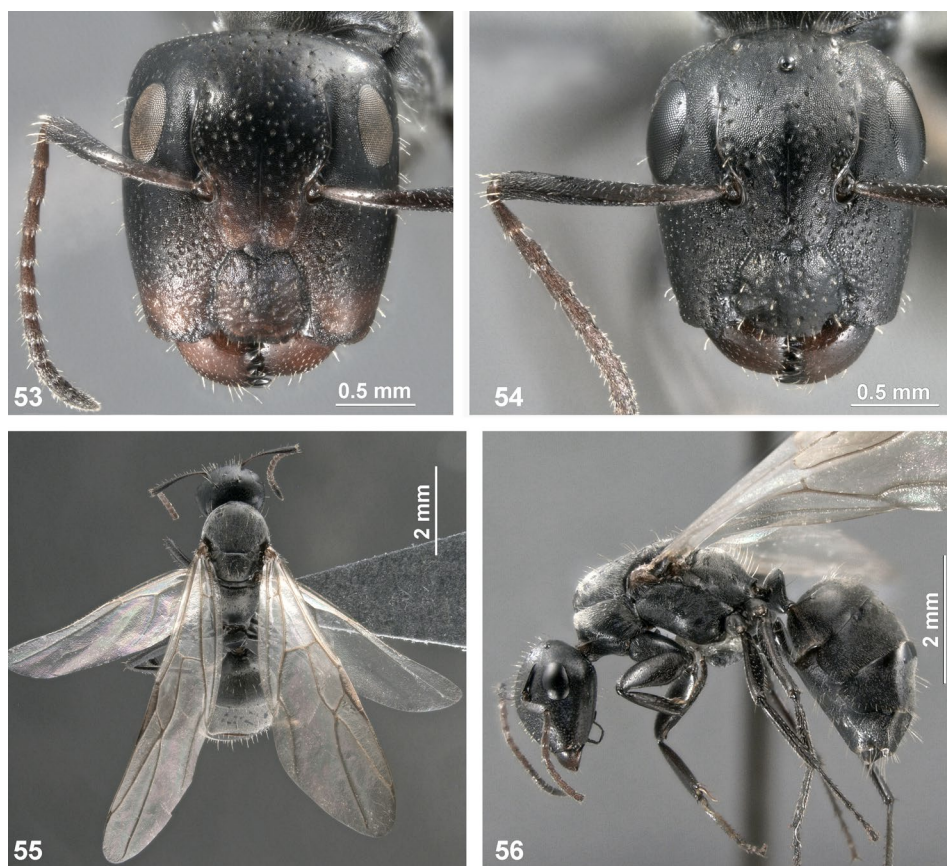
Description of major worker: Measurements of paratypes (n = 6): HW 1.76–2.02; HL 2.00–2.28; SL 1.22–1.35; SW 0.17–0.23; EL 0.54–0.58; ML 2.35–2.67; HaL 0.28–0.33; FeL 1.60–1.76; CI 85–90; SI 67–70; EI 28–33; FeI 84–97.

Structures: Head squared, moderately longer than wide. Eyes small, laterally not reaching sides of head. Ocellar scars absent. Frontal carinae prominent, curved. Entire head with reticulate microsculpture, ventrally more superficial and slightly shiny. In addition,



Figs. 51–52: *Camponotus (Myrmamblys) paracolobopsis* ZETTEL & YAMANE sp.n., paratype, major worker, (51) lateral and (52) dorsal view. © P. Balàka.

vertex, frons, clypeus, and temples with two types of punctures, medium-sized and very large, the latter bearing the standing setae; number of large groove-like punctures on clypeus 12–16. Genae only with large punctures bearing no or very short setae. Clypeus moderately narrow, about 1.3 times as long as wide; basal margin with distinct emargination; base with short, narrow median impression, in one specimen inconspicuous; anterior



Figs. 53–56: *Camponotus (Myrmamblys) paracolobopsis* ZETTEL & YAMANE sp.n., paratype, major worker, (53) frontal view, and paratype, alate gyne, (54) frontal, (55) dorsal, and (56) lateral view. © P. Balàka.

margin strongly protruded, but hardly surpassing genae. Mandibles with fine, widely spaced punctures and very fine micropunctures. – Mesosoma similar to minor regarding microsculpture and dorsal outline, but slightly higher, somewhat broader at pronotum. – Node of petiole similar to minor, but apex less acute in lateral view and straighter in anterior view. – Gaster similar as in minor.

Pilosity: Similar to minor, except white setae on head, pronotum, and mesonotum comparatively shorter; short pubescence absent from head.

Colour: Black, similar to minor, with the following exceptions: anterior part of genae yellowish or reddish brown; anterior part of clypeus medium to dark brown; anterior part of frons light to medium brown; mandibles reddish brown, except black teeth; orange-brown colour of funiculus more extended.

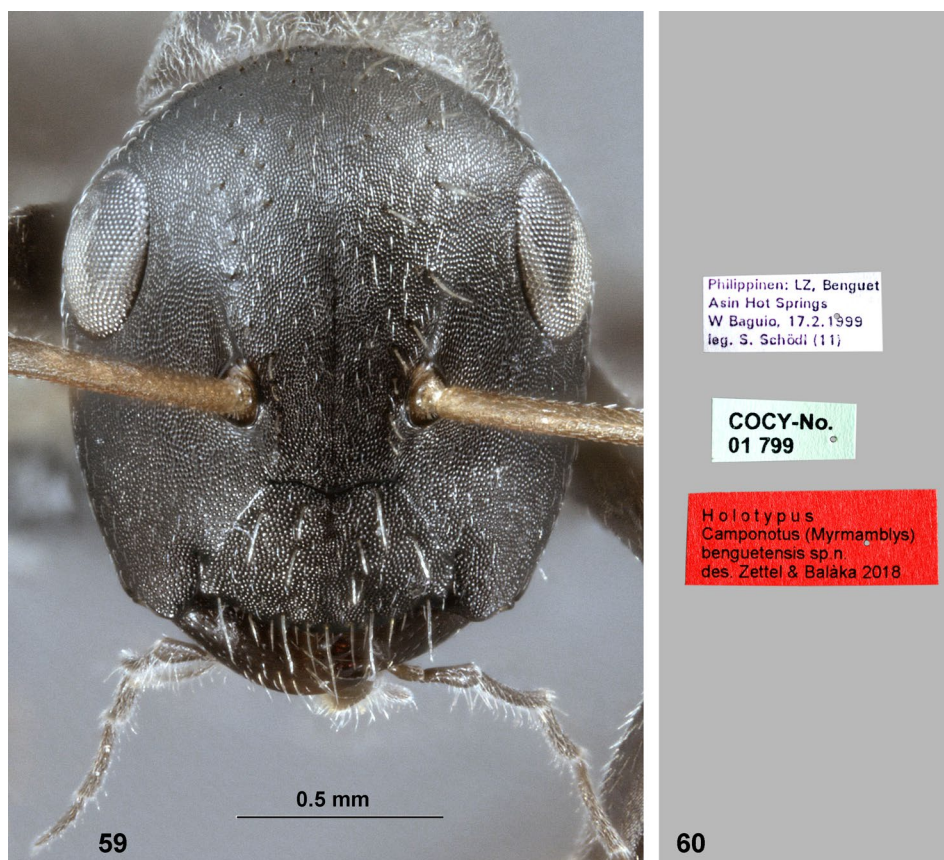
Description of gyne: Measurements of paratypes (n = 2): HW 1.65, 1.67; HL 1.78, 1.83; SL 1.37, 1.39; SW 0.17, 0.19; EL 0.62, 0.63; ML 3.13, 3.26; HaL 0.28, 0.29; FeL 1.83, 1.84; OcW 0.11; FWL 8.87; CI 92, 93; SI 83; EI 37, 38; FeI 110, 111.





Figs. 57–58: *Camponotus (Myrmamblys) benguetensis* ZETTEL & BALÁKA sp.n., holotype, minor worker, (57) lateral and (58) dorsal view. © P. Baláka.

Structures: Intermediate between minor and major in many characters. Head roundish, somewhat elongated. Eyes large, slightly surpassing outline of head. Ocelli present. Sculpture of head similar as in major. Clypeus with emarginated base and medially protruded anterior margin. – Mesosoma with gyne-specific structures, entirely bearing reticulated microsculpture, slightly shiny; mesoscutum anteriorly with short, narrow, deep median impression. – Petiole similar as in major. – Gaster larger than in workers, translucent margins of tergites 3–4 somewhat broader.



Figs. 59–60: *Camponotus (Myrmamblys) benguetensis* ZETTEL & BALÁKA sp.n., holotype, minor worker, (59) frontal view and (60) labels. © P. Balàka.

**Pilosity:** Similar to major. Standing setae on thoracic nota short, completely absent from pronotum. Short pubescence absent from head.

**Colour:** Black, similar to minor, except anterior margin of clypeus dark brown, mandibles reddish brown, except black teeth, and orange-brown colour of funiculus more extended. Wings grayish-yellow; veins yellow to yellow-brown.

**Comparative notes:** Among the (almost) entirely black species, *C. paracolobopsis* sp.n. has the major workers with the most strongly sculptured head (major worker of *C. paraleonardi* sp.n. unknown). *Camponotus paraleonardi* sp.n. differs by the golden hair on mesosoma and gaster, *C. kutteri* by distinct pale hind margins of gaster tergites. *Camponotus benguetensis* sp.n. from the Philippines is most similar; see the comparative notes of this species.

The paratype series from Kalimantan differs from the Brunei series by very dark antennae and, in major workers, by less obvious grooves on clypeus and genae between the very pronounced microsculpture, but is regarded as conspecific. These specimens resemble *C. benguetensis* sp.n., but differ in the structures at clypeus base.







**Distribution and biological notes:** This species is currently only known from Borneo (Brunei, North Kalimantan, Sarawak). One colony was discovered in an artificial nest close to the “visitor canopy walkway” in the Ulu Temburong National Park, Brunei. The nest contained only specimens of *C. paracolobopsis* sp.n. and may have been a complete colony (or fragment thereof) with minor workers, major workers, gynes and brood (see notes on *C. inquilinus* sp.n.).

**Etymology:** The species epithet (a noun in apposition) refers to the similarity with the genus *Colobopsis*.

***Camponotus (Myrmamblys) benguetensis* ZETTEL & BALÁKA sp.n. (Figs. 57–63)**

**Type material:** Holotype (minor worker #1799; NHMW) from the Philippines, Luzon, Benguet, W Baguio, Asin Hot Springs, 17.II.1999, leg. S. Schödl. Paratypes (NHMW, CZW, NMNH): 4 minor workers (#85, 1796–1798), 2 major worker (#86, 240), same label data; 5 minor workers (#1800–1804), 2 major workers (#1805, 1806), from Benguet, W Baguio, Asin Road-km 7, 17.II.1999, leg. H. Zettel.

**Diagnosis for worker castes:** Minor worker: Black species with orange scape and first funicular segment. Long white standing setae abundant all over dorsum. Clypeus basally almost straight. Flagellum of normal length. Pronotum with distinct sculpture, but somewhat shiny. Dorsal outline of mesonotum and propodeum slightly convex, propodeum rather abruptly downcurved. Petiolar node high and narrow in lateral aspect. – Major worker: Colour as in minor, except anterior part of head and mandibles medium to light brown. Head with scattered medium-sized punctures, denser on genae and clypeus. Clypeus with 6–8 groove-like punctures, base with deep medial impression.

**Description of minor worker:** Measurements of holotype: HW 1.30; HL 1.39; SL 1.39; SW 0.13; EL 0.41; ML 1.89; HaL 0.32; FeL 1.63; CI 94; SI 107; EI 32; FeI 125. – Ward’s Indices: ASM/HW<sub>ex</sub> 0.28; ASM/CLW 0.61; CLW/CLL 1.40.

Measurements of paratypes (n = 9): HW 1.17–1.43; HL 1.41–1.54; SL 1.41–1.52; SW 0.14–0.17; EL 0.43–0.46; ML 1.76–2.15; HaL 0.30–0.39; FeL 1.61–1.74; CI 79–95; SI 98–128; EI 31–38; FeI 118–142. – Ward’s Indices: ASM/HW<sub>ex</sub> 0.28–0.33; ASM/CLW 0.59–0.67; CLW/CLL 1.29–1.45.

**Structures:** Head roundish, uniformly reticulated and matt dorsally and laterally, ventrally with slightly reduced microsculpture and somewhat shiny. Lateral outline of eye and head contiguous. Vertex moderately raised, not domed. Frons with hardly discernable shiny midline. Clypeus with an almost straight, slightly angular basal margin, with distal margin slightly protruded in middle, with reduced shiny midline at base. Mandible scarcely punctured, with five teeth. – Mesosoma slender and low, entirely reticulated, but with a silky shimmer; dorsal outline convex, on pronotum and propodeum moderately convex, without distinct indentations. – Petiolar node posteriorly high, its anterior and posterior face parallel, apex obliquely truncated. – Gaster tergites entirely with dense reticulation, including very narrow translucent margins on tergites 2–4.

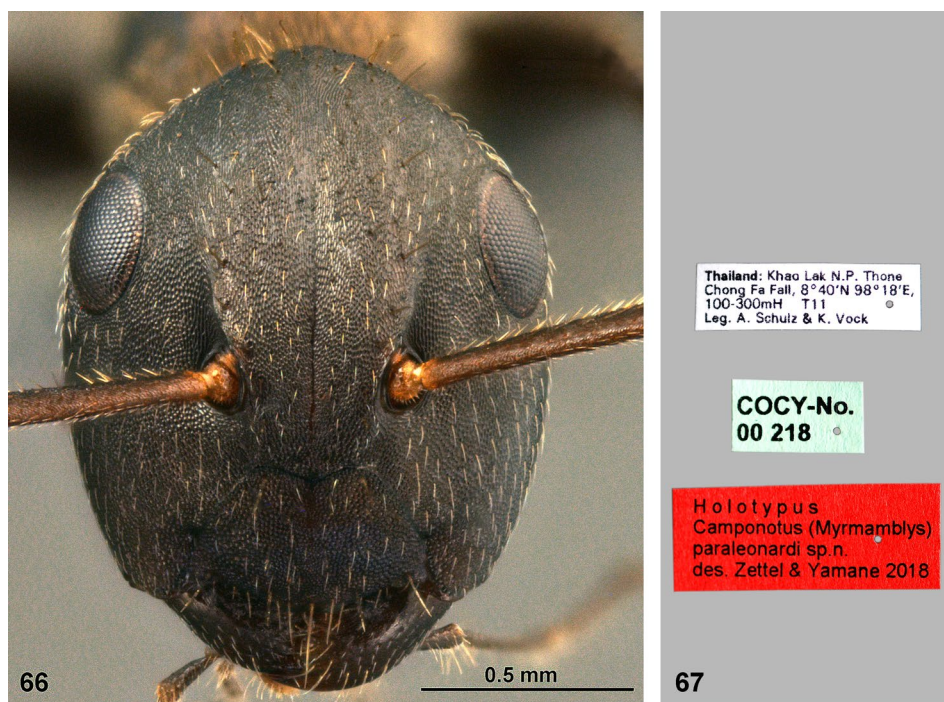
**Pilosity:** White long standing setae abundant all over dorsum, longest on mesonotum, propodeum, gaster tergites 1 and 4. Subdecumbent pubescence short, thin, whitish, extremely sparse and inconspicuous on head, dense and distinct on mesosoma, petiole, and gaster.

Figs. 61–63: *Camponotus (Myrmamblys) benguetensis* ZETTEL & BALÁKA sp.n., paratype, major worker, (61) frontal, (62) lateral, and (63) dorsal view. © P. Baláka.



Figs. 64–65: *Camponotus (Myrmamblys) paraleonardi* ZETTEL & YAMANE sp.n., holotype, minor worker, (64) lateral and (65) dorsal view. © P. Balàka.

Colour: Trunk, palpi, and legs black. Mandibles brown. Antenna black; scape orange, brownish infuscated towards apex; first funicular segment entirely orange or pale brown, strongly contrasting with black second segment. Tergites 3–4 with very narrow translucent margins.



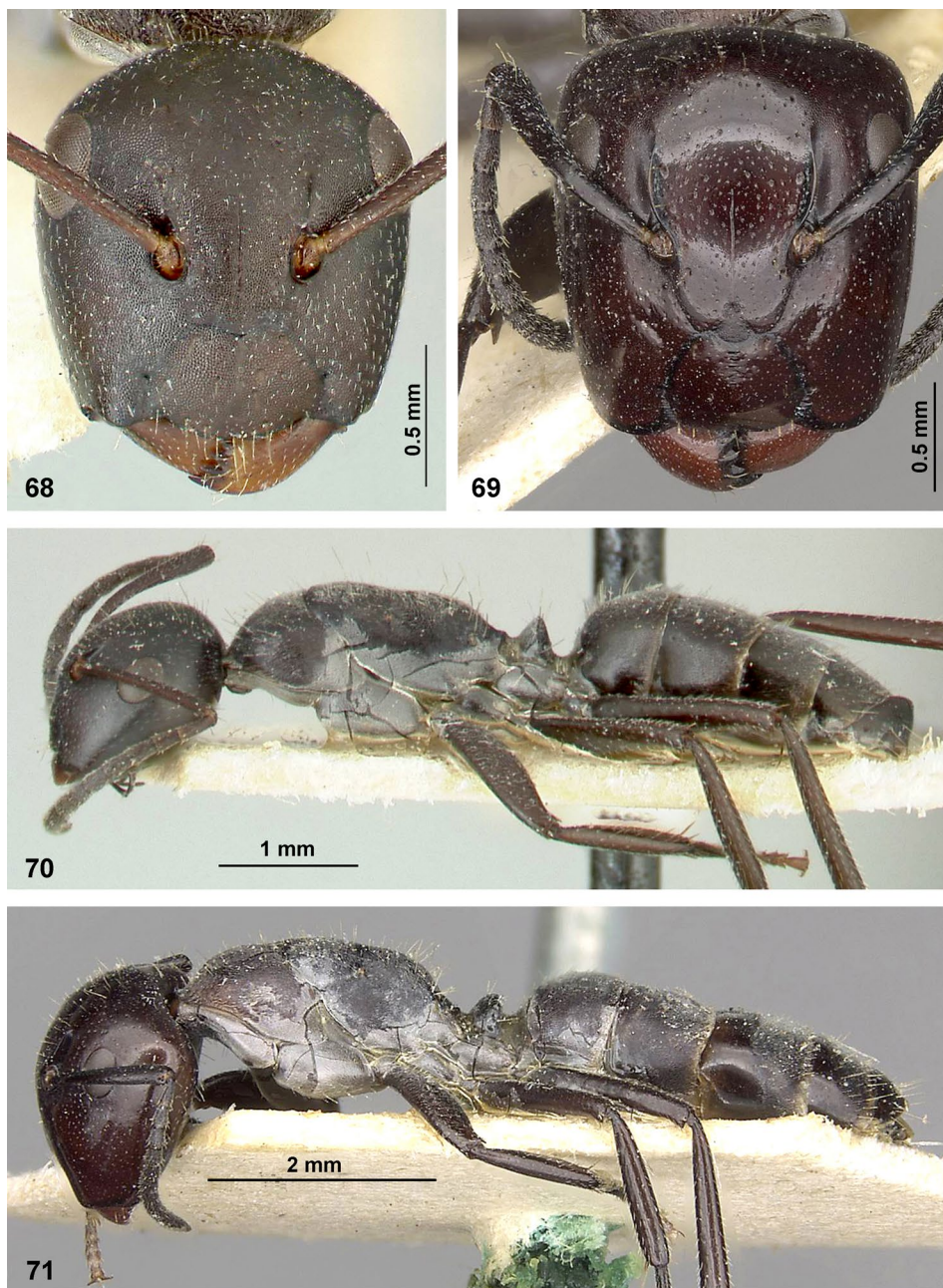
Figs. 66–67: *Camponotus (Myrmamblys) paraleonardi* ZETTEL & YAMANE sp.n., holotype, minor worker, (66) frontal view and (67) labels. © P. Baláka.

Description of major worker: Measurements of paratypes ( $n=4$ ): HW 1.72–1.96; HL 2.00–2.25; SL 1.17–1.28; SW 0.20–0.22; EL 0.50–0.56; ML 2.15–2.54; HaL 0.21–0.31; FeL 1.53–1.63; CI 86–90; SI 60–72; EI 25–29; FeI 78–91.

Structures: Head squared, longer than wide. Eyes small, laterally not reaching sides of head. Ocellar scars absent. Frontal carinae prominent, curved. Entire head with reticulate microsculpture, ventrally more superficial and slightly shiny. In addition, vertex, frons, clypeus, and temples with two types of punctures, medium-sized and large, the latter bearing the standing setae; number of large groove-like punctures on clypeus 6–8. Genae only with moderately large punctures bearing no setae. Clypeus moderately narrow, about 1.3 times as long as wide; base slightly elevated over frontal triangle and deeply incised along midline; anterior margin strongly protruded, but hardly surpassing genae. Mandibles with fine, widely spaced punctures and very fine micropunctures. – Mesosoma similar to minor regarding microsculpture and dorsal outline, slightly higher and somewhat broader at pronotum. – Node of petiole similar to minor, but apex less acute in lateral view and straighter in anterior view. – Gaster similar as in minor.

Pilosity: Similar to minor, except that white setae on head, pronotum, and mesonotum comparatively shorter; short pubescence absent from head.





Figs. 68–71: *Camponotus (Myrmamblys) kutteri* FOREL, 1915, syntypes: frontal views of (68) minor and (69) major worker; lateral views of (70) minor and (71) major worker. © 68, 70: Christiana Klingenberg, State Museum of Natural History Karlsruhe; 69, 71: Zach Lieberman, ANTWEB.

Colour: Black, similar to minor, except head anterior of antennal grooves medium brown (laterally less far); mandibles reddish brown, except black teeth, and orange colour of funiculus more extended.

Gyne: Unknown.

Comparative notes: This species is very similar to *C. paracolobopsis* sp.n. The major workers are well separable by structure and sculpture of genae and clypeus (see key and Figs. 53 and 61), whereas the differentiating characters for minors are more subtle: In *C. benguetensis* sp.n., the basal margin of the clypeus is straighter, the propodeum more abruptly downcurved, and the apex of the petiole less acute than in *C. paracolobopsis* sp.n. Differences in the colour of the antenna (see key) are not very reliable due to considerable variation in both species.

Distribution: Only known from the type locality in northern Luzon. Most likely restricted to the Philippines.

Etymology: Named after the province of origin, Benguet.

***Camponotus (Myrmamblys) paraleonardi* ZETTEL & YAMANE sp.n. (Figs. 64–67)**

Type material: Holotype (minor worker, #218, NHMW) from Thailand, Phang-nga Province, Khao Lak N.P., Thone Chong Fa Falls, N8°40', E98°18', 100–300 m a.s.l., leg. A. Schulz & K. Vock, #T11. Paratypes (NHMW): 1 minor worker (#214), same locality data as holotype; 1 minor worker (#6) from Myanmar, Mandalay Division, Mt. Popa, Popa village environment, N20°54.175', E95°14.049', 28.X.1998, leg. H. Schillhammer.

Diagnosis for worker castes: Minor worker: Black species with brown antennae and legs; long pale standing setae abundant all over dorsum; dense golden pubescence on dorsum of mesosoma and on gaster tergites characteristic. Vertex elevated. Clypeus basally with small emargination at middle. Flagellum of normal length. Pronotum with reduced sculpture, somewhat shiny. Dorsal outline of pronotum moderately convex, of mesonotum and propodeum almost straight, propodeum gently downcurved. Petiolar node high and narrow in lateral aspect. – Major worker unknown.

Description of minor worker: Measurements of holotype: HW 1.21; HL 1.39; SL 1.36; SW 0.14; EL 0.37; ML 1.83; HaL 0.29; FeL 1.63; CI 87; SI 113; EI 31; FeI 135. – Ward's Indices: ASM/HW<sub>ex</sub> 0.31; ASM/CLW 0.61; CLW/CLL 1.47.

Measurements of paratypes (n = 2): HW 1.22, 1.24; HL 1.39, 1.48; SL 1.36, 1.39; SW 0.15, 0.16; EL 0.38, 0.44; ML 1.89, 1.96; HaL 0.30, 0.35; FeL 1.37, 1.70; CI 82, 89; SI 110, 114; EI 31, 37; FeI 111, 139. – Ward's Indices: ASM/HW<sub>ex</sub> 0.36, 0.30; ASM/CLW 0.67, 0.61; CLW/CLL 1.33.

Structures: Head roundish, uniformly reticulated and matt dorsally and laterally, with slightly reduced microsculpture and somewhat shiny ventrally. Lateral outline of eye and head contiguous. Vertex raised. Frons and basal half of clypeus with shiny midline. Clypeus with very small emargination at middle of basal margin, distal margin slightly protruded in middle. – Mesosoma slender and low, densely reticulated and matt except for slightly shiny pronotum where reticulation is weakly developed; dorsal outline of pronotum and posterior slope of propodeum moderately convex, of mesonotum and anterior part of propodeum almost straight. – Petiole with high node, its anterior and posterior face parallel, apex obliquely truncated. – Gaster tergites with dense reticulation.

**Pilosity:** Long standing setae abundant all over dorsum, of white or pale yellow colour, longest on pronotum and propodeum. Pubescence very dense, golden to yellow on dorsum of mesosoma and on gaster tergites, on other parts pale yellowish and sparse, very short on dorsum of head.

**Colour:** Trunk black; translucent margins on tergites 3 and 4 very narrow, hardly discernable. Antenna and legs dark brown; scape lighter, pale to medium brown.

**Variation:** The worker from Myanmar differs in some characters, but is considered as conspecific: base of scape yellowish; vertex of head less convex (but head of this specimen deformed); dorsal outline of mesonotum and propodeum very straight.

**Major worker and gyne:** Unknown.

**Comparative notes:** This species can be easily recognized by the dense golden pubescence on the dorsal mesosoma and gastral tergites, which makes it very similar to *Colobopsis leonardi*. The single specimen from Myanmar differs by a yellowish base of the scape and shows fewer setae dorsally on the head, but is supposedly conspecific.

**Distribution:** Recorded from Phang-nga Province in Thailand and from Mandalay Division in Myanmar.

**Etymology:** Named after its great similarity to *Colobopsis leonardi*.

### ***Camponotus (Myrmamblys) kutteri* FOREL, 1915 (Figs. 68–71)**

*Camponotus (Myrmamblys) kutteri*: FOREL 1915: 40 (minor, major, queen, male), Sumatra.

*Camponotus (Myrmamblys) kutteri* FOREL, 1915 in “group 1 (*reticulatus*)”. EMERY 1925: 138.

*Camponotus (Myrmamblys) kutteri* FOREL, 1915; BOLTON 1995: 107.

*Camponotus kutteri*, subgenus *Colobopsis*: McARTHUR 2012: 44.

**Illustrations of type material examined:** AntWeb illustrates three syntypes (1 major CASENT0910520, 2 minor workers CASENT0910521, FOCOL2278) deposited in MNHG and MHUB.

**Diagnosis for worker castes:** Trunk, antennae and legs black; only mandibles orange; tergites with narrow but distinct pale hind margins. – Minor worker: Body matt to moderately shiny. Vertex moderately high. Posterior margin of clypeus concave. Dorsal outline of mesosoma strongly convex, with a shallow depression between mesonotum and propodeum. – Major worker: Head squared, about as long as wide; strongly shiny, with scattered punctures; some notably large punctures on frons.

**Descriptive notes on minor worker:** Measurements of syntypes, taken from illustration: Ward's Indices: ASM/HW<sub>ex</sub> 0.31, 0.30; ASM/CLW 0.65, 0.62; CLW/CLL 1.54, 1.61.

**Structures:** Head roundish, uniformly reticulated and matt dorsally and laterally. Lateral outline of eye and head contiguous. Vertex moderately raised, not domed. Frons with shiny midline. Clypeus with a slightly concave basal margin, with distal margin roundly protruded. Mandible scarcely punctured. – Mesosoma slender and low, entirely reticulated; dorsal outline convex, with a shallow impression between mesonotum and propodeum; on pronotum and propodeum moderately convex. – Petiolar node with obliquely truncated apex. – Gaster tergites with reticulation; translucent margins on tergites 1–4 distinct.



**Pilosity:** Long white standing setae abundant all over dorsum, longest on mesonotum, propodeum, gaster tergites 1 and 4. Subdecumbent pubescence short, thin, whitish, extremely sparse and inconspicuous on head, dense on mesosoma, petiole, and gaster.

**Colour:** Dark brown to black, except scape brown and mandibles orange.

**Descriptive notes on major worker:** Structures: Head squared, longer than wide, sides slightly converging anteriorly. Eyes small, laterally not reaching sides of head. Ocellar scars absent. Frontal carinae prominent, curved. Dorsal surface of head with strong, widely spaced punctures; interspaces with reduced, hardly visible microsculpture, except area between high frontal carinae and eye clearly reticulated. Clypeus moderately narrow; basal margin with strong concavity in middle; anterior margin moderately protruded, not surpassing genae; disk with a few transverse wrinkles near base. Mandibles with widely spaced punctures. – Mesosoma similar to minor regarding microsculpture and dorsal outline, but slightly higher and somewhat broader at pronotum. – Node of petiole similar to minor, but apex less acute in lateral view. – Gaster similar as in minor.

**Pilosity:** Similar to minor, except white setae on head, pronotum, and mesonotum comparatively shorter; short pubescence absent from head.

**Colour:** Black, similar to minor, except head and anterior part of pronotum medium brown; mandibles reddish brown, except black teeth.

**Comparative notes:** The species fits relatively well in the species group, except for the distinct pale yellowish hind margins of gaster tergites in both major and minor workers, which resemble some species of *Myrmamblys*. The major worker strongly differs from other related black species by the shiny head, the minor worker by the more concave base of the clypeus.

**Further notes:** FOREL (1915) described all morphs including males. He compared *C. kutteri* with *C. punctaticeps* MAYR, 1867 from Java, which has been listed as either a member of the subgenus *Myrmamblys* (FOREL 1914, EMERY 1925) or *Colobopsis* (MCARTHUR 2012) by previous authors. According to the same publication (FOREL 1915), the species lives in Sinabang in sympatry (but not necessarily at the same localities) with “*Camponotus (Colobopsis) pilosus* SMITH”. This taxon is a member of the *Colobopsis cylindrica* group and is presently under investigation.

**Distribution:** Only known from the type locality on Simeulue Island, Indonesia.

## Discussion

EMERY (1925) treated *Myrmamblys* as a very diverse subgenus of *Camponotus* and included 57 species from the Eastern Hemisphere. Even after the splitting by SANTACHI (1926), who excluded the African and some Asian species, *Myrmamblys* remains a very heterogeneous assemblage and is possibly not monophyletic. There are no strong morphological characters defining this subgenus. A distinct dimorphism of the worker castes including a pronounced phragmotic doorkeeper caste (“Eastern False Cork-head Ants”, ANTWIKI 2018), similar to some other subgenera of *Camponotus* and especially to *Colobopsis*, may be a result of parallelism as an adaptation to nesting in hard wood. In the present assembly of *Myrmamblys*, the *C. inquilinus* species group can be defined only by two negative characters, the absence of distinct modifications of the propodeum and of yellow patches on gaster tergites. The only “common character” of the species is

coevolution with syntopic or sympatric *Colobopsis cylindrica* group species, which makes a monophyly of the group plausible.

The ecological role of the herein established *C. inquilinus* species group remains a mystery in many regards: Based on the hitherto conducted fieldwork and observations in Brunei, at least two species (*C. inquilinus* sp.n. and *C. paracolobopsis* sp.n.) have been found to occupy their own nests containing all castes and brood. A minor worker of one species (*C. inquilinus* sp.n.) was found inside an artificial nest occupied by an undescribed COCY species (LACINY et al. 2017). Minor workers of most other species were found within nest- or trail samples of other COCY species, but only identified as belonging to the *C. inquilinus* group after sampling, when specimens were examined under a microscope and the morphological differences became apparent. Thus, they were obviously in close proximity to their “hosts” and not readily distinguishable from them in the field, due to similarity of size, colouration and behaviour. Only minor workers have hitherto been found in mixed samples and no instances of aggression between the species have ever been observed in the wild.

The exact nature of the species’ relationship is still an open question. As ants of the *C. inquilinus* group obviously possess all castes, have the ability to found their own nests and reproduce without a host, they are certainly not socially parasitic in the true sense of the word (HÖLLDOBLER & WILSON 1990, BUSCHINGER 2009). While true social parasitism (“inquilism”) is quite common among ants in general, it is hitherto only known from two Palearctic species of *Camponotus*, *C. universitatis* FOREL, 1890 (TINAUT et al. 1992) and *C. rusei* KARAMAN, 2012 (KARAMAN 2012), both currently in the subgenus *Tanaemyrmex* ASHMEAD, 1905. In contrast, the species group established herein may be considered xenobiotic (BUSCHINGER 2009) or simply engaging in tolerated commensalism with the respective COCY species. The observed similarity in appearance also points to the possibility of mimicry to gain protection from predators by blending into trails of the dominant and defensive COCY ants (see DAVIDSON et al. 2016, LACINY et al. 2017, 2018). This leads to the question of how members of the *C. inquilinus* group avoid detection by their host species. Ant colonies rely strongly on mutual recognition via cuticular hydrocarbons (CHCs) and parasitic or parabiotic species are known to possess special modifications of their CHC profiles to facilitate acceptance by the host colony (MENZEL & SCHMITT 2012, GUILLEM et al. 2014). Due to the lack of observed aggression by the usually very defensive COCY ants, similar adaptations of CHC profiles in the *C. inquilinus* group are highly probable and will be investigated in the near future (Hoenigsberger et al., in prep.).

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Authors' addresses: Dr. Herbert ZETTEL, Pia BALÁKA and Alice LACINY,  
2<sup>nd</sup> Zoological Department, Natural History Museum Vienna,  
Burgring 7, 1010 Vienna, Austria.

E-mail: [herbert.zettel@nhm-wien.ac.at](mailto:herbert.zettel@nhm-wien.ac.at); [pia@balaka.at](mailto:pia@balaka.at);  
[alice.laciny@nhm-wien.ac.at](mailto:alice.laciny@nhm-wien.ac.at)

Prof. Dr. Seiki YAMANE, Kagoshima University Museum,  
Kôrimoto 1-21-30, Kagoshima-shi, 890-0065 Japan.  
E-mail: [mayiopa0@gmail.com](mailto:mayiopa0@gmail.com)

Prof. Dr. Linda LIM, Chemical Sciences, Universiti Brunei  
Darussalam, Jalan Tungku Link, Bandar Seri Begawan, BE 1410,  
Brunei Darussalam. E-mail: [linda.lim@ubd.edu.bn](mailto:linda.lim@ubd.edu.bn)

Prof. Dr. Irina S. DRUZHININA, Research Area Biochemical  
Technology, Institute of Chemical, Environmental and Bioscience  
Engineering, TU Wien, Gumpendorfer Straße 1a, 1060 Vienna,  
Austria. E-mail: [irina.druzhinina@tuwien.ac.at](mailto:irina.druzhinina@tuwien.ac.at)

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