



## The ant genus *Rhopalomastix* (Hymenoptera: Formicidae: Myrmicinae) in Southeast Asia, with descriptions of four new species from Singapore based on morphology and DNA barcoding

WENDY Y. WANG<sup>1,4</sup>, GORDON W.J. YONG<sup>2</sup> & WEEYAWAT JAITRONG<sup>3</sup>

<sup>1</sup>Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377

<sup>2</sup>Department of Biological Sciences, Faculty of Science, National University of Singapore, 16 Science Drive 4, Singapore 117558

<sup>3</sup>Natural History Museum, National Science Museum, Technopolis, Khlong 5, Khlong Luang, Pathum Thani, 12120 Thailand

<sup>4</sup>Corresponding author. E-mail: [nhmwyw@nus.edu.sg](mailto:nhmwyw@nus.edu.sg)/[wywang24@gmail.com](mailto:wywang24@gmail.com)

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### Abstract

The true diversity of the Asian ant genus *Rhopalomastix* Forel is poorly understood. We use an integrated approach to review the known species and subspecies of *Rhopalomastix* in Southeast Asia. Based on morphology and supporting DNA evidence, we recognize six species. We raise two subspecies of *R. rothneyi* Forel to species rank (*R. johorensis* Wheeler **stat. n.**, *R. javana* Wheeler **stat. n.**), synonymize *R. janeti* Donisthorpe (**syn. nov.**) with *R. johorensis*, and describe four new species from Singapore: *R. glabricephala* **sp. n.**, *R. murphyi* **sp. n.**, *R. striata* **sp. n.**, and *R. tenebra* **sp. n.** All six species found in Southeast Asia are distinct from each other based on morphology; morphological delimitation of these species is further supported by and congruent with mOTUs generated from objective clustering of short fragment COI barcodes using the best close match criteria. Different castes and sexes of most species are described, including redescrptions of the queen of *R. javana* and male of *R. johorensis*. A key to the Southeast Asian species based on the worker caste is also provided. Variation among sympatric and also geographically distant populations, and the possibilities of cryptic species, are discussed.

**Key words:** Crematogastrini, Southeast Asia, integrative taxonomy, DNA barcoding

## Introduction

*Rhopalomastix* is a genus of Asian ants, all of which nest only under tree bark. Six species and two subspecies are known, but the true diversity is poorly understood and possibly severely underestimated, in part because the cryptic nesting habits of the genus make colonies difficult to find. Here we report on the fauna of Singapore, with evidence for six sympatric species. The presence of six species in Singapore alone suggests that species diversity could be far higher for the genus as a whole.

The genus was first established by Forel in 1900, with type species *R. rothneyi* Forel, based on a winged queen collected by G.A.J. Rothney at Barrackpore, near Calcutta, India. Forel (1911) subsequently found the worker and male of the same species, together with a queen of a second species (*R. escherichi* Forel) among ants collected by Professor K. Escherich in Ceylon. Only then did Forel notice the similarities of *Rhopalomastix* to *Melissotarsus* Emery. The two genera were recently confirmed as sister clades in the tribe Crematogastrini (Ward *et al.* 2015). In both *Rhopalomastix* and *Melissotarsus*, workers have very short antennae, each with two apical segments forming an expanded, robust club. The frontal lobes are narrow and very closely approximated, separated by a small impressed line and slightly overlapping the posterior clypeal margin. The mesosoma is typically short and box-like, with the dorsum devoid of sutures or obvious deep impressions. Both genera nest in and under bark of living trees. The two genera can, however, be separated by multiple morphological characters, such as: number of antennal segments (10 in *Rhopalomastix*; six in *Melissotarsus*), relative size of procoxa (*Rhopalomastix*—procoxa as large as or larger than remaining coxae; *Melissotarsus*—procoxa much smaller than the other coxae), and condition of the basitarsus (not swollen in *Rhopalomastix*; swollen with apical circlets of teeth in *Melissotarsus*). The two genera are geographically separated: *Melissotarsus* is confined to the Afrotropics and is widespread in Africa and Madagascar; *Rhopalomastix* has a tropical Oriental and Indo-Australian distribution.

Six *Rhopalomastix* species are currently recognized. *Rhopalomastix rothneyi* is considered widespread throughout India, Borneo, and Indo-Australia, with two subspecies in Southeast Asia (*R. rothneyi javana* and *R. rothneyi johorensis*). The other five species are more localized: *R. escherichi* in Sri Lanka, *R. janeti* in Thailand, *R. mazu* Terayama in Taiwan, *R. omotoensis* Terayama in Japan, and *R. umbracapitata* Xu in South China. However, the actual diversity and taxonomy of *Rhopalomastix* is poorly understood, largely due to the difficulty of destructive bark sampling, which is necessary to obtain nest series of the genus. In this study we revise the genus *Rhopalomastix* in Southeast Asia, which prior to the present study contained only *R. janeti* and the two subspecies of *R. rothneyi*.

In recent times, multi-disciplinary approaches to species delimitation, involving both molecular and morphological methods, have gained popularity. Despite being of poor utility in discerning deeper phylogenetic relationships, DNA barcodes have nevertheless been shown to be extremely useful for rapid and accurate species delimitation in invertebrates (Wang *et al.* 2018), especially in cases where species show low levels of morphological divergence (e.g. Hebert *et al.* 2004; Schlick-Steiner *et al.* 2006; Fisher & Smith 2008; Liu *et al.* 2013; Doña *et al.* 2015). *Rhopalomastix* species are small (ca. 2-3 mm total length) and similar in appearance; morphological differences are often subtle and only observable under high-powered microscopes. Considering the lack of conspicuous morphological differences amongst *Rhopalomastix* species, we adopt an integrated approach towards deciphering the systematics of *Rhopalomastix* in Southeast Asia, supporting morphological species with additional molecular evidence in the form of DNA barcodes where fresh material is available.

## Materials and methods

This study is based mainly on material deposited in the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum (Singapore), the Natural History Museum of the Thai National Science Museum (Thailand), and the Seiki Yamane reference collection (Japan). Colonies of *Rhopalomastix* were collected from bark samples across forests and forest fragments varying in levels of disturbance. Morphological observations were made using an Olympus SZX16 stereomicroscope, while measurements were made using micrometres on the same microscope. All measurements are given in millimetres and recorded to the second decimal place. Specimens were imaged with a Dun Inc.<sup>TM</sup> Passport II macrophotography imaging system, using a Canon MP-E 65 mm lens, and additional 20x telephoto zoom extension where necessary.

The abbreviations used for measurements and indices are as follows:

EL	Maximum eye length measured along its maximum horizontal diameter.
EW	Maximum eye width perpendicular to EL.
HL	Maximum head length in full-face view, measured in a straight line, from the anterior clypeal margin to the midpoint of a straight line drawn across the posterior margin of the head.
HW	Maximum head width behind the eyes, measured in full-face view.
ML	Mesosomal (Weber's) length, measured as the diagonal length of the mesosoma in profile, from the anteriormost point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.
MsW	Maximum width of the mesoscutum (queens and males only) in dorsal view.
PL	Petiole length, measured in profile view from the anterior margin of the peduncle to posteriormost point of the petiolar tergite.
PronW	Maximum width of pronotum in dorsal view.
SL	Maximum length of the antennal scape measured in a straight line, excluding the basal constriction and condylar bulb.
TL	Total body length, roughly measured in profile view from the anterior margin of the head to the apex of the gaster for outstretched specimens.
CI	Cephalic index, $HW/HL \times 100$
REL	Relative eye length, $EL/HW \times 100$
SI	Scape index, $SL/HW \times 100$

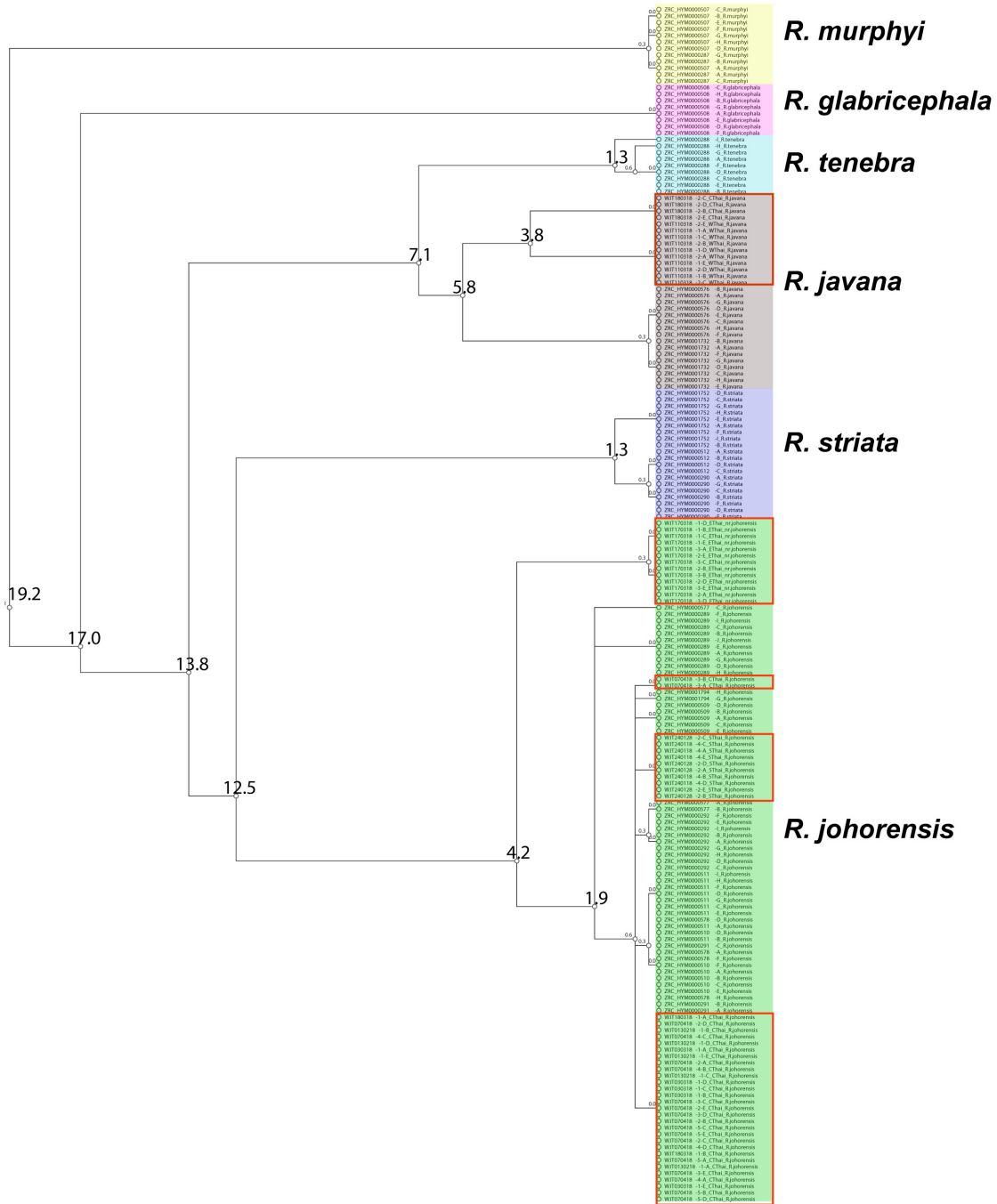
#### Specimen Depositories, Collections and their Abbreviations

MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
SKYC	Seiki Yamane Collections, Kagoshima, Japan
USNM	Smithsonian Museum of Natural History, Washington DC, USA
THNHM	Thailand Natural History Museum of National Science Museum, Pathum Thani, Thailand
ZRC	Zoological Reference Collection, Lee Kong Chian Natural History Museum, Singapore

**Note:** register numbers beginning with 'ZRC\_ENT' or 'ZRC\_HYM' are unique catalogue numbers that may be assigned to individual specimens or multiple specimens as collective entities (i.e. individuals from one colony) in the Zoological Reference Collection of the Lee Kong Chian Natural History Museum.

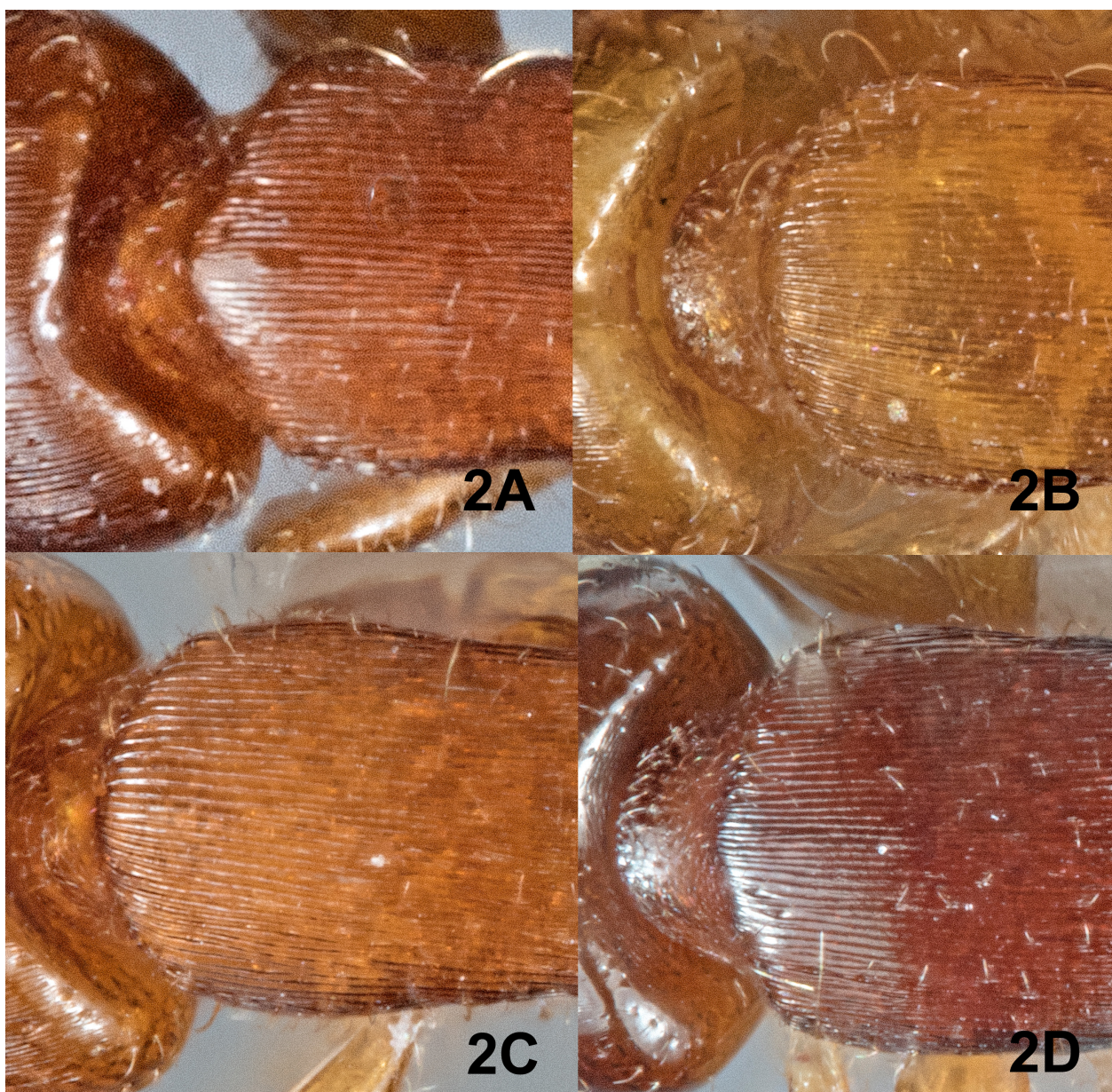
**DNA Barcoding.** DNA barcoding was conducted on *Rhopalomastix* specimens collected from Singapore and Thailand to strengthen support for species delimitation. Polymerase chain reactions (PCR) were performed to amplify DNA barcodes from representative specimens of colonies collected from Singapore. DNA extracts were obtained per specimen using QuickExtract™ DNA extraction solution (Kranzfelder *et al.* 2016), following manufacturer's protocol. A 313 bp fragment of cytochrome oxidase I within the 658 bp Folmer COI barcoding region [COI; m1COLintF: 5'-GGWACWGGWTGAACWGTWTAYCCYCC-3' (Leray *et al.* 2013) and modified jgHCO2198: 5'-TANACYTCNGGRTGNCCRAARAAYCA-3' (Geller *et al.* 2013)/ 5'-TAAACYTCAGGRTGCCRAARAAYCA-3' (Meier *et al.* 2016)] was amplified using labelled forward and reverse primers. Each label was 9 bp long, differing from other labels by  $\geq 3$  bp; labels were generated using the online freeware "Barcode Generator" ([http://comailab.genomecenter.ucdavis.edu/index.php/Barcode\\_generator](http://comailab.genomecenter.ucdavis.edu/index.php/Barcode_generator)). PCR mixtures of 20  $\mu$ l reaction volume each were prepared (2  $\mu$ l of 10x BioReady rTaq 10x Reaction Buffer, 1.5  $\mu$ l of 2.5 mM dNTP mix, 0.2  $\mu$ l of BioReady rTaq DNA polymerase, 2  $\mu$ l each of 5  $\mu$ M forward and reverse primers, 2  $\mu$ l of 1mg/ml Bovine Serum Albumin, RNase/DNase-free sterile water), and cycling conditions were as follows: initial denaturation at 94 °C for 5 min, 35 cycles of denaturation at 94 °C for 1 min, annealing at 45-47°C for 2 min, and extension at 72 °C for 1 min, thereafter a final extension at 72 °C for 5 min. Amplified PCR products were combined and cleaned in aliquots of up to 100  $\mu$ l using SureClean (Bioline Inc., London, UK); cleaned amplicon products were re-eluted in RNase/DNase-free water. Next Generation Sequencing (NGS) libraries were prepared

with the combined PCR products using the TruSeq Nano DNA Library Preparation kit and then sequenced on an Illumina MiSeq 2x300 bp platform. Paired-end (PE) read data (.fastq) were assembled using PEAR ver.0.9.6 (Zhang *et al.* 2014).



**FIGURE 1.** Cluster dendrogram of COI (313 bp) barcodes of *Rhopalomastix* from Singapore and Thailand. Objective clustering of barcodes was performed based on uncorrected *p*-distances using the ‘best close match’ criteria; the number at each ‘node’ represents the percentage divergence or pairwise distance threshold at which clusters split or lump together. Each cluster identified as a species is highlighted in one colour per respective species. Sequences of Thai *Rhopalomastix* are outlined in red.

**mOTU Estimation.** Barcodes were aligned using MAFFT v7 (Kato & Standley 2013), and alignments were checked on MEGA 6 (Tamura *et al.* 2013). We determined the number of molecular operational taxonomic units (mOTUs) over a range of percentage thresholds using “objective clustering”, using a custom-built Python script-based software *obj\_clust* v 0.1.2 (Srivathsan, A. unpublished; an implementation of objective clustering in SpeciesIdentifier (Meier *et al.* 2006)). In objective clustering, sequences are grouped according to uncorrected *p*-distances using the ‘best close match’ criteria (Meier *et al.* 2006, 2008)—members of a set of putative conspecific sequences have at least one match to a sequence in that set, which falls within a given percentage distance threshold. Multiple thresholds were applied (0–10%) to test stability of results. Cluster splitting and/or merging events amongst individual sequences were visualized using the same custom-designed software. We performed clustering on two sets of barcodes separately: 1) barcodes of *Rhopalomastix* from Singapore (SRB), and 2) barcodes of *Rhopalomastix* from Singapore (SRB) and Thailand (TRB) combined. This allows for assessment of potential effects on objective clustering that may result from the inclusion of sequences from geographically distant (allopatric) populations. The inter-species threshold for COI divergence across most arthropods ranges from 2–4% (Hebert 2003; Meier *et al.* 2008); however, intra-species divergences can vary greatly between allopatric regional populations because of local adaptation or genetic drift (Bickford *et al.* 2006; Moe & Weiblen 2010).



**FIGURE 2.** Dorsal views of anterior pronotal margin of four *Rhopalomastix* species. 2A, *R. striata*; 2B, *R. javana*; 2C, *R. johorensis*; 2D, *R. tenebra*.

## Results

A total of 184 *Rhopalomastix* specimens—116 across 18 nest series from Singapore, 68 across 15 nest series from Thailand—were successfully barcoded. Objective clustering (Meier *et al.* 2006) of only SRB yielded 20, 10, and 6 mOTUs at 0, 1, 2–9% thresholds respectively, i.e. number of clusters remained the same across the threshold range of 2–9% and no specimens were involved in mOTU reassignment between those thresholds. The 6 clusters of SRB that remained consistent within the broad threshold range of 2–9% were thus considered most representative of actual species.

Next, clustering of TRB in combination with SRB yielded 27, 13, 7, 6, and 5 mOTUs at 0, 1, 4, 6 and 9% thresholds respectively. The mOTU reassignments between thresholds 4–6 % mostly involved TRB (Fig. 1). Specimens of colonies from which SRB and TRB were derived were further examined for morphological differences among putative species clusters. In addition, we made careful comparisons of the TRB specimens and the SRB specimens they clustered with or were neighbours to. Two TRB clusters diverged from the closest SRB clusters within the threshold range of 4–6 % (i.e. splits at 5.8 and 4.2%, Fig. 1). Despite the divergences of these two TRB clusters from SRB clusters by > 4 %, we could not find any unambiguous morphological differences between the TRB and SRB specimens involved. Thus, based on morphological similarity and considering the possibility of greater genetic differentiation between allopatric populations, we inferred that the TRB specimens involved in the respective cluster splits were the same species as corresponding SRB specimens (i.e. *R. javana* and *R. johorensis*). We do not rule out the possibility of future changes to our current species assignments, should additional genetic information support the existence of cryptic species.

The breakdown of nest series from Singapore (SG) and/or Thailand (TH) barcoded per mOTU/species is as follows: *R. glabricephala*—1(SG); *R. javana*—2(SG), 3(TH); *R. johorensis*—9(SG), 9(TH); *R. murphyi*—2(SG); *R. striata*—3(SG), *R. tenebra*—1(SG). All COI (313 bp) barcodes obtained for this study are available in .fasta format from the corresponding author on request.

## Systematics

### Genus *Rhopalomastix* Forel

*Rhopalomastix* Forel, 1900: 24. Type-species: *Rhopalomastix rothneyi*, by monotypy

*Rhopalomastix* in Myrmicinae, Solenopsidini: Wheeler, W.M., 1910: 140.

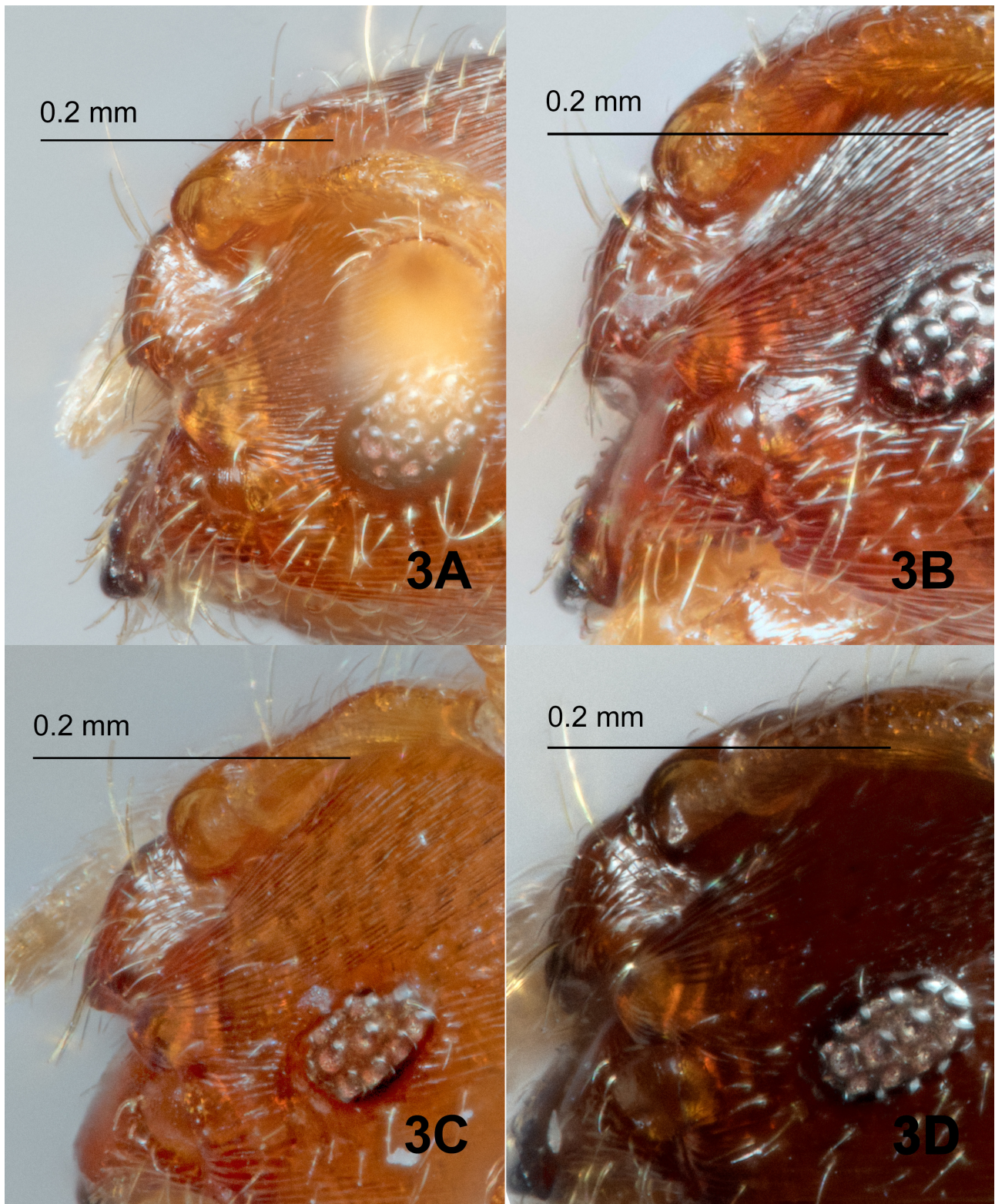
*Rhopalomastix* in Myrmicinae, Melissotarsini: Emery, 1914: 40; Forel, 1917: 242; Emery, 1922: 118; Wheeler, W.M. 1922: 661.

*Rhopalomastix* in Myrmicinae, Crematogastrini: Ward *et al.*, 2015: 71, 77.

**Diagnosis of genus. Worker.** Total length approximately 1.59–2.62 mm, HL 0.39–0.58, HW 0.36–0.56. Worker monomorphic with variation in size. Head in full-face view subrectangular or subquadrate; frontal carina and antennal scrobe weak; frontal lobes touching or separated only by a narrow longitudinal impression. Median portion of anterior clypeal margin weakly convex anteriorly and projected forward slightly from lateral clypeal margin, lined with minute denticles. Mandible short, subtrapezoidal, its masticatory margin with a few teeth, usually one large apical tooth, a smaller pre-apical tooth, and 2–3 minute, reduced denticles. Antenna with 10 segments, antennal club 2-segmented; antennal scape short, extending a little beyond midlength of head when laid backwards; antennal funiculus flattened in appearance. Eye relatively large, with 5–6 ommatidia in the longest axis, located well in front of midlength of side of head. Mesosoma box-shaped; promesonotal suture absent dorsally; metanotal groove absent; propodeum unarmed; metapleural gland bulla large; propodeal lobe reduced and indistinct. Procoxa subtriangular and anteriorly expanded into smooth and rounded lobe. Fore- and hind femora extremely widened and flattened distally. Petiole nodiform, with relatively high node, anteroventrally with well-developed subpetiolar process, globular in dorsal view. Postpetiole much shorter than high, broadly attached to anteriormost portion of gaster. Gaster in dorsal view elliptical in shape, first gastral tergite much larger compared to the rest.

**Queen.** Differing from associated workers in the following characteristics: body slightly larger; eye very large in size (>100 ommatidia); ocelli present; promesonotal suture deeply impressed; metapleuron large, in profile view

rounded subrectangular, with distinct metapleural furrow that is oblique and linear, directed posterodorsally. Sculpturing on head usually weaker than in worker. Clypeus usually with two pairs of erect hairs—one pair of setae on the median anterior clypeal margin, another pair of longer hairs closer to the posterior clypeal margin.



**FIGURE 3.** Profile views of clypeus of four *Rhopalomastix* species. 3A, *R. striata*; 3B, *R. javana*; 3C, *R. johorensis*; 3D, *R. tenebra*.

**Male.** Head including eye in full-face view rounded or broadly ovate. Eye extremely large (>100 ommatidia) and bulging; ocelli relatively larger than in queen. Mandible reduced and nub-like; clypeus in profile strongly

projected from anterior margin of head. Ventrolateral corner of head roundly convex. Antenna 12-segmented, without obvious antennal club, scape very short. Mesosoma elongate, not box-shaped. Petiole sometimes similar to that in worker but relatively longer than high, anterior margin always longer than posterior, in dorsal view, petiole including anterior face subcylindrical. Subpetiolar process besides distal anteroventral point typically lighter in colour and more translucent than adjacent sclerites. Postpetiole relatively flat, broadly attached to anteriormost portion of gaster; gaster elliptical in dorsal view. Hairs on dorsum of mesosoma usually most abundant on mesoscutum, sparser or absent on mesoscutal disc and propodeum.

### Checklist of Southeast Asian species

*Rhopalomastix glabricephala* sp. n.

*Rhopalomastix javana* Wheeler, W. M., 1929 stat. n.

*Rhopalomastix johorensis* Wheeler, W. M., 1929 stat. n.

= *Rhopalomastix janeti* Donisthorpe, 1936 syn. n.

*Rhopalomastix murphyi* sp. n.

*Rhopalomastix striata* sp. n.

*Rhopalomastix tenebra* sp. n.

### Key to the Southeast Asian species based on worker caste

1. In profile, lateral surface of posterior half of head largely smooth and shiny (Figs. 6, 50); ventral surface of head largely smooth and shiny, with sparse superficial reticulate sculpture or feeble striations; outer surface of femora largely smooth and shiny, sometimes feebly reticulate. . . . . 2
- In profile, lateral surface of posterior half of head largely striate and/or reticulate (Figs. 10, 14, 26, 30, 54, 66); ventral face of head striate, punctate and/or reticulate with smooth and shiny interspaces; outer face of femora superficially reticulate with smooth and shiny interspaces . . . . . 3
2. Anterior face of petiole smooth and shiny, without short appressed or decumbent hairs. . . . . *R. murphyi* sp. n.
- Anterior face of petiole weakly punctate or smooth, with short appressed or decumbent hairs. . . . . *R. glabricephala* sp. n.
3. In dorsal view, anterior pronotal margin strongly convex, distinctly angulate medially (Fig. 2A); clypeus in profile view evenly and roundly convex (Fig. 3A). . . . . *R. striata* sp. n.
- In dorsal view, anterior pronotal margin broadly convex or weakly angulate medially (Figs. 2B–D); clypeus in profile view variable—almost entirely straight and flat, or very weakly convex (Figs. 3B–D) . . . . . 4
4. Vertexal lobe of head largely smooth and shining, sometimes with sparse and fragmented striae; head and dorsum of mesosoma darker blackish-brown than rest of body. . . . . *R. tenebra* sp. n.
- Vertexal lobe of head largely finely striated and shining, sometimes striae fragmented and sparse; body colour uniformly brown. . . . . 5
5. Posteriormost portion of vertex just above occiput in posterodorsal view largely unsculptured, smooth and shiny; petiolar node in dorsal view more strongly convex anteriorly than posteriorly . . . . . *R. javana* stat. n.
- Posteriormost portion of vertex striate but slightly shiny; petiolar node in dorsal view similarly convex anteriorly and posteriorly. . . . . *R. johorensis* stat. n.

### *Rhopalomastix glabricephala* sp. n.

(Figs. 4–7)

**Type.** Holotype. Worker, SINGAPORE, Mandai Road (1.41379°N, 103.79820°E), nest in bark of Tembusu tree (*Fagraea fragrans* Roxb), 16 Nov 2016, G.W. Yong & K.H. Pwa leg., ZRC\_ENT\_00000873 (ZRC).

**Paratypes.** Thirty-six workers (MCZ, THNHM, USNM, ZRC), same data as holotype, colony no. GY-SG16-RhoE, ZRC\_HYM\_0000508.

**Diagnosis. Worker.** Small (HL 0.43–0.45, HW 0.39–0.42), monomorphic, with little variation in size. In profile, clypeus projected slightly forward from dorsal margin of head, almost entirely flat or straight; posterior half of head smooth and shiny; ventral surface of head largely smooth and shiny; outer surface of femora mostly smooth and shiny, with very feeble superficial reticulation; petiole rather small, anterior face weakly concave and covered with short appressed hairs. Head and dorsum of mesosoma darker brown compared to rest of yellowish-brown body; legs and tips of antennae pale yellow.



**Worker measurements.** Holotype. TL 1.93; HL 0.44; HW 0.42; SL 0.18; ML 0.54; PronW 0.28; EL 0.09; EW 0.05; CI 95; REL 21; SI 43.

Paratype workers (n = 6): TL 1.73–1.86; HL 0.43–0.45; HW 0.39–0.42; SL 0.16–0.18; ML 0.44–0.52; PronW 0.26–0.28; EL 0.06–0.08; EW 0.04–0.05; CI 91–95; REL 15–20; SI 38–46.

**Description. Worker.** Monomorphic with little variation in size. Head in full face view subrectangular, slightly longer than wide, posterior margin with a weak median concavity, posterolateral corner of head roundly convex, lateral margin broadly convex. Eye with 13–17 ommatidia. Median portion of anterior clypeal margin broadly convex and lined with minute denticles. In profile, clypeus projected slightly forward from dorsal margin of head, almost entirely flat or straight. Antennal scape short, gradually swollen distally, reaching midlength of head when laid backwards. In profile, mesosoma box-shaped, subcylindrical, dorsal outline weakly convex, propodeal declivity shallowly concave. In dorsal view, mesosoma subrectangular, anterior pronotal margin strongly convex and rounded, posterior propodeal margin weakly concave. In profile, petiole inclined posteriorly, much longer than high, anterior rising margin weakly concave, forming a smooth continuous curve with rounded apical margin, junction between both margins indistinct; petiolar node bell-shaped, apex convex, posterior declivity roughly half as long and as steep as anterior rising margin. Petiole as high as and longer than postpetiole, dorsal margin of postpetiole broadly convex in profile view. In dorsal view, petiole elliptical in shape, about twice as broad as long in large workers, less broad and more oval in smaller workers; postpetiole globular and sub-oblong in shape, lateral margin rounded, wider than long, larger than petiole.



**FIGURES 4–7.** Holotype worker of *Rhopalomastix glabricephala* sp. nov. 4, habitus in profile; 5, head in full-face view; 6, closeup of head in profile view; 7, body in dorsal view.

Posterior half of head including dorsum, lateral surfaces and venter mostly smooth and shiny, anterior half of head including antennal scrobe and area surrounding eye with feeble striations. Median clypeal surface carinate and punctate but still shiny. Mandible mostly smooth and shining with sparse and feeble striations, area close to

masticatory margin lightly punctate. Lateral surface of mesosoma weakly striate-reticulate and shining; dorsum of mesosoma striated. Lateral surfaces of petiole, postpetiole weakly punctate, largely smooth and shiny. Dorsal surfaces of petiolar and postpetiolar nodes weakly strigate with sparse punctures, still shining. Gaster mostly smooth and shining, with sparse and weak transverse sculpture and scattered punctures.

Dorsal surface of head with numerous short erect and suberect hairs, interspersed by sparser and much longer erect hairs; ventral surface and gena with abundant short appressed and decumbent hairs. Mesosoma dorsum with sparse, scattered short standing hairs mainly aligned close to dorsolateral margin, sparser and longer erect hairs on the same margin. Petiole and postpetiole relatively more pilose, anterior face of petiole with dense decumbent hairs, petiolar and postpetiolar nodes with abundant short standing hairs, and sparser and longer erect hairs. Gaster pilose, both ventral and dorsal surfaces with dense erect and suberect hairs.

Head and dorsum of mesosoma relatively dark brown in colour, rest of body lighter and uniformly yellowish-brown, legs and tips of antennae pale yellow.

**Etymology.** The specific name refers to the smooth and shining, i.e. glabrous, posterior half of head in this species.

**Distribution.** Singapore.

**Habitat.** *Rhopalomastix glabricephala* appears to be a rare species in Singapore, currently found only in its type locality. The type series was collected from a nest within deeper bark layers of a Tembusu tree in a secondary forest.

**Remarks.** *Rhopalomastix glabricephala* is most similar to *R. murphyi* in having small body size, smooth and shining posterior half of head, largely smooth and shining femora and first gastral tergite. However, *R. glabricephala* can be distinguished from *R. murphyi* by the following characteristics: 1) deeper, more pronounced central median concavity of the posterior margin of the head, 2) petiolar node small and usually not higher than postpetiole, 3) anterior rising face of petiole pilose with decumbent hairs (anterior petiolar face is largely smooth and shining without hairs in *R. murphyi*).

**DNA barcoding.** Eight workers from the same colony as the type series (ZRC\_HYM\_0000508) were successfully barcoded. Based on the combined cluster dendrogram (Fig. 1), barcode divergences from other species are as follows: *R. murphyi*, 19.2%; *R. javana*, *R. johorensis*, *R. striata*, *R. tenebra*, 17%.

### ***Rhopalomastix javana* Wheeler, W.M., 1929 stat. n.**

(Figs. 8–23)

*Rhopalomastix rothneyi* subsp. *javana* Wheeler, W.M., 1929: 96.

**Types.** *Rhopalomastix rothneyi* subsp. *javana*: Numerous workers, four females and three males from INDONESIA, Eastern Java, Besoeki, Bondowoso. Three syntype workers on 1 pin (USNM, cotype: MCZ.6.9.20783/ SNM.595.31) were examined. One worker (top on pin) is selected as the lectotype.

**Diagnosis. Worker.** Workers monomorphic with little size variation (lectotype and paralectotypes: HL 0.48–0.52, HW 0.45–0.48). Head in full face view subrectangular, longer than wide, posterior margin with a shallow median concavity. In profile, clypeus broadly and weakly convex; entire dorsum finely striated; posterior half of head striate-reticulate and weakly shining; ventral surface of head largely superficially reticulate; outer surface of femora reticulate with shining interspaces; petiole bell-shaped, anterior face weakly concave. Head, mesosoma dorsum and gaster dark brown, rest of body yellowish brown.

**Queen.** Small-medium size (non-types: HL 0.48–0.49, HW 0.44–0.45), head slightly less rectangular than that of worker. In profile view, clypeus very weakly convex, almost flat; posterior half and ventral surface of head largely smooth and shiny, vertex feebly striated; outer surface of femora and gaster superficially reticulate; dorsum of mesosoma finely striate and shiny; anterior pronotal margin roundly convex; anterior face of petiole evenly concave, petiole distinctly narrower apically. Body colour generally uniformly dark brown; head, dorsum of mesosoma and gaster slightly darker brown, tibia and tarsus yellowish brown.

**Male.** Small size (non-types: HL 0.39–0.41, HW 0.38–0.4). Head almost entirely spherical in full face view, posterior margin broad and round; eye relatively smaller than other species, maximum diameter of eye only slightly exceeding midline of head; clypeus in profile roundly convex, strongly projecting from dorsum of head, rugulose

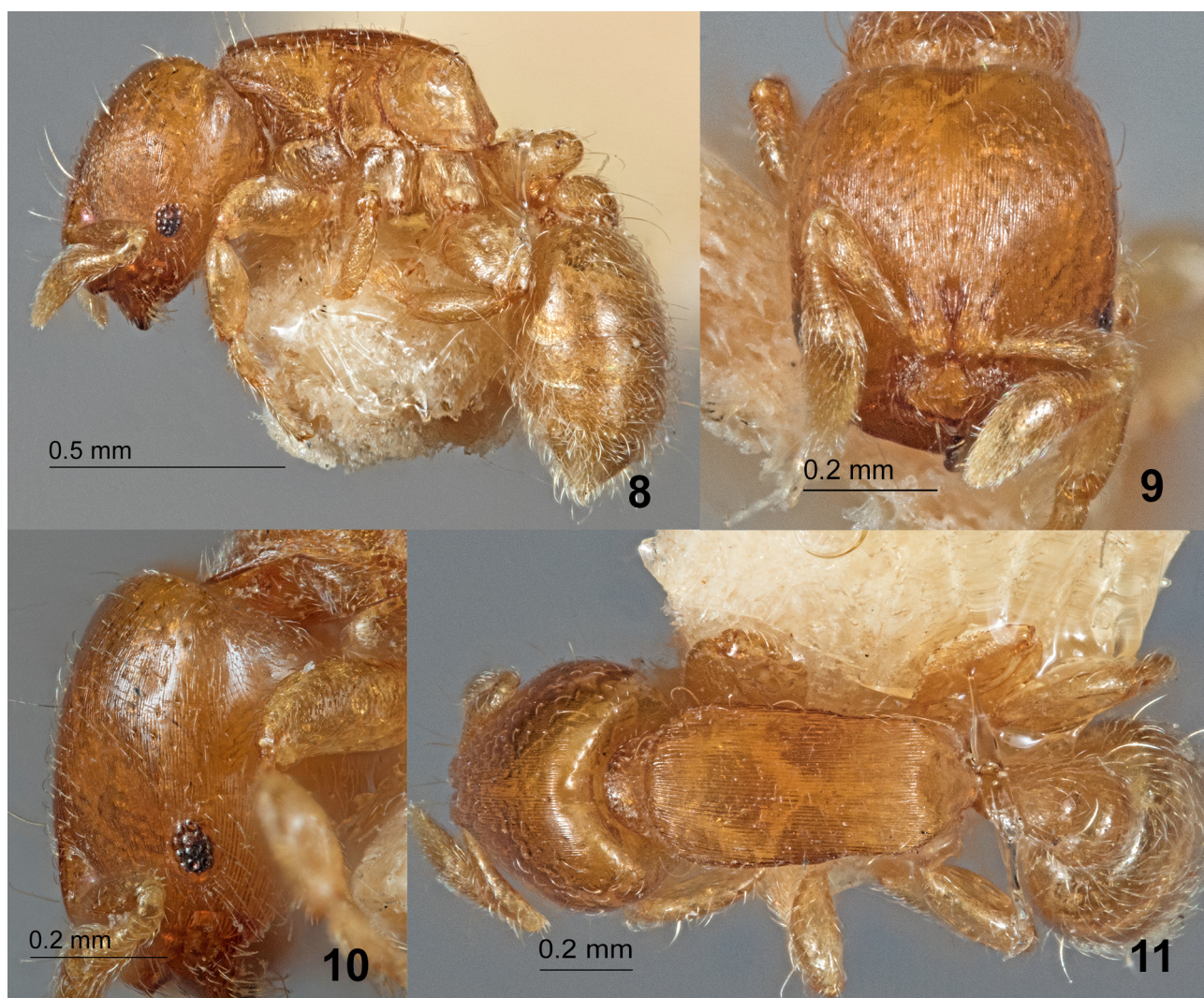
with punctured interspaces and weakly shining; petiole short and sub-trapezoidal, apex smooth and blunt; entire head substrate-reticulate with smooth and shining interspaces, rest of body superficially reticulate; short standing hairs on entire dorsum including petiole and postpetiole.

**Worker measurements.** Lectotype and paralectotypes (n = 3): TL 1.83–1.98; HL 0.48–0.52; HW 0.45–0.48; SL 0.18–0.20; ML 0.48–0.50; PronW 0.28–0.32; EL 0.08; EW 0.04–0.06; CI 92–94; REL 17–18; SI 39–42.

Nine non-types (n = 9): TL 1.69–2.02; HL 0.46–0.48; HW 0.41–0.44; SL 0.17–0.19; ML 0.50–0.54; PronW 0.28–0.32; EL 0.08–0.1; EW 0.04–0.06; CI 89–93; REL 18–23; SI 40–44.

**Queen measurements.** Three non-types (n = 3; 1 alate and 2 dealate): TL 2.21–2.43; HL 0.48–0.49; HW 0.44–0.45; SL 0.18–0.20; ML 0.70–0.72; MsW 0.36–0.40; EL 0.15–0.16; EW 0.09–0.10; CI 92–94; REL 33–36; SI 40–45.

**Male measurements.** Two non-types (n = 2): TL 1.98–1.99; HL 0.39–0.41; HW 0.38–0.40; SL 0.06; ML 0.66–0.70; MsW 0.40–0.44; EL 0.18–0.20; EW 0.14; CI 97–98; REL 45–53; SI 15–16.



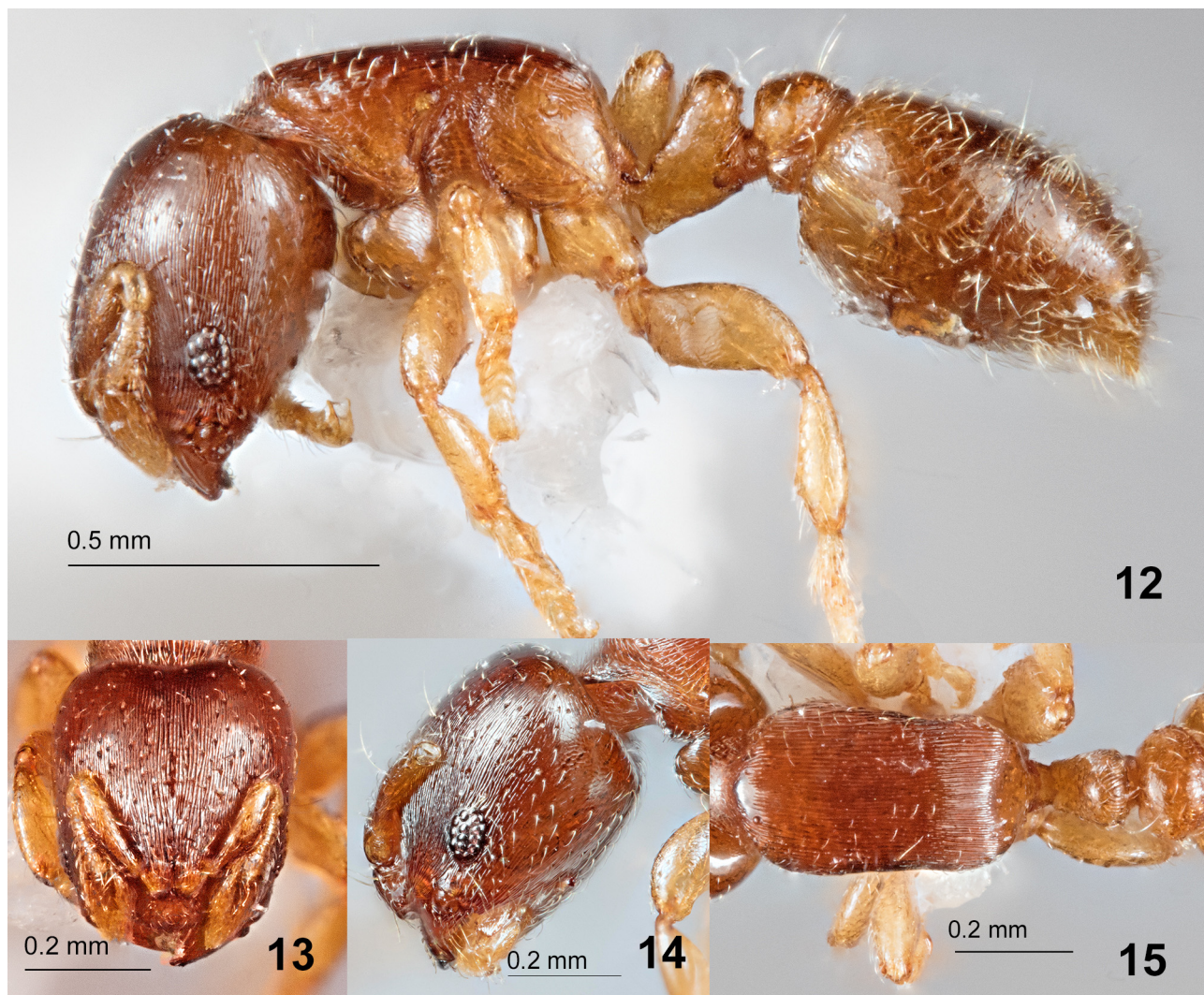
**FIGURES 8–11.** Lectotype worker of *R. javana* **stat. n.** 8, habitus in profile; 9, head in full-face view; 10, closeup of head in profile view; 11, body in dorsal view.

**Redescription. Worker** (lectotype, paralectotypes and non-types). Workers monomorphic with little variation in size. Head in full face view subrectangular, longer than wide, posterior margin with a shallow median concavity, posterolateral corners roundly convex, lateral margins of head broadly convex and weakly converging anteriorly— anterior clypeal margin less wide than posterior margin of head. Eye with 11–16 ommatidia. In profile view, outline of clypeus evenly and weakly convex, projecting slightly forward from dorsal margin of head. Mesosoma in profile box-shaped, subcylindrical, dorsal outline weakly convex and almost straight, propodeal declivity steep and shallowly concave. In dorsal view, mesosoma subrectangular, anterior pronotal margin broadly convex, sometimes

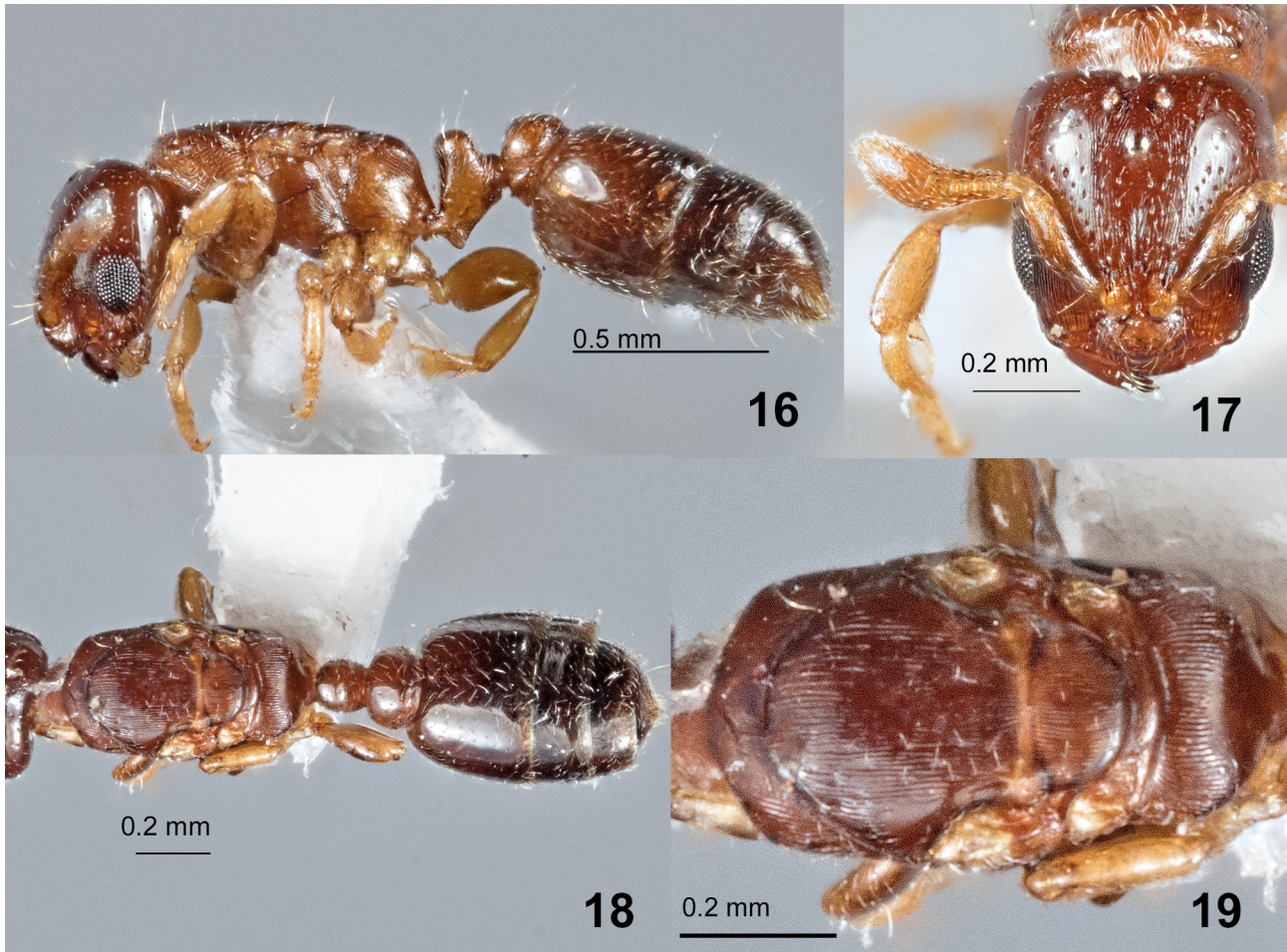
angulate at its median point, humeral angles rounded, posterior propodeal margin weakly concave. In profile, petiole inclined posteriorly, slightly longer than high, apex distinctly narrower than base, anterior margin broadly concave; petiolar node bell-shaped, apex rounded and smooth, posterior face nearly straight and almost as steep as anterior face; petiole higher and longer than postpetiole, dorsal margin of postpetiole weakly convex and nearly flat. In dorsal view, petiole suboval, wider than long; postpetiole globular and larger than petiole.

Dorsum and lateral surface of head finely striated and shining, posterolateral corners also feebly reticulate, interspaces smooth and shining; posterior-most portion of vertex of head just above occiput in posterodorsal view largely unsculptured, smooth and shiny. Ventral surface of posterior half of head mostly superficially reticulate with smooth and shining interspaces. Mandible mostly smooth and shining, area close to masticatory margin punctate. Lateral surface of mesosoma striate-reticulate and shining; dorsum of mesosoma striated. Petiole, postpetiole and gaster superficially reticulate with smooth and shining interspaces.

Dorsal and ventral surfaces of head with abundant short standing and suberect hairs interspersed by sparse longer erect hairs, gena with abundant short appressed hairs. Mesosoma dorsum with sparse, scattered short standing hairs and sparse longer erect hairs close to dorsolateral margin. Anterior rising face of petiole with uniformly short appressed hairs, posterior declivity covered with short erect and subdecumbent hairs; apex of petiolar node with short erect hairs and 1–2 pairs of much longer erect hairs. Postpetiole with abundant short erect and suberect hairs, and 1 pair of long erect hairs. Gaster very pilose, all surfaces covered with abundant short suberect and erect hairs, interspersed by sparse longer erect hairs.



**FIGURES 12–15.** Non-type worker of *R. javana* **stat. n.** from Singapore, Mandai Track, ZRC\_HYM\_0000576; 12, habitus in profile; 13, head in full face view; 14, closeup of head in profile view; 15, body in dorsal view.



**FIGURES 16–19.** Non-type queen of *R. javana* from Singapore, Bukit Timah Nature Reserve, ZRC\_HYM\_0001732; 16, habitus in profile; 17, head in full face view; 18, body in dorsal view; 19, closeup of mesosoma in dorsal view.

Head, dorsum of mesosoma and gaster generally darker brown in colour, rest of body more yellowish brown, tips of antennae and legs pale in tone.

**Queen** (non-types). Small-medium size. Head in full face view subrectangular, slightly less rectangular than that of worker, longer than wide; lateral margins almost entirely straight and parallel to each other, posterolateral corners smooth and rounded, posterior margin nearly straight with a shallow median concavity. Eye large (>100 ommatidia); posterior margin of eye located slightly below midline of head in full face view. In profile, clypeus very weakly convex, almost entirely flat. Scape short, not exceeding midline of head when laid back. In profile, mesosoma sub-cylindrical, more elongate than that of worker, dorsal outline weakly and broadly convex, propodeal junction rounded and smooth, posterior face of propodeum steep and almost vertical, shallowly concave. In dorsal view, mesosoma sub-cylindrical, anterior pronotal margin roundly convex, humeral angles distinctly obtuse though rounded and smooth, mesoscutum wider than long. In profile view, petiole inclined posteriorly, longer than high, anterior margin weakly concave; petiolar node bell-shaped, apex roundly convex, posterior face steeper than anterior face; dorsal margin of postpetiole weakly convex, not as long as postpetiole, dorsal margin weakly convex. In dorsal view, petiole suboval, less than twice as wide as long; postpetiole globular, much larger and wider than petiole.

Posterior half of head mostly smooth and shining, feeble striations on frons and venter, anterior half of head finely striated and shiny, clypeus striated but with a median spot that is smooth and shining. Mandible mostly smooth and shining, area next to masticatory margin slightly striate-punctate. Lateral surface of mesosoma weakly substriate-reticulate, interspaces smooth and shining. Dorsum of mesosoma mostly striated and shining, median section of pronotum superficially reticulate with smooth and shining interspaces. Lateral surfaces of petiole and postpetiole reticulate, interspaces smooth and shining; apices of petiole and postpetiole feebly and superficially

reticulate, mostly smooth and shining. Gaster largely smooth and shining, partly superficially and weakly reticulate.

Dorsum and ventral surface of head covered with abundant short erect and suberect hairs, with sparse longer erect hairs. Dorsum of mesosoma with sparse short standing hairs and sparser long erect hairs, mainly along dorsolateral margin. Anterior face of petiole with short appressed and/or decumbent hairs, posterior face with multiple short erect hairs, apex with short erect hairs, 1–2 pairs of longer erect hairs; postpetiole with multiple short standing hairs and a pair of longer erect hairs. Gaster pilose, with abundant short appressed hairs, scattered short standing hairs and sparse long erect hairs.

Entire body generally uniform dark brown; head, dorsum of mesosoma and gaster slightly darker brown; tibia and tarsus paler and more yellowish brown.

**Male** (non-types). Small size. Head in full face view almost entirely spherical, posterior margin broad and round; eye relatively smaller as compared to other species, maximum diameter of eye only slightly exceeding midline of head, outline of eye exceeding lateral margin of head by a little. In profile, head broad-ovate, lateral corners smooth and rounded, ventral and posterior margins forming a continuous curved outline; clypeus roundly convex and strongly projecting from dorsum of head. In profile, mesosoma sub-oblong, dorsal margin almost completely straight, propodeal junction roundly convex, posterior face of propodeum steep and almost entirely vertical. In dorsal view, mesosoma obovate, notauli absent. In profile view, petiole inclined posteriorly, short and subtrapezoidal, longer than high, anterior margin weakly concave, apex smooth and blunt, weakly convex and sloping downwards gently, posterior margin very short; anteroventral extension of subpetiolar process shallow and subtriangular, longer at base than apex. Dorsal outline of postpetiole weakly convex, differentiated from gaster by a weak but distinct cinctus.

Entire head mostly substrate-reticulate, with smooth and shining interspaces and scattered punctures; clypeus rugulose with punctured interspaces and weakly shining. Lateral surface of mesosoma weakly striate-reticulate, interspaces smooth and shining; dorsum largely striated and shining, propodeum superficially reticulate with smooth and shiny interspaces. Petiole, postpetiole and gaster superficially reticulate with smooth and shiny interspaces.

Dorsum of head with abundant short standing hairs, lateral and ventral surfaces with numerous short decumbent and appressed hairs. Dorsal surfaces of mesosoma, petiole, postpetiole and gaster mostly with abundant short standing hairs, propodeum with visibly much sparser standing hairs.

Generally dark greyish-brown; head, dorsum of mesosoma and gaster darker blackish-brown; funiculi of antennae light brown; joints of legs, tarsus pale brownish-yellow.

**Distribution.** Indonesia (eastern Java), Singapore, Thailand (Fig. 76).

**Habitat.** Non-type specimens from Singapore were collected from bark of common native trees, e.g. *Camptosperma auriculatum* (Blume) Hook.f., in secondary forests and nature reserves which used to be abandoned plantations; specimens from Thailand were collected from bark of mango trees. Nests do not appear to occupy large expanses of tree bark.

**Remarks.** We compared the queen specimens of *R. javana* from Singapore with the holotype queen (head missing) of *Rhopalomastix rothneyi* from India. We found the Singapore queen specimens of *R. javana* (SQJV) to be quite different from the holotype queen of *R. rothneyi* (QR): 1) in SQJV, pronotal length in dorsal view is more than half of propodeal length; in QR, the pronotal length is less than half of propodeal length; 2) mesoscutellar disc of SQJV less than twice as wide as long; in QR, mesoscutellar disc more than twice as wide as long; 3) SQJV propodeum in dorsal view more than twice as wide as long, with broadly concave posterior margin; in QR, propodeum less than twice as wide as long, with roundly convex posterior margin; 4) anterior margin of petiole of SQJV broadly concave, posterior margin steep and nearly flat; in QR, anterior margin not distinctly concave, as steep and flat as posterior margin; 5) SQJV is generally smaller (MsW 0.36–0.40 in SQJV, MsW 0.42 in QR)

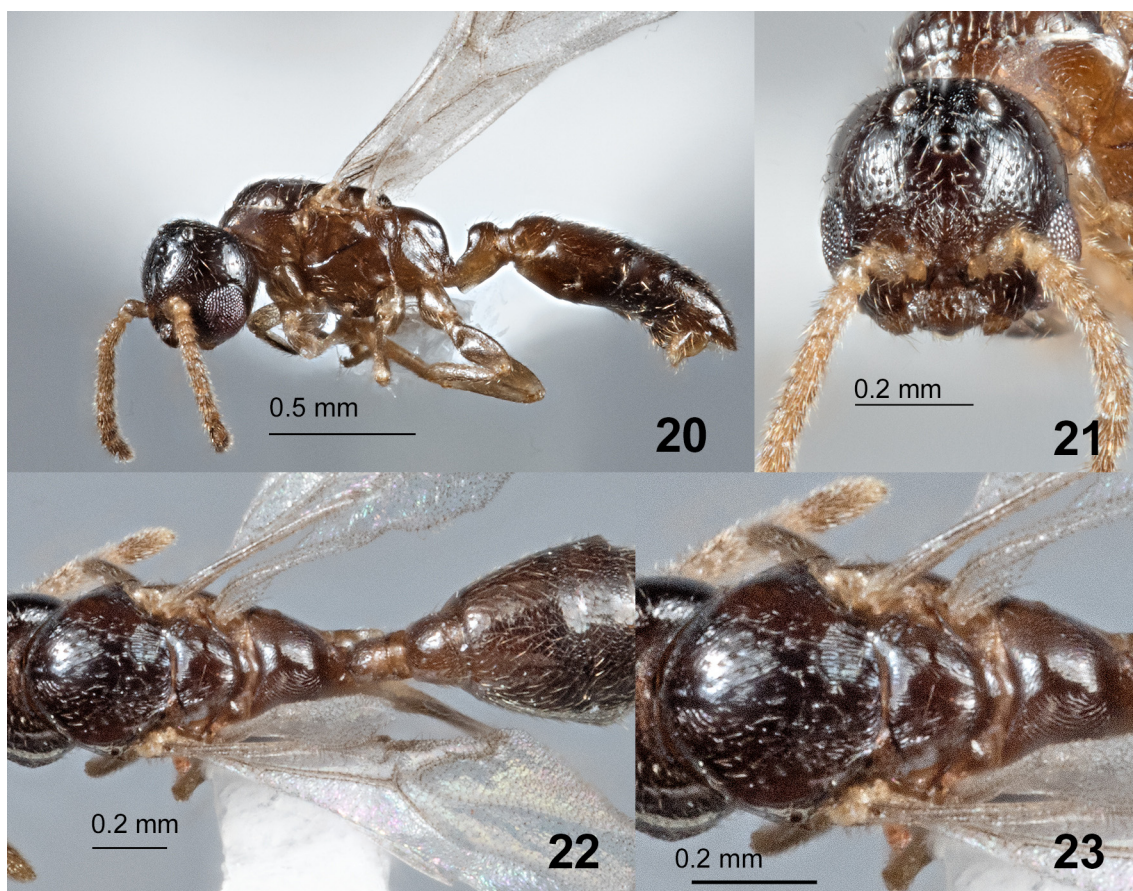
Three workers, two males on two pins each with ‘typus’ labels (MHNG) and 23 workers on pins with ‘cotypus’ labels of *R. rothneyi* (MHNG) from Peradineya [sic], Sri Lanka were also examined. Although labeled as such, they are not type specimens of *R. rothneyi*. We compared workers of the Sri Lankan specimens (SLW) with the lectotype and paralectotypes of *R. javana* from Java (JVW). We found the following differences between SLW and JVW: 1) for SLW, straight-line distance of eye to mandibular insertion in profile view  $\leq$  maximum diameter of eye; in JVW, distance of eye to mandibular insertion  $>$  maximum diameter of eye; 2) in JVW, mesosoma relatively short in proportion to head length (HL/ML 89–91); in SLW, mesosoma slightly more elongate (HL/ML 83–87); 3)

in JVW, slope of the propodeal declivity is more deeply concave, with a distinctly concave posterior propodeal margin in dorsal view; for SLW, slope of the propodeal declivity is steep and mostly flat.

The male of *R. javana* from Singapore (SMJV) differs from the Sri Lankan male (SLM) by the following traits: 1) SMJV has a more orbicular head, broadly and evenly rounded posteriorly in full face view; SLM has a more longitudinally oval head, with posterior margin more elongate; 2) SMJV is smaller (SMJV HL 0.39–0.41, HW 0.38–0.40, MsW 0.4–0.44; SLM HL 0.44, HW 0.40–0.42, MsW 0.48–0.5); 3) mesoscutum of SMJV in profile view roughly as high as pronotum; in SLM, mesoscutum distinctly much higher than pronotum, with a roundly convex anterior margin.

Given the character differences between *R. rothneyi* and both the types and the Singapore populations of *R. javana*, especially those between the holotype queen of *R. rothneyi* and SQJV, we thereby choose to raise the subspecies *javana* to species status. There remains the strong possibility of future revision of *R. rothneyi* and its previous subspecies, when fresh material from across the species range is available for DNA/molecular investigation.

The lectotype and paralectotypes of *R. javana* (JVW) are morphologically similar to the Singapore (SWJV) and Thai (TWJV) specimens, except for a few minor differences: 1) JVW is overall uniformly yellowish brown with pale yellow antennal tips, but SWJV and TWJV are in general not uniform in colour, with head and mesosoma usually darker brown than rest of body, antennal tips and legs paler yellowish brown; 2) eye size of JVW relatively smaller in proportion to head width compared to SWJV and TWJV (JVW: REL 17–18; SWJV, TWJV: REL 18–23). On the other hand, the heads of JVW and TWJV are generally larger than that of SWJV (JVW, TWJV: HL 0.48–0.52, HW 0.45–0.48; SWJV: HL 0.46–0.48; HW 0.41–0.44). These minor differences may simply be morphological variation or polyphenism among geographically distant allopatric populations. For now, given the lack of DNA/molecular evidence and the minor morphological differences, we here choose to treat the Singapore and Thai populations as *R. javana*, until fresh specimens of *R. javana* can be obtained from its type locality (Java), and more compelling DNA information from different genetic markers (nuclear and mitochondrial) is available for comparison with the Singapore and Thai specimens.



**FIGURES 20–23.** Non-type male of *R. javana* from Singapore, Mandai track, ZRC\_HYM\_0000576; 20, habitus in profile; 21, head in full face view; 22, body in dorsal view; 23, closeup of mesosoma in dorsal view.

Workers of *R. javana* are similar to small workers of *R. johorensis*, but may be differentiated from the latter based on characters indicated in couplet (5) of the species key. Workers of *R. javana* are also similar to small workers of *R. tenebra*, but can be distinguished from the latter based on characters as explained in “Remarks” under the latter description.

**Non-type material examined.** SINGAPORE: 18 workers, 1 queen, 1 male, Mandai Track (1.40337°N, 103.77824° E), 4 Jan 2017, G.W. Yong leg., colony no. GY-SG17-RhoN, ZRC\_HYM000576 (THNHM, ZRC); 12 workers, 2 queens, Bukit Timah Nature Reserve (1.35449°N, 103.78211°E), nest in bark of *Camposperma auriculatum*, 21 Jun 2017, C. Peeters leg., colony no. WW-SG17-015, ZRC\_HYM\_0001732 (ZRC). THAILAND: W. Thailand, Kanchanaburi Prov., Sai Yok Dist., Ban Tha Sao, 280 m a.s.l. (14.33389° N, 98.98° E), collected from a mango tree, 11 Mar 2018, W. Jaitrong leg., colony no. WJT110318-1 (THNHM, ZRC); same locality, date and collector, colony no. WJT110318-2 (THNHM, ZRC); Central Thailand, Saraburi Prov., Phu Kae Botanical Garden, 89 m a.s.l. (14.67056°N, 100.88500°E), 18 Mar 2018, W. Jaitrong leg., colony no. WJT180318-2 (THNHM, ZRC).

**DNA Barcoding.** SINGAPORE: 16 workers were successfully barcoded, 8 each from a colony in Mandai (ZRC\_HYM\_0000576) and another colony in BTNR (ZRC\_HYM\_0001732). THAILAND: 14 workers were successfully barcoded, 5 each from 2 colonies in West Thailand (WJT110318-1, WJT110318-2), and 4 from a colony in Central Thailand (WJT180318-2). Based on the combined cluster dendrogram (Fig. 1), barcode divergences from other species are as follows: *R. murphyi*, 19.2%, *R. glabricephala*, 17%; *R. johorensis*, 13.8%; *R. striata*, 13.8%; *R. tenebra*, 7.1%.

### ***Rhopalomastix johorensis* Wheeler W.M., 1929 stat. n.**

(Figs. 24–39)

*Rhopalomastix rothneyi* subsp. *johorensis* Wheeler, W.M., 1929: 96

*Rhopalomastix janeti* Donisthorpe, 1936: 55 (w.q.m). **syn. n.**

**Types.** *Rhopalomastix rothneyi* subsp. *johorensis*. Three syntype workers (on 1 pin) from Singapore (Overbeck) (MCZ, MCZ\_ENT00023066, examined). One worker (top on pin) is selected as the lectotype. *Rhopalomastix janeti*. Holotype and paratype workers (BMNH, USNM) from Thailand, Bangkok (A. Manjikul). Paratype workers (USNM, USNM\_ENT00529551) were examined. New synonym.

**Diagnosis. Workers.** Monomorphic workers with broad size variation (types and non-types: HL 0.44–0.58; HW 0.42–0.56). Head of large worker slightly more rectangular than small worker; posterior margin with shallow and gentle median depression. In profile, clypeus projected slightly forward from dorsal margin of head, almost entirely flat or straight; dorsum and lateral surfaces of head with fine and dense striations; ventral surface of head reticulate with smooth and shiny interspaces; outer surface of femora and first gastral tergite superficially reticulate with smooth and shiny interspaces; angle of propodeal junction in profile obtuse and rounded, posterior propodeum face steeply sloped. Head and dorsum of mesosoma darker brown compared to rest of yellowish-brown body; legs and tips of antennae slightly paler in tone. Large workers generally darker brown compared to small workers, tonal patterns identical.

**Queen.** Relatively large size (non-types: HL 0.54–0.56, HW 0.51–0.53), head not much more rectangular compared to large worker. In profile, clypeus very weakly convex and almost entirely flat. Dorsal view, anterior pronotal margin angulate at median point, posterior propodeal margin weakly convex; posterior face of propodeum rounded and smooth. Anterior half of head striated; posterior half mostly smooth and shining. Entire dorsum of mesosoma finely striated and shiny; lateral surface of mesosoma striate-reticulate, interspaces smooth and shining. Overall darker blackish brown as compared to worker, tonal patterns identical.

**Male.** Relatively large size (non-types: HL 0.44, HW 0.4–0.42). Head in full face view broad ovate; clypeus in profile weakly convex and almost flat anteriorly, rugulose and weakly shining; petiole subtriangular, apex blunt; dorsal outline of postpetiole almost entirely flat, cinctus between postpetiole and gaster indistinct. Anterior half of head dorsum rugulose-reticulate, interspaces punctured and weakly shining, rest of head substriate-reticulate and shiny, with scattered punctures; body mostly superficially substriate-reticulate with smooth and shining interspaces. Body colour generally dark grey-brown, head blackish; joints of legs and antennae paler in tone.

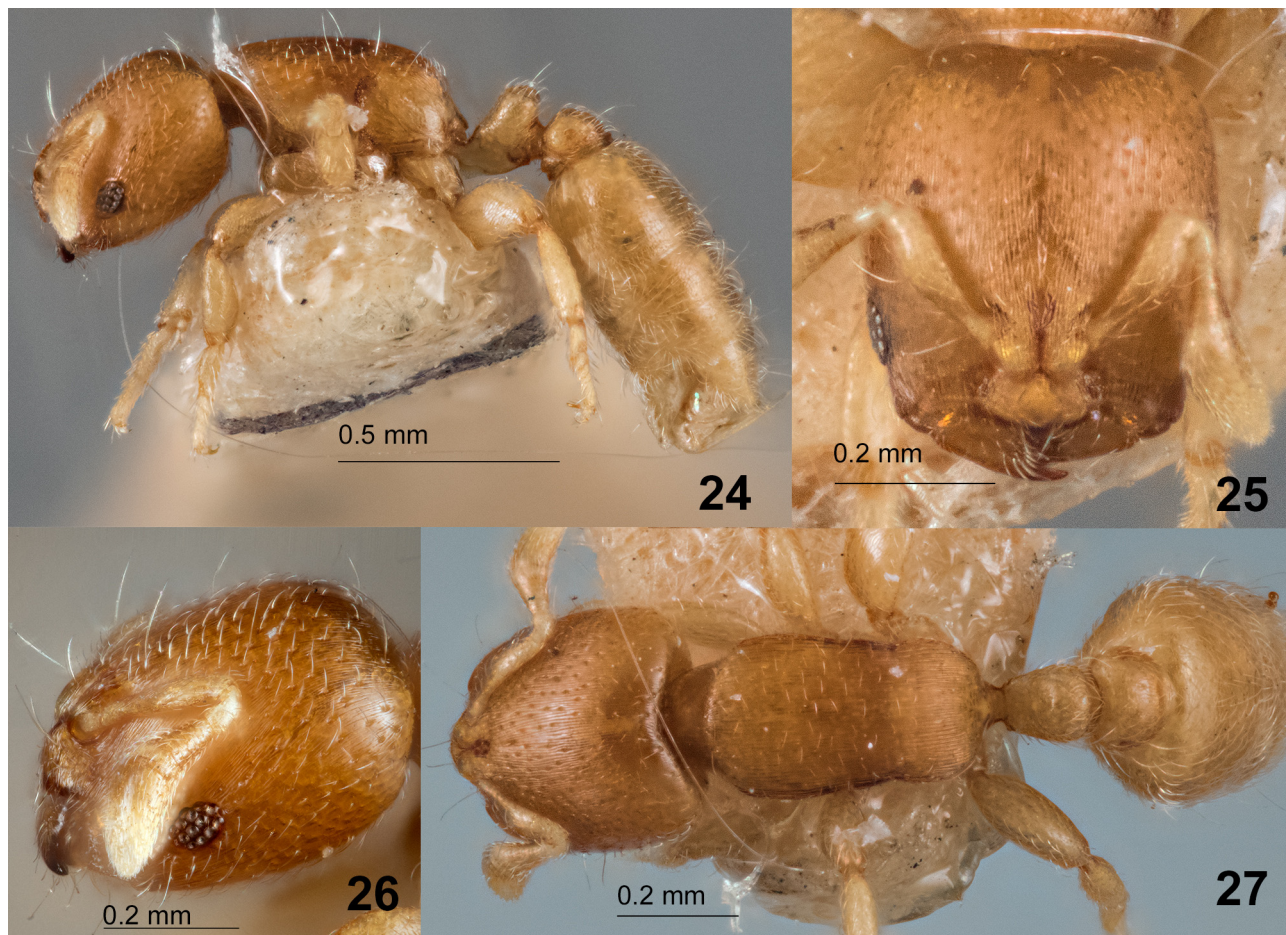
**Worker measurements.** Three syntypes (n = 3): TL 2.11–2.20; HL 0.50–0.52; HW 0.48–0.50; SL 0.18–0.20; ML 0.50–0.52; PronW 0.32–0.36; EL 0.08; EW 0.06; CI 96 ; REL 16–17; SI 38–40.



Eighteen non-types (n = 18): TL 1.84–2.43; HL 0.44–0.58; HW 0.42–0.56; SL 0.17–0.22; ML 0.52–0.74; PronW 0.28–0.42; EL 0.08–0.12; EW 0.05–0.08; CI 92–97; REL 16–21; SI 37–45.

**Queen measurements.** Three non-types (n = 3, 1 alate, 2 dealate): TL 2.53–3.1; HL 0.54–0.56; HW 0.51–0.53; SL 0.2–0.22; ML 0.8–0.88; MsW 0.42–0.46; EL 0.16–0.18; EW 0.12–0.13; CI 94–96; REL 31–35; SI 38–43.

**Male measurements.** Two non-types (n = 2): TL 2.4–2.53; HL 0.46–0.48; HW 0.44; SL 0.08; ML 0.88–0.92; MsW 0.52; EL 0.25–0.26; EW 0.2–0.21; CI 92–96; REL 57–59; SI 18.



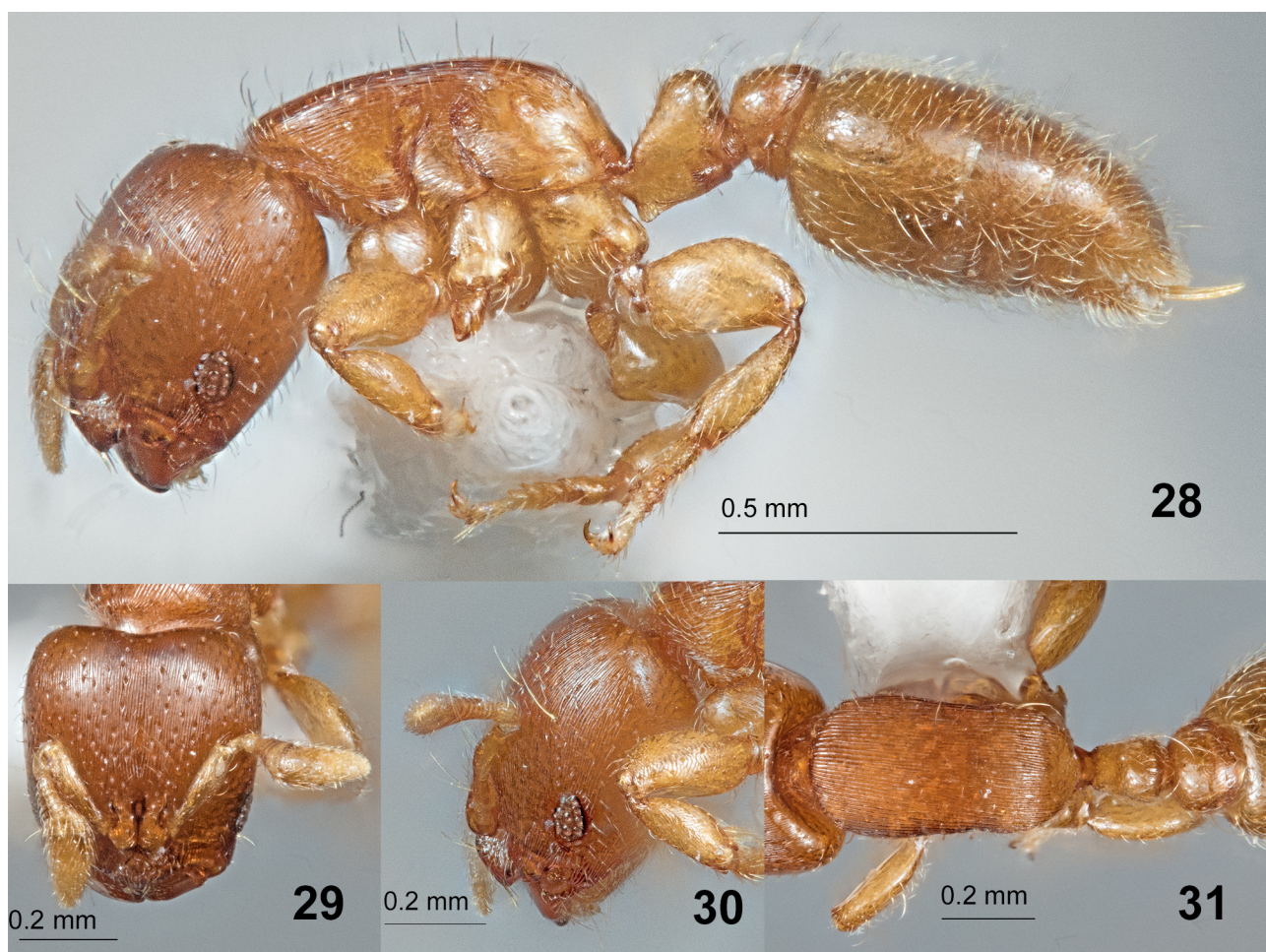
**FIGURES 24–27.** Lectotype worker of *R. johorensis* **stat. n.** 24, habitus in profile; 25, head in full-face view; 26, closeup of head in profile view; 27, body in dorsal view.

**Redescription of Worker** (lectotype, paralectotypes and non-types). Workers monomorphic with broad size variation. Head in full face view sub-rectangular, clearly longer than broad (only slightly in smaller worker), posterolateral corners smooth and rounded, lateral margins broadly and weakly convex, almost parallel to each other, posterior margin with shallow median depression. Eye relatively large, with 17–29 ommatidia (10–15 in smaller workers). In absolute profile, clypeus projecting forward slightly from dorsal margin of head, flat or weakly convex for most of its length. Antennal scape short and thin, extending slightly beyond midlength of head when laid backwards. Mesosoma in profile box-shaped, dorsal outline weakly convex, propodeal junction curved and obtuse, posterior face of propodeum shallowly concave and steeply sloped; mesopleuron demarcated from lateral face of pronotum and propodeum by distinct sutures. In dorsal view, mesosoma subrectangular, anterior pronotal margin broadly convex, sometimes slightly angulate at median point in large worker, humeral corners obtuse and rounded; lateral sides almost parallel and straight, not much narrower posteriorly than anteriorly, posterior margin of propodeum weakly concave. In profile, petiole inclined posteriorly, anterior margin weakly concave, slightly higher than broad, petiolar node bell-shaped, apex of node convex and blunt, about as high as post-petiole; dorsal margin of postpetiole in profile weakly convex. In profile, anteroventral extension of subpetiolar process short, subtriangular, variable in size across individuals, posterior margin of subpetiolar process

usually almost straight or weakly and broadly convex. In dorsal view, both petiole and post-petiole oblong or elliptical, both broader than long; post-petiole larger and wider than petiole.

Dorsal and lateral surfaces of head striated but shining; clypeal surface also striated, mandible mostly smooth and shining, with weak basal striations; ventral surface of head striate-reticulate and shining. Lateral surfaces of mesosoma substriate-reticulate and shiny, sculpture coarser closer to dorsal surface, interspaces punctate and weakly shining. Petiole and postpetiole superficially reticulate, interspaces mostly smooth and shining, apices also weakly striated. Gaster largely superficially reticulate with smooth and shining interspaces, scattered punctures.

Head and antenna covered with a mix of short standing and suberect hairs; sparse longer standing hairs present mainly on the clypeus, mandible and antennal scape. Mesosoma with abundant but scattered short standing hairs and sparse longer erect hairs around dorsal margin. Dorsal surface of petiole, postpetiole each with abundant short standing hairs of nearly uniform length, with a pair of long erect hairs. Dorsal and ventral surfaces of gaster covered with abundant and dense erect, suberect and decumbent short hairs, much denser and longer hairs relative to head and mesosoma, interspersed by sparse long erect hairs.



**FIGURES 28–31.** Non-type worker of *R. johorensis* from Singapore, Hougang Ave 3, ZRC\_HYM\_0000511; 28, habitus in profile; 29, head in full-face view; 30, closeup of head in profile view; 31, body in dorsal view.

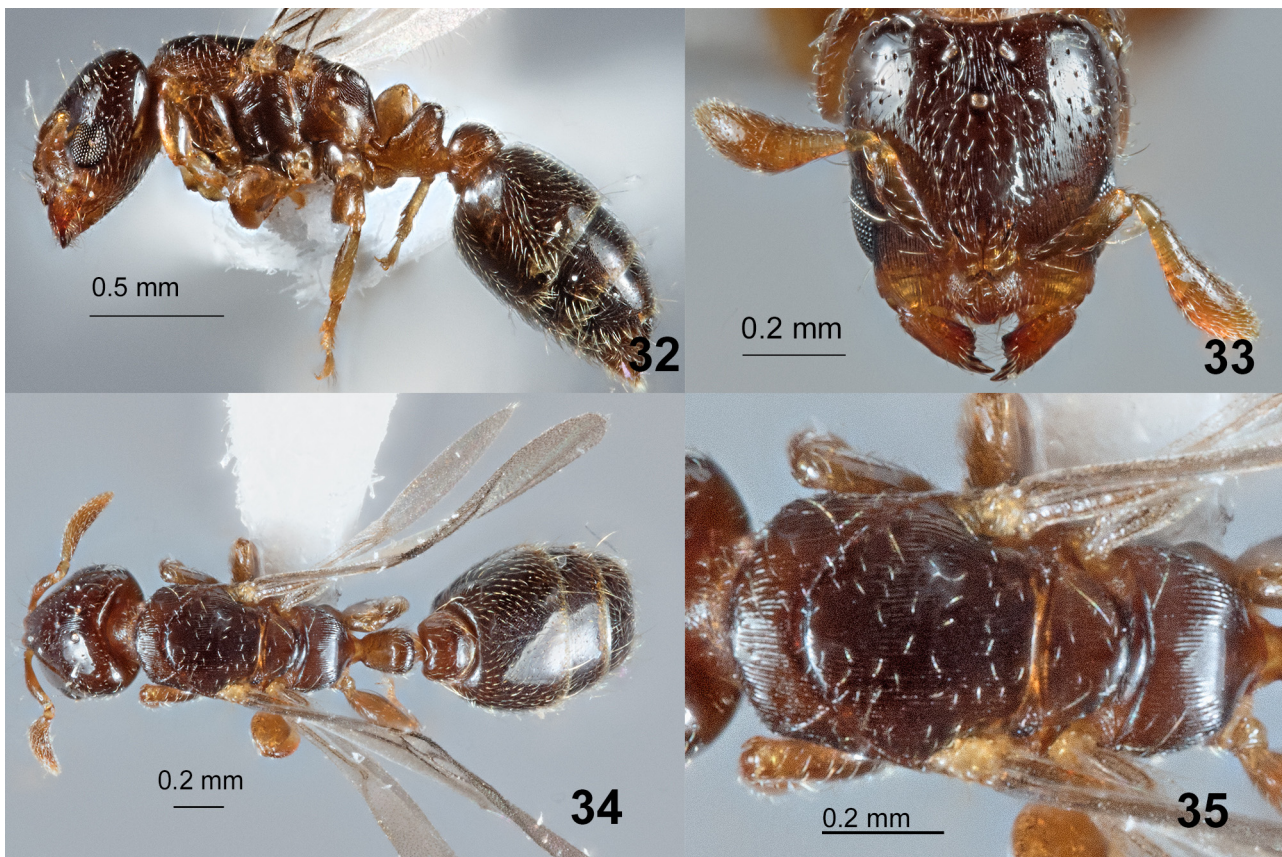
Small workers generally uniform pale yellowish-brown in colour; head and mesosoma of slightly darker tone, especially the dorsal surface of the mesonotum. Large workers darker brown or more reddish brown compared to small workers, tonal patterns identical.

**Description. Queen.** Relatively large size. Head in full face view subrectangular, not much more rectangular than that of large worker; posterolateral corners smooth and rounded, posterior margin nearly straight with a weak median depression. Posterior margin of eye located below midline of head in full face view. In profile, clypeus projected slightly forward from dorsal margin of head, very weakly convex and almost straight. Scape short, barely surpassing posterior margin of eye when laid back on head. In profile, mesosoma subcylindrical, more elongate

than worker, dorsal outline broadly and weakly convex, propodeal junction rounded and smooth, posterior face of propodeum weakly convex and smooth; sutures and sulci on lateral surface of mesosoma distinct. In dorsal view, mesosoma sub-cylindrical, anterior margin of pronotum strongly convex humeral corners angulate though rounded, mesoscutum almost as wide as long, sides of propodeum roundly convex, posterior propodeal margin indistinct and weakly convex. In profile view, petiole subtrapezoidal, slightly inclined posteriorly, anterior margin weakly concave; apex of petiolar node smooth and rounded, slightly higher than postpetiole. In dorsal view, petiole suboval, less than twice as wide as long; postpetiole globular, broader and larger than petiole.

Anterior half of head striated and shining, posterior half of head mostly smooth and shining with scattered punctures, feeble striations on and around the vertex; ventral surface of head mostly smooth and shining. Median section of clypeus striate-reticulate, interspaces punctured and weakly shining. Mandible mostly smooth and shining with very feeble striations. Lateral surface of mesosoma weakly striate-reticulate, interspaces smooth and shining; entire dorsum finely striated and shiny. Lateral and dorsal surfaces of petiole and postpetiole superficially reticulate, interspaces smooth and shining. Gaster superficially reticulate, interspaces smooth and shining with scattered punctures.

Dorsal and ventral surfaces of head with numerous scattered short standing and decumbent hairs, with sparse longer erect hairs; antennal scape with many short suberect hairs and sparse longer erect hairs. Dorsum of mesosoma with sparse short standing hairs, and sparser long erect hairs on anterodorsal and dorsolateral margins. Petiole and postpetiole pilose, with abundant short standing hairs, and sparse long erect hairs. Gaster very pilose, covered with abundant appressed and decumbent hairs, hairs on ventral surface denser than on dorsum.



**FIGURES 32–35.** Non-type queen of *R. johorensis* from Singapore, Pulau Tekukur, ZRC\_HYM\_0000578; 32, habitus in profile; 33, head in full-face view; 34, body in dorsal view; 35, closeup of mesosoma in dorsal view.

Overall uniformly dark-brown; legs lighter brown in tone, becoming progressively paler from femur to tarsus. Antennal funiculus and lateral surfaces of petiole, postpetiole also lighter brown. Generally darker in colour relative to worker.

**Male.** Relatively large size. Head in full face view broad ovate, distinctly narrower posteriorly than anteriorly,

posterior margin strongly convex; eye below transverse midline of head, outline of eye roundly convex and exceeding lateral margin of head. In profile, head broad-ovate and lobular, lateral corners smooth and rounded, ventral and posterior margins forming a continuous curved outline; clypeus projected strongly from dorsal margin of head, anterior outline weakly convex and almost flat. In profile, mesosoma subcylindrical and relatively elongate, dorsal outline broadly and weakly convex, propodeal junction rounded and smooth, posterior face of propodeum steep and almost vertical. In dorsal view, mesosoma obovate, narrower posteriorly, notauli absent. In profile view, petiole inclined posteriorly, longer than high, short and subtriangular with blunt and rounded apex, posterior slope weakly convex, forming a continuous curved outline with apex; anteroventral extension of subpetiolar process reduced to a short and shallow translucent lamella. Dorsal outline of postpetiole almost entirely flat, differentiated only a little from gaster by an indistinct cinctus.

Anterior half of head dorsum rugulose-reticulate, interspaces punctured and weakly shining, rest of head substriate-reticulate and shiny, with scattered punctures. Dorsum of mesosoma mostly sub-striated and shiny; lateral surface of mesosoma and dorsum of propodeum superficially striate-reticulate with smooth and shining interspaces. Petiole, postpetiole and gaster superficially reticulate, interspaces smooth and shining.

Dorsum of head with abundant evenly distributed and uniform short standing hairs, lateral surface with sparse standing hairs; ventral surface of head with numerous short appressed hairs. Dorsum of mesosoma, petiole and postpetiole with scattered short standing hairs. Gaster pilose, with numerous standing and decumbent hairs.

Body generally dark grey-brown, head more blackish and darker than rest of body; joints of legs and antennae paler in tone.

**Distribution.** Singapore, Thailand (Fig. 76).

**Habitat.** Often found in bark of common relatively large native tree species in secondary or disturbed forests, and abandoned or operational plantations. Colonies have frequently been collected from fruit trees, in particular mango trees (in both Singapore and Thailand).

**Remarks.** We carefully compared our queen specimens with the holotype queen (head missing) of *Rhopalomastix rothneyi* from India (QR), as we did for *R. javana*. We found the Singapore queen specimens (SJHQ) similar to the holotype, except for the following differences: 1) in SJHQ, pronotal length in dorsal view is more than half of propodeal length; in QR, pronotal length is less than half of propodeal length; 2) in SJHQ, posterior face of propodeum in profile view sloped at a slight angle, propodeal junction correspondingly obtuse; in QR posterior face of propodeum nearly entirely vertical, propodeal junction almost right-angled, though rounded; 3) SJHQ generally larger than QR (MsW 0.44–0.46 in SJHQ, MsW 0.42 in QR).

We compared workers and males of the Sri Lankan specimens (non-types of *R. rothneyi*) with the Singaporean specimens of *R. johorensis*, as we did for *R. javana*. The worker from Singapore (SJHW) differs from the Sri Lankan worker (SLW) by three main characters: 1) SJHW is of a generally larger size—SJHW PronW > 0.3, SLW PronW ≤ 0.3; 2) for SJHW, dorsal margin of mesosoma in profile view distinctly broadly convex with dorsum of propodeum sloped downwards, in SLW, dorsum of mesosoma is nearly entirely straight with propodeal dorsum flatly level for most of its length; 3) slope of the propodeal declivity in SJHW is gentler with an obtuse propodeal junction; in SLW, the slope of the propodeal declivity is steep with its propodeal junction almost right-angled. Our observations mostly concur with Wheeler's (1929), except his observation of smaller eyes; large Singaporean workers in this study can have 17–29 ommatidia, eye size relative to head very variable among all workers (REL 16–20).

The male from Singapore (SJHM) differs from the Sri Lankan male (SLM) in four main character traits. Firstly, SGM's head is generally larger than SLM's head—SJHM HL 0.46–0.48, HW 0.44; SLM HL 0.44, HW 0.4–0.42. Secondly, the mesoscutal width of SJHM is larger than that of SLM—SJHM MsW 0.52, SLM MsW 0.48–0.5. Thirdly, for SJHM the dorsum of mesosoma is mostly sub-striated and shiny; in SLM, dorsum of mesosoma is mostly smooth and shiny with scattered punctures. Lastly, for SJHM the petiole is more subtriangular, apex forming a continuous curve with the posterior margin; in SLM the petiole is more subtrapezoidal, apical and posterior petiolar margins joined at a distinct angle.

Given the character differences between the Singapore populations of *R. johorensis* and *R. rothneyi*, especially between the holotype queen of *R. rothneyi* and SJHQ, we thereby choose to raise the subspecies *johorensis* to species status.

Workers of *R. johorensis* are also quite similar to the workers of *R. striata*, but can be distinguished from the latter based on characters as explained in "Remarks" under the latter description.

**Variation.** Out of 6 examined colonies of *R. johorensis* from Singapore, 1 colony (ZRC\_HYM\_0000289) stood apart from the others in terms of minor differences in morphology and DNA. For COI (313 bp), barcodes obtained from this colony diverged from other specimens identified as *R. johorensis* at 1.9 % uncorrected *p*-distance clustering threshold, when only Singapore specimens were considered. An objective clustering threshold range of 3–4% is usually taken to best reflect actual species delimitation for insects (Hebert *et al.* 2003); thus, based on this criterion alone, the colony remains within the percentage threshold for species and can still be considered *R. johorensis*. As for morphology, worker size variation seemed more constrained in this colony—workers from the colony mostly resemble larger workers from other colonies, with more ommatidia per eye and darker body colour. No distinctly different small workers were collected. Furthermore, there are morphological traits that differ from large workers in other colonies. The mesosoma is more elongate (ML 0.64–0.74, *n*=10; vs. 0.52–0.62, *n*=8), the pronotum is wider (PronW 0.36–0.42; vs. PronW 0.28–0.36), and there is more intranidal variation in the number of ommatidia per eye (11–29 vs. 10–17, 11–16). These differences may simply constitute variation among different colonies and/or phenotypic plasticity under different living conditions, e.g. colonies established in different tree species. Therefore, before more convincing molecular and/or morphological evidence is gathered, we tentatively consider this slightly aberrant colony as *R. johorensis*.

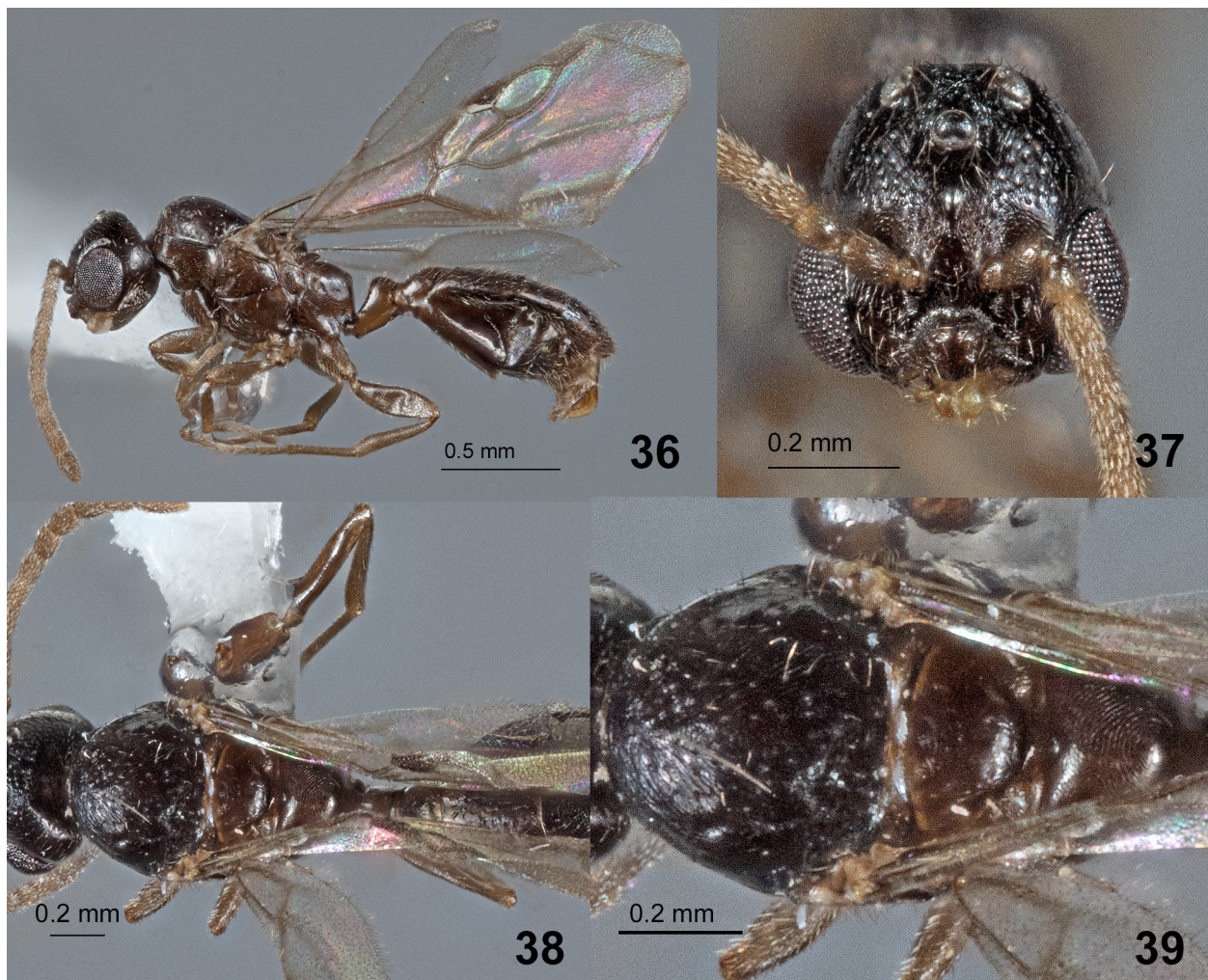
Barcodes of most specimens of *R. johorensis* identified from Thailand clustered with Singapore specimens between 0–0.6% (Fig. 1), except for specimens from East Thailand which diverged from all other *R. johorensis* specimens by 4.2% (Fig. 1). The East Thailand workers (EJHW) are morphologically identical to the types and other populations of *R. johorensis* examined in this study, except for one minor character: the sculpture on the lateral surface of the head is visibly weaker than on the dorsum of the head, and the interspaces are more smooth and shining. Given the absence of stronger morphological differences, and insufficient DNA support for cryptic species, we currently consider EJHW as *R. johorensis*.

**Non-type material examined.** SINGAPORE: 7 workers, 1 queen, Mandai Road (1.41385°N, 103.80481°E), nest behind bark of living tree, 29 Nov 2016, G.W. Yong and B. Ho leg., ZRC\_HYM\_0000509 (ZRC); 12 workers, 1 queen, Hougang Ave 3 (1.34769°N, 103.88838°E), mango tree, 12 Dec 2016, G.W. Yong and S.X. Chui leg., ZRC\_HYM\_0000511 (ZRC); 12 workers, 1 queen, Pulau Tekukor (1.23081°N, 103.83774°E), 15 Jan 2017, G.W. Yong leg., ZRC\_HYM\_0000578 (ZRC); 12 workers, Mandai Road (1.41318°N, 103.79405°E), nest behind bark of *Aquilaria malaccensis*, 21 Nov 2016, G.W. Yong and S.X. Chui leg., ZRC\_HYM\_0000291; 6 workers, 1 male, Mandai Road (1.41318°N, 103.79405°E), nest behind bark of *Macaranga gigantea*, 21 Nov 2016, G.W. Yong and S.X. Chui leg., ZRC\_HYM\_0000292 (ZRC); 12 workers, Pulau Tekukor (1.23081°N, 103.83774°E), mango tree, 9 Dec 2016, G.W. Yong and Y.G. Tan leg., ZRC\_HYM\_0000510 (ZRC); 12 workers, Mandai Road (1.41333°N, 103.79839°E), 13 Jan 2017, G.W. Yong leg., ZRC\_HYM\_0000577 (ZRC); 12 workers, 1 male, Mandai Road (1.41333°N, 103.79839°E), 18 Nov 2016, nest behind bark of *Camposperma auriculatum*, G.W. Yong and S.X. Chui leg., ZRC\_HYM\_0000289 (ZRC); 12 workers, 2 queens, Bukit Timah Nature Reserve (1.35127°N, 103.78161°E), nest in bark of *Artocarpus integer* (Thunb.) Merr./cempedak, 1 Nov 2017, W. Wang leg., colony no. WW-SG17-022, ZRC\_HYM\_0001794 (ZRC). THAILAND: Central Thailand, Pathum Thani Prov., Khlong Luang Dist., Kholng 5, 3 m a.s.l. (14.18083°N, 100.71000°E), mango tree, 3 Mar 2018, W. Jaitrong leg., colony no. WJT030318-1 (THNHM, ZRC); same locality, date and collector, colony no. WJT130218-1 (THNHM, ZRC); Central Thailand, Pathum Thani Prov., Khlong Luang Dist., Kholng 3, 10 m a.s.l. (14.17528°N, 100.66333°E), mango tree, 9 May 2018, W. Jaitrong leg., colony no. WJT090518-1 (THNHM); same locality, date and collector, colony no. WJT090518-2 (THNHM); Central Thailand, Ang Thong Prov., Chaiyo Dist., Lakfa Subdist., 14 m a.s.l. (14.68278°N, 100.46444°E), 7 Apr 2018, W. Jaitrong leg., colony no. WJT070418-2 (THNHM, ZRC); same locality, date and collector, colony no. WJT070418-1 (THNHM); same locality, date and collector, colony no. WJT070418-3 (THNHM, ZRC); same locality, date and collector, colony no. WJT070418-4 (THNHM, ZRC); same locality, date and collector, WJT070418-5 (THNHM, ZRC); Central Thailand, Saraburi Prov., Phu Kae Botanical Garden, 89 m a.s.l. (14.67056°N, 100.88500°E), 18 Mar 2018, W. Jaitrong leg., colony code. WJT180318-1 (THNHM, ZRC); Central Thailand, Saraburi Prov., Kang Koi Dist., Ban Chaom, nr. Ched Kod waterfall (14.47111°N, 101.16111°E), 8 Jan 2018, W. Jaitrong leg., colony no. WJT080118-3 (THNHM); Central Thailand, Nakhon Nayok Prov., Banna Dist., from mango tree, 11 May 2018, W. Jaitrong leg., colony no. WJT110518-1 (THNHM); E. Thailand, Chanthaburi Prov., Tha Mai Dist., Burapecholathid Road, 5 m a.s.l. (12.57083°N, 101.91611°E), 17 Mar 2018, W. Jaitrong leg., colony no. WJT170318-1 (THNHM, ZRC); E. Thailand, Chanthaburi Prov., Tha Mai Dist., Khlong Khud Subdist., 18 m a.s.l. (12.57167°N, 101.93111°E), 17 Mar

2018, W. Jaitrong leg., colony no. WJT170318-2 (THNHM, ZRC); same locality, date and collector, colony no. WJT170318-3 (THNHM, ZRC); S. Thailand, Trang Prov., Nayong Dist., Ban Nakhaw Sia, 28 m a.s.l. (7.50833°N, 99.71639°E), under bark of *Azadirachta excelsa* (Jack) Jacobs, 24 Jan 2018, W. Jaitrong leg., colony no. WJT240118-2 (THNHM, ZRC); same locality, date and collector, colony no. WJT240118-3 (THNHM); same locality, date and collector, colony no. WJT240118-4 (THNHM, ZRC).

**DNA Barcoding.** SINGAPORE: 46 workers from 9 different colonies collected from various localities were successfully barcoded, breakdown as follows (no. of workers per colony in parentheses): ZRC\_HYM\_0000291(3), ZRC\_HYM\_0000292(9), ZRC\_HYM\_0000509(5), ZRC\_HYM\_0000510(6), ZRC\_HYM\_0000511(9), ZRC\_HYM\_0000577(3), ZRC\_HYM\_0000578(4), ZRC\_HYM\_0001794(2), ZRC\_HYM\_0000289(10). THAILAND: 54 workers from 12 colonies were successfully barcoded, breakdown as follows: WJT240118-4(5), WJT240128-2(5), WJT130218-1(5), WJT030318-1(5), WJT170318-1(4), WJT170318-2(4), WJT170318-3(5), WJT180318-1(2), WJT070418-2(5), WJT070418-3(5), WJT070418-4(4), WJT070418-5(5).

Based on the combined cluster dendrogram (Fig. 1), barcode divergences from other species are as follows: *R. glabricephala*, 17%; *R. javana*, 13.8%; *R. murphyi*, 19.2%; *R. striata*, 12.5%; *R. tenebra*, 13.8%.



**FIGURES 36–39.** Non-type male of *R. johorensis* from Singapore, Mandai Road, ZRC\_ENT0000289; 36, habitus in profile; 37, head in full-face view; 38, body in dorsal view; 39, closeup of mesosoma in dorsal view.

***Rhopalomastix murphyi* sp. n.**

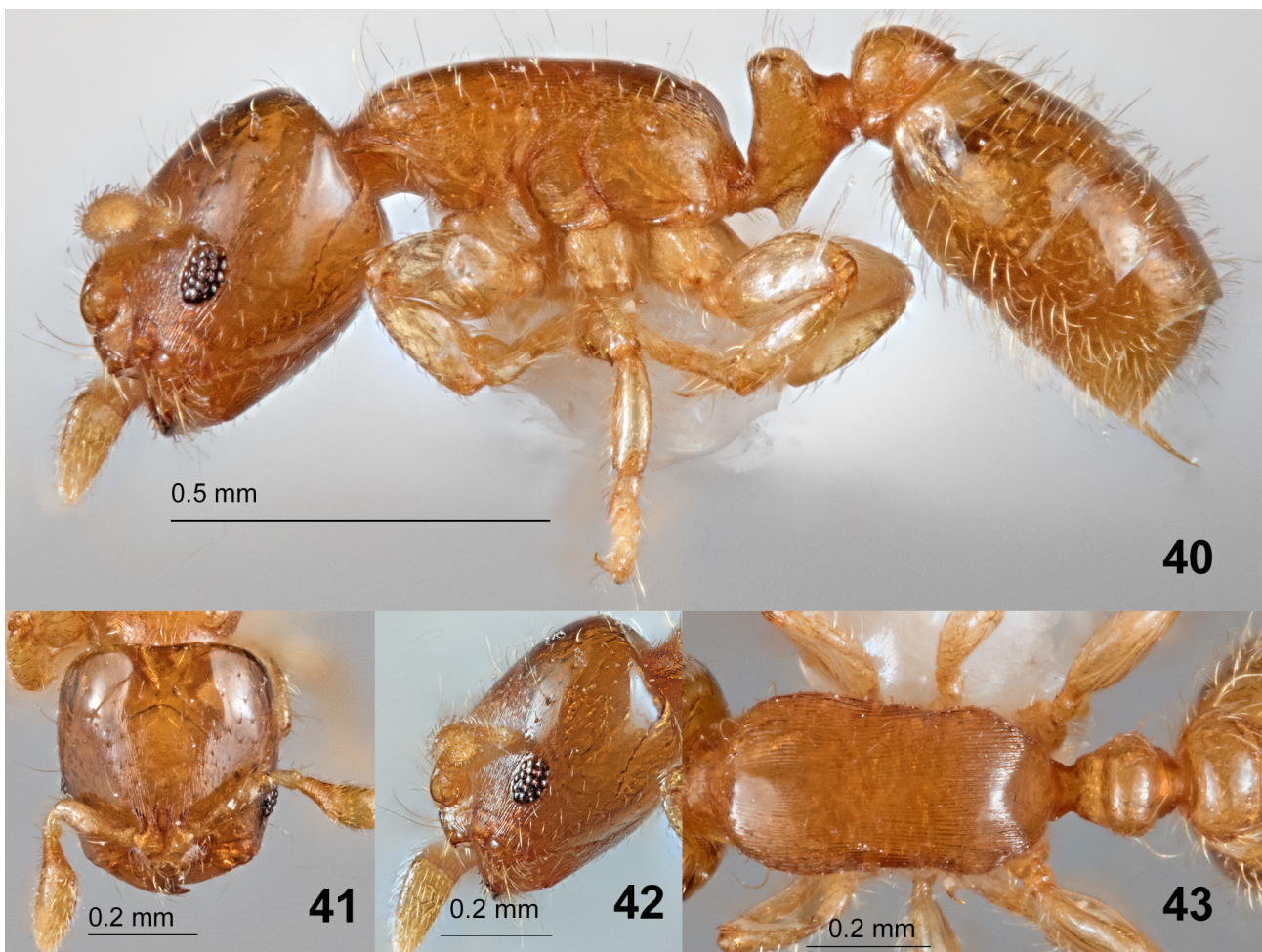
(Figs. 40–51)

**Type.** Holotype. Worker. SINGAPORE, Upper Thomson Nature Park (1.38653°N, 103.81938°E), in bark of *Durio zibethinus* L. tree, 24 Oct 2016, G.W. Yong & S.X. Chui leg., ZRC\_ENT\_00000874 (ZRC).

**Paratypes.** Fifty-five workers (MCZ, THNHM, USNM, ZRC), 3 dealate queens (ZRC), 6 males (THNHM, ZRC), same data as holotype, colony no. GY-SG16-RhoA, ZRC\_HYM\_0000287.

**Diagnosis. Worker.** Workers monomorphic with little size variation; small size (HL 0.40–0.44, HW 0.36–0.41). In profile view, clypeus evenly and broadly convex, projected forward slightly from dorsal margin of head; posterior half of head smooth and shiny; ventral surface of head and outer surface of femora largely smooth and shiny; upper part of mesopleuron rugulose-reticulate, interspaces punctured and dull; anterior face of petiole weakly concave, smooth and shiny without hairs. Body colour generally uniform yellowish-brown, head and mesosoma slightly darker in tone.

**Queen.** Small size (HL 0.42–0.45, HW 0.38–0.42), head slightly more rectangular than that of worker. In profile view, clypeus broadly and evenly convex; posterior half and ventral surface of head, outer surface of femora, dorsum of mesosoma and gaster largely smooth and shiny; pronotum in dorsal view short, anterior pronotal margin roundly convex; anterior face of petiole weakly concave and steep, smooth and shiny without hairs. Body colour generally uniform light brown, head, dorsum of mesosoma and gaster slightly darker in tone.



**FIGURES 40–43.** Paratype worker of *R. murphyi* sp. nov. 40, habitus in profile; 41, head in full-face view; 42, closeup of head in profile view; 43, body in dorsal view.

**Male.** Small size (HL 0.4–0.42, HW 0.37–0.4). Head in profile view subtrapezoidal, ventral margin below eye almost entirely straight; ocelli large; clypeus in profile short and rounded, punctate but shiny; petiole very short and wedge-shaped, apex smooth and blunt; dorsal outline of postpetiole flat, much longer than ventral margin; cinctus

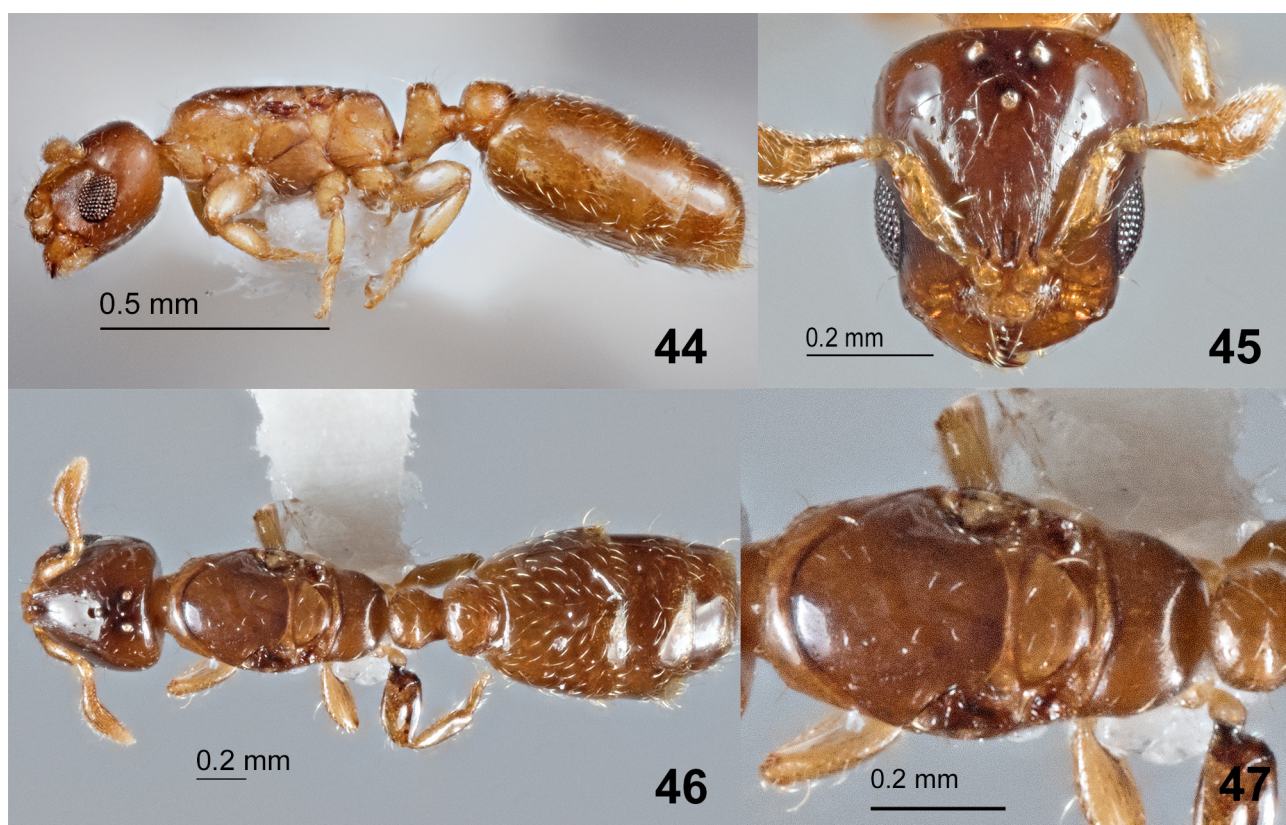
between postpetiole and gaster very weak. Entire body mostly smooth and shiny; petiole and postpetiole with sparse standing hairs. Body colour generally grey-brown; head, dorsum of mesosoma and distal half of gaster darker in tone.

**Worker measurements.** Holotype: TL 1.69; HL 0.43; HW 0.39; SL 0.15; ML 0.48; PronW 0.26; EL 0.08; EW 0.04; CI 91; REL 21; SI 38.

Two paratypes and eight non-types (n = 10): TL 1.59–2.07; HL 0.40–0.44; HW 0.36–0.41; SL 0.15–0.18; ML 0.44–0.50; PronW 0.26–0.29; EL 0.07–0.08; EW 0.04–0.05; CI 90–95; REL 18–21; SI 40–47.

**Queen measurements.** Three paratypes and three non-types (n = 6): TL 1.94–2.46; HL 0.42–0.45; HW 0.38–0.42; SL 0.18–0.19; ML 0.62–0.70; MsW 0.32–0.42; EL 0.15–0.16; EW 0.09–0.10; CI 89–93; REL 36–40; SI 43–47.

**Male measurements.** Six paratypes (n = 6, except for HW, CI, REL, SI (n=2)): TL 2.11–2.31; HL 0.40–0.42; HW 0.37–0.4; SL 0.07–0.10; ML 0.70–0.74; MsW 0.32–0.42; EL 0.18–0.22; EW 0.16–0.18; CI 93–95; REL 54–55; SI 19–25.



**FIGURES 44–47.** Paratype queen of *R. murphyi*. 44, habitus in profile; 45, head in full-face view; 46, body in dorsal view; 47, closeup of mesosoma in dorsal view.

**Description. Worker.** Small sized, with little size variation. Head in full-face view subrectangular, slightly longer than broad, lateral margins weakly convex or almost parallel to each other, posterior margin broadly convex with a weak median depression. Eye relatively small, with 10–13 ommatidia. In profile view, clypeus evenly and broadly convex, projected forward slightly from dorsal margin of head. Antennal scape short and almost uniformly thin, reaching midlength of lead when laid backwards. Mesosoma in profile subcylindrical and elongate, slightly longer than head length, anterior rising margin of pronotum truncate compared to posterior declining face of propodeum, dorsal outline almost straight; dorsolateral corner of propodeum rounded and smooth, propodeal declivity shallowly concave. In dorsal view, mesosoma subrectangular, anterior pronotal margin strongly convex and rounded, posterior propodeal margin weakly concave. In profile, petiole inclined posteriorly, slightly longer than high, anterior margin steep and weakly concave, anterior face distinct from apical face, petiolar node subtrapezoidal, apex smooth and blunt, directed postero-diagonally. Petiole higher and longer than postpetiole, postpetiole in profile view quadrant in shape, dorsal margin broadly convex. In dorsal view, petiole elliptical in shape, nearly twice as broad as long; postpetiole globular, wider than long, slightly wider and longer than petiole.



Posterior half of head including dorsum, lateral surfaces and venter mostly smooth and shiny, anterior half of head including antennal scrobe and area surrounding eye with feeble striations, partly superficially reticulate. Median clypeal surface with sparse punctures. Mandible mostly smooth and shining with punctures concentrated to small area close to masticatory margin. Lateral surface of mesosoma mostly weakly striate-reticulate and shiny, upper part of mesopleuron, i.e. anepisternum, rugulose-reticulate, interspaces punctured and dull; dorsal surface of mesosoma striated and shining, except for smooth and shining spot antero-median of pronotal dorsum. Lateral and dorsal surfaces of petiole, postpetiole weakly punctate, largely smooth and shining. Gaster mostly smooth and shining, with scattered punctures.

Dorsal surface of head with abundant short erect hairs and sparse long erect hairs; no standing hairs on central median shiny strip, and antennal scrobe; no hairs on gena, ventral surface with short appressed hairs, antenna with many short standing hairs. Sparse pilosity on mesosoma dorsum, scattered short erect hairs and sparse longer hairs concentrated close to dorsolateral sides. Petiolar node with short erect hairs of generally uniform length, and 1–2 pairs of much longer erect hairs; dorsal surface of postpetiole also with multiple short erect hairs of uniform length and a pair of much longer erect hairs. Gaster pilose, surfaces covered with abundant short standing hairs, sparse long standing hairs.

Overall generally uniformly yellowish-brown, head and mesosoma slightly darker in tone, legs and antennae brownish yellow and lighter in tone, tips of antennae pale yellow.

**Queen.** Relatively small size. Head in full face view subrectangular, slightly more rectangular than that of worker; lateral margins weakly and broadly convex, almost parallel to each other; posterolateral corners smooth and rounded, posterior margin nearly straight with a weak median depression. Posterior margin of eye located approximately at transverse midline of head in full face view. In profile, clypeus broadly and evenly convex. Antennal scape short, exceeding transverse midline of head by less than a quarter its length when laid back. In profile, mesosoma sub-cylindrical, more elongate than that of worker, dorsal outline broadly and weakly convex, posterior propodeal declivity steep and almost vertical; oblique mesopleural sulcus distinct but not deeply impressed, metapleural outline indistinct. In dorsal view, mesosoma sub-cylindrical, anterior margin of pronotum roundly convex, humeral corners rounded and smooth, pronotum relatively short, mesoscutum almost as wide as long. In profile view, petiole slightly inclined posteriorly, anterior rising margin steep and weakly concave; petiolar apex rounded and smooth, posterior declivity steep and weakly convex, about half the length of anterior margin. In dorsal view, petiole sub-oblong, about twice as wide as long; postpetiole globular, larger than petiole, wider than long.

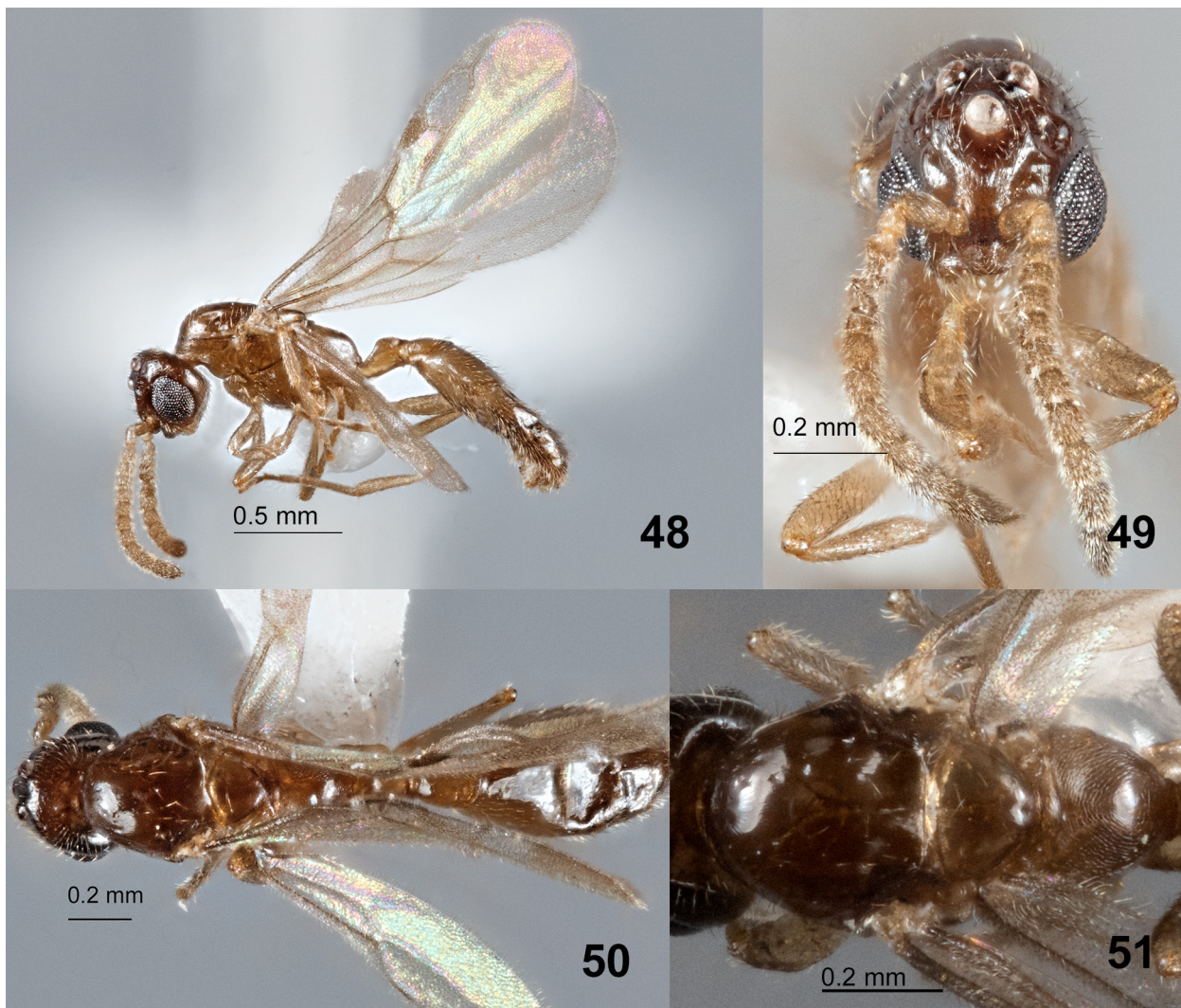
Posterior half of head, including dorsum and venter, and ventral head surface mostly smooth and shining; anterior half of head striate-reticulate and shiny; interspaces surrounding eye punctured but shining. Median section of clypeus largely smooth and shining. Mandible mostly smooth and shining with very feeble striations, area close to masticatory margin with sparse punctures. Lateral surface of mesosoma weakly striate-reticulate, interspaces smooth and shining; dorsal surface mostly smooth and shining, with superficial striate-reticulate sculpture. Lateral and dorsal surfaces of petiole and postpetiole superficially reticulate, interspaces smooth and shining; anterior rising face of petiole smooth and shining. Gaster largely smooth and shining.

Dorsum of head with short standing hairs of nearly uniform length, arranged approximately along two rows on frons, sometimes with up to 2 longer erect hairs; antennal scape with scattered uniformly short standing hairs, interspersed by sparse longer erect hairs; hairs on gena short and sparse, appressed or standing. Ventral surface of head with scattered short appressed hairs. Dorsum of mesosoma with sparse pilosity, sparse short standing hairs mainly on anterior half of mesoscutum; longer erect hairs scattered along dorsolateral margin, mainly on anterodorsal margin of pronotum. Rising face of petiole without hairs, apex with sparse short standing hairs, and two pairs of longer erect hairs. Dorsal surface of postpetiole with many short suberect hairs and at least a pair of longer erect hairs. Gaster pilose, dorsal surfaces mainly with abundant suberect and decumbent short hairs, ventral surfaces with abundant appressed and subdecumbent short hairs, both surfaces with sparse longer standing hairs. Pilosity denser close to distal end of gaster, around pygidium.

Entire body generally uniform light-brown; head, dorsum of mesosoma and gaster slightly darker in tone.

**Male.** Small size. Head in full face view broad-ovate, posterior margin strongly convex; ocelli large relative to head width; eye very large, extending past midline of head and close to posterior head margin at its maximum diameter, outline of eye strongly convex and exceeding lateral margin of head. In profile, head subtrapezoidal, ventral margin below eye almost entirely straight, lateral corners smooth and rounded; clypeus short and rounded,

strongly projected from dorsal margin of head. In profile, mesosoma sub-cylindrical and relatively elongate, dorsal outline broadly and weakly convex, posterior face of propodeum short and weakly convex. In dorsal view, mesosoma slightly obovate, notauli absent. In profile view, petiole inclined posteriorly, longer than high, anterior margin gently concave and longer than posterior margin, very short and wedge-shaped, apex smooth and blunt, posterior face gently sloping and broadly convex; anteroventral extension of subpetiolar process reduced to a translucent shallow and narrow lamella. Dorsal outline of postpetiole flat, much longer than ventral margin, forming an almost continuous outline with dorsum of gaster, only differentiated from the latter by a very weak cinctus.



**FIGURES 48–51.** Paratype male of *R. murphyi*. 48, habitus in profile; 49, head in full-face view; 50, body in dorsal view; 51, closeup of mesosoma in dorsal view.

Surfaces of head mostly smooth and shining, anterior half of dorsum and ventral surface of head weakly striate-punctate, clypeus punctate but shiny. Lateral surface of mesosoma superficially reticulate, interspaces smooth and shining, dorsum mostly smooth and shining, with feeble superficial striate-reticulate sculpture. Lateral and dorsal surfaces of petiole and postpetiole, and gaster superficially reticulate, largely smooth and shining.

Dorsal and ventral surfaces of head with abundant short erect and sub-decumbent hairs, posterior surface of head also with abundant subdecumbent and appressed hairs. mesoscutum with well-spaced subdecumbent and suberect hairs; ventral surface of episternum, coxa and legs with abundant short, erect, subdecumbent and appressed hairs. Petiole, postpetiole with sparse short standing hairs of uniform length. Gaster very pilose, both dorsal and ventral surfaces covered with abundant standing and subdecumbent hairs of moderate length.

Entire body generally uniform grey-brown; head, dorsum of mesosoma, and posterior half of gaster slightly darker brown in colour.

**Distribution.** Singapore.

**Etymology.** The specific name is dedicated to D.H. Murphy, who first collected *Rhopalomastix* in 1981; these specimens were deposited in ZRC and later identified as this species.

**Habitat.** The type series was derived from a rather large colony with numerous workers and multiple dealate queens, occupying an extensive area of bark on a durian tree (*Durio zibethinus*) in an abandoned plantation forest.

**Remarks.** *Rhopalomastix murphyi* sp. n. is most similar to *R. glabricephala*. See ‘Remarks’ under *R. glabricephala*.

**Non-type material examined.** SINGAPORE: 3 workers, locality unknown, secondary forest, 14 Apr 1993, Sk. Yamane leg., ZRC\_HYM\_0000584, 585 (ZRC); 12 workers, Mandai Lake Road (1.40915°N, 103.78234°E), durian tree, 03 Nov 2016, G.W. Yong & C. Peeters leg., ZRC\_HYM\_0000507 (THNHM; ZRC); 16 workers, 10 males, Upper Thomson Nature Park, 2 Nov 2016, G.W. Yong & C. Peeters leg., colony no. SP021116-1 (THNHM); Bukit Timah forest, 2 Jan 1981, D.H. Murphy leg., colony no. DHM-SG81-Rho1, ZRC\_HYM\_0000009 (ZRC).

**DNA barcoding.** Four individuals from the same colony as the type series (ZRC\_HYM\_0000287), and eight others from another colony (ZRC\_HYM\_0000507) collected from a different locality—Mandai Lake Road—were successfully barcoded. These barcodes clustered into two near-identical (0.3% divergence) haplotypes, 19.2% differentiated from all other species of *Rhopalomastix* (Fig. 1)

### ***Rhopalomastix striata* sp. n.**

(Figs. 52–63)

**Type.** Holotype. Worker, SINGAPORE, Mandai Road (1.41440°N, 103.79845°E), behind bark of Dipterocarpaceae, 18 Nov 2016, G.W. Yong & S.X. Chui leg., colony no. GY-SG16-RhoG, ZRC\_ENT\_00000876 (ZRC).

**Paratypes.** Thirty-six workers (MCZ, THNHM, USNM, ZRC), five males (ZRC), same data as holotype, ZRC\_HYM\_0000290.

**Diagnosis. Worker.** Workers generally monomorphic with broad size variation, relatively large size (HL 0.45–0.54 mm; HW 0.42–0.50 mm). Head sub-rectangular in full face view, distinctly longer than wide; in profile clypeus projected slightly forward from dorsal margin of head, roundly and evenly convex; dorsum and lateral surfaces of head with dense striations; ventral head surface mostly reticulate with smooth and shining interspaces; anterior pronotal margin strongly convex and angulate at its median point in both small and large workers, outer face of femora superficially reticulate with smooth and shiny interspaces; in profile, petiole sub-trapezoidal, its anterior margin steep and nearly straight. Head and dorsum of mesosoma darker brown than rest of lighter yellowish-brown body; legs and antennae paler yellowish-brown in some workers. Small workers with generally lighter body colours.

**Queen.** Medium size (HL 0.54–0.55, HW 0.46). Head more rectangular than worker. In profile view, clypeus broadly and evenly convex; posterior half and ventral surface of head largely smooth and shiny, frons and vertex with feeble striations; lateral surface of pronotum, outer surface of femora and gaster superficially reticulate and shining; dorsum of mesosoma finely striate and shiny; anterior pronotal margin strongly convex and angulate at median point; humeral corners angulate; pronotum about as wide as propodeum in dorsal view; posterior face of propodeum shallowly concave, in posterior view, lateral sides of propodeum strongly concave; anterior face of petiole steep and almost straight, petiole subtrapezoidal. Head, dorsum of mesosoma and gaster dark blackish brown, rest of body slightly lighter in tone, lateral surfaces of petiole, pronotum, and metapleuron more yellowish brown.

**Male.** Relatively large size (HL 0.45–0.47, HW 0.4–0.42). Head in full face view sub-oval; clypeus in profile strongly and evenly convex, rugulose-punctate and weakly shining; petiole subtrapezoidal, apex broadly and smoothly convex; anteroventral extension of subpetiolar process greatly reduced and small; dorsal outline of postpetiole broadly and weakly convex. Head mostly substriate-reticulate, interspaces smooth and shining, dorsum punctate; mesoscutum striated and shiny, with deep punctures. Entire body including head generally uniform blackish-brown, antennae and tips of legs pale yellowish-brown.

**Worker measurements.** Holotype: TL 2.23; HL 0.54; HW 0.48; SL 0.2; ML 0.66; PronW 0.34; EL 0.1; EW 0.07; CI 88.89; REL 20.83; SI 41.67. Four paratype workers and 7 non-types (n=11): TL 1.86–2.38; HL 0.45–0.54;

HW 0.42–0.50; SL 0.16–0.22; ML 0.52–0.70; PronW 0.28–0.35; EL 0.07–0.10; EW 0.05–0.06; CI 87–93; REL 17–21; SI 38–47.

**Queen measurements.** Two non-types (n = 2): TL 2.59–2.62; HL 0.54–0.55; HW 0.46; SL 0.2–0.22; ML 0.82–0.86; MsW 0.42–0.43; EL 0.16–0.17; EW 0.1–0.11; CI 84–85; REL 35–37; SI 43–48.

**Male measurements.** Five paratypes (n = 5): TL 2.33–2.61; HL 0.46–0.47; HW 0.4–0.42; SL 0.07–0.08; ML 0.86–0.92; MsW 0.46–0.54; EL 0.22–0.24; EW 0.18–0.20; CI 87–91; REL 52–60; SI 18–20.



**FIGURES 52–55.** Holotype worker of *R. striata* sp. nov. 52, habitus in profile; 53, head in full face view; 54, closeup of head in profile view; 55, body in dorsal view.

**Description. Worker.** Workers monomorphic with broad variation in size. Head in full face view subrectangular, distinctly longer than wide, posterolateral corners smooth and rounded, lateral margins broadly and weakly convex, almost parallel to each other, posterior margin with a shallow median depression, lateral margins broadly and weakly convex. Eye relatively small, larger worker with 12–15 ommatidia, smaller worker with 10–11 ommatidia. In absolute profile, clypeus projecting forward from dorsal margin of head, roundly and evenly convex. Mesosoma in profile box-shaped, dorsal outline weakly convex; dorsolateral corner of propodeum roundly convex; metapleuron demarcated from lateral face of pronotum and metapleuron by distinct sutures. In dorsal view, mesosoma subrectangular, anterior pronotal margin strongly convex and angulate at its median point, humeral angles obtuse but smooth and rounded, lateral margins almost entirely parallel with each other, posterior margin of propodeum feebly concave or nearly straight, four corners including pronotal humeri rounded and smooth. In profile, petiole slightly inclined posteriorly, its anterior margin steep and nearly straight, higher than broad, petiolar node sub-trapezoidal, apex weakly convex, posterior declivity of petiole short. Petiole slightly higher than postpetiole; dorsal margin of postpetiole weakly convex; subpetiolar process with subtriangular anteroventral

extension; posterior margin of subpetiolar process almost entirely straight or weakly concave. In dorsal view, petiole oval in shape, broader than long; postpetiole globular and larger than petiole.

Dorsal and lateral surfaces of head striated and shining. Median clypeal surface carinate with punctured interspaces and weakly shining; mandible mostly smooth and shining with few feeble striations, area close to masticatory margin with dense punctures; ventral surface of head mostly reticulate with smooth and shiny interspaces. Lateral surfaces of mesosoma weakly substrate-reticulate and shining; dorsal surface densely striated and shining. Outer face of femora superficially reticulate with smooth and shiny interspaces. Lateral surfaces of petiole and postpetiole including subpetiolar process reticulate, interspaces shining; dorsal surfaces of petiole and postpetiole striated and shining. Gaster superficially reticulate and weakly shining.

Dorsal surface of head with abundant short erect and suberect hairs, interspersed by sparse longer erect hairs. Ventral surface with numerous short appressed and decumbent hairs, ventrolateral area directly below eye with dense patch of short standing hairs, visibly more pilose than sparse hairs in adjacent genal region. Mesosoma less pilose than head, with scattered short erect and suberect hairs, sparse longer erect hairs, mostly aligned close to dorsolateral and anterodorsal sides. Petiole and postpetiole relatively more pilose, dorsal surfaces of both covered with abundant short erect and suberect hairs, generally longer than most hairs on head dorsum, each with a pair of longer erect hairs. Anterior rising face and posterior declivity of petiole also covered with dense short standing and decumbent hairs. Gaster very pilose, dorsal surface with abundant and dense erect and suberect hairs, ventral surface with thick layer of appressed and decumbent hairs.

In larger workers, head and dorsum of mesosoma dark brown, rest of body lighter in colour and roughly uniform yellowish-brown; legs and antennae may be paler yellowish light brown in some workers. For smaller workers, tonal patterns identical to larger workers, i.e. head and mesosomal dorsum darker than rest of body, but overall body colours lighter compared to large workers.

**Queen.** Medium size, not much larger than large worker. Head in full face view subrectangular, more rectangular than that of worker; lateral margins broadly convex and nearly parallel to each other, posterolateral corners smooth and rounded, posterior margin of head distinctly wider than anterior clypeal margin, with a shallow median concavity. Posterior margin of eye located approximately at transverse midline of head in full face view. In profile, clypeus broadly and evenly convex. Scape slightly exceeding transverse midline of head when laid back. In profile, mesosoma subcylindrical, more elongate than that of worker, dorsal outline broadly and weakly convex; posterior face of propodeum steep and shallowly concave; in posterior view, posterolateral sides of propodeum strongly concave; oblique mesopleural sulcus distinct. In dorsal view, mesosoma sub-elliptical, anterior pronotal margin strongly convex and angulate at median point; humeral corners angulate; pronotum about as wide as propodeum, clearly narrower than mesoscutum; mesoscutum about as wide as long. In profile view, petiole slightly inclined posteriorly, almost as high as long, anterior margin steep and weakly concave; petiolar node subtrapezoidal, apex rounded and blunt, slightly higher than postpetiole. In dorsal view, petiole globular, less than twice as wide as long, postpetiole also globular, much larger and wider than petiole.

Posterior half of head mostly smooth and shining, except for feeble striations and scattered punctures on frons and venter; anterior half of head largely striate-reticulate and shiny; ventral head surface mostly smooth and shining. Mandible mostly smooth and shining, area close to masticatory margin with dense punctures and weakly shining. Lateral surface of mesosoma including pronotum substrate-reticulate, interspaces smooth and shining; dorsal surface mostly striated, interspaces punctate but still shining, pronotum with weak striations, its median section almost entirely smooth and shining. Lateral surfaces of petiole and postpetiole reticulate, interspaces smooth and shining, dorsal surfaces superficially reticulate and mostly smooth and shining. Gaster largely smooth and shining, base of first tergite superficially reticulate.

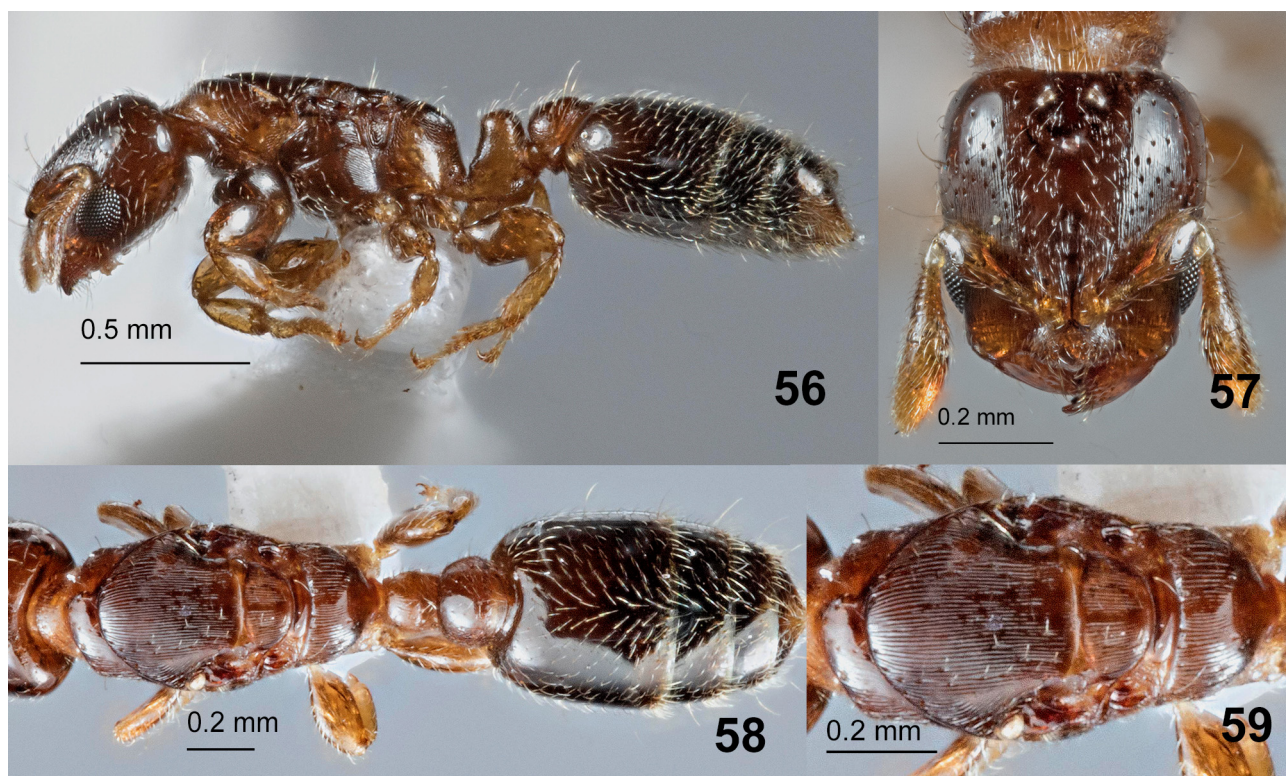
Dorsum of head with abundant short standing hairs of roughly uniform length, and sparse longer erect hairs; antennal scape lined with short erect hairs of roughly uniform height, and at least one longer erect hair; standing hairs on gena short and sparse. Ventral surface of head with abundant erect and suberect short hairs. Dorsum of mesosoma with sparse pilosity, sparse short standing hairs scattered mainly on the mesoscutum and along dorsolateral margin; sparse long erect hairs along dorsolateral margin, two pairs on anterior pronotal margin. Petiole pilose, anterior face with dense, short decumbent hairs, apex and posterior declining face with abundant short standing hairs, a pair of long erect hairs on apex. Dorsal surface of postpetiole with many short suberect hairs and a pair of long erect hairs. Gaster pilose, dorsal surfaces with abundant suberect and subdecumbent short hairs, sparse long erect hairs; ventral surfaces with abundant appressed and decumbent short hairs. Pilosity denser close to distal end of gaster, around pygidium.

In general, uniformly dark blackish-brown, petiole and postpetiole lighter brown, lateral surface of petiole much paler in colour. Legs also lighter brown, colour progressively paler in tone from femur to tarsus.

**Male.** Relatively large size. Head in full face view sub-oval, posterior margin roundly convex; eye just below transverse midline of head, outline of eye roundly convex and exceeding lateral margin of head. In profile, head broad-ovate and lobular, posterior margin almost straight, forming a continuous curved outline with rounded ventral margin; clypeus strongly projected from dorsal margin of head, outline strongly and roundly convex. In profile, mesosoma sub-oblong, dorsal outline very weakly convex and nearly straight, propodeal junction smooth and rounded, posterior face of propodeum short and weakly convex. In dorsal view, mesosoma obovate, narrower posteriorly, notauli absent. In profile view, petiole inclined posteriorly, subtrapezoidal and slightly longer than high, anterior margin weakly concave, apex blunt and weakly convex, posterior margin short and weakly convex; anteroventral extension of subpetiolar process greatly reduced to a very short and shallow translucent lamella. Dorsal outline of postpetiole broadly and weakly convex, separated from gaster by a weak but distinct cinctus.

Head surfaces mostly substriate-reticulate, interspaces smooth and shining, dorsum of head with scattered punctures, clypeus and its periphery more rugulose-reticulate, interspaces punctate and weakly shining. Dorsally, mesoscutum weakly and finely striated, shining and with scattered deep punctures; mesoscutal disc and dorsum of propodeum superficially reticulate, with smooth and shining interspaces; lateral surface mostly superficially reticulate with feeble substriations, interspaces smooth and shining. Petiole, postpetiole and gaster largely superficially reticulate with smooth and shining interspaces, apices of petiole and postpetiole almost completely smooth and shining.

Dorsum of head with abundant and evenly distributed short standing hairs; sparser standing hairs on lateral surface; ventral surface with abundant short appressed and decumbent hairs. Dorsum of mesosoma abundant short standing hairs, mainly concentrated on the mesoscutum. Dorsal surfaces of petiole, postpetiole with uniformly-short standing hairs. Gaster pilose, dorsum with abundant short decumbent and erect hairs roughly uniform in length, ventral surface visibly less pilose, with sparser short decumbent hairs.



**FIGURES 56–59.** Non-type queen of *R. striata* from Singapore, Bukit Timah Nature Reserve, ZRC\_HYM\_0001752; 56, habitus in profile; 57, head in full face view; 58, body in dorsal view; 59, closeup of mesosoma in dorsal view.

Entire body including head generally uniform blackish-brown, antennae and tips of legs pale yellowish-brown.

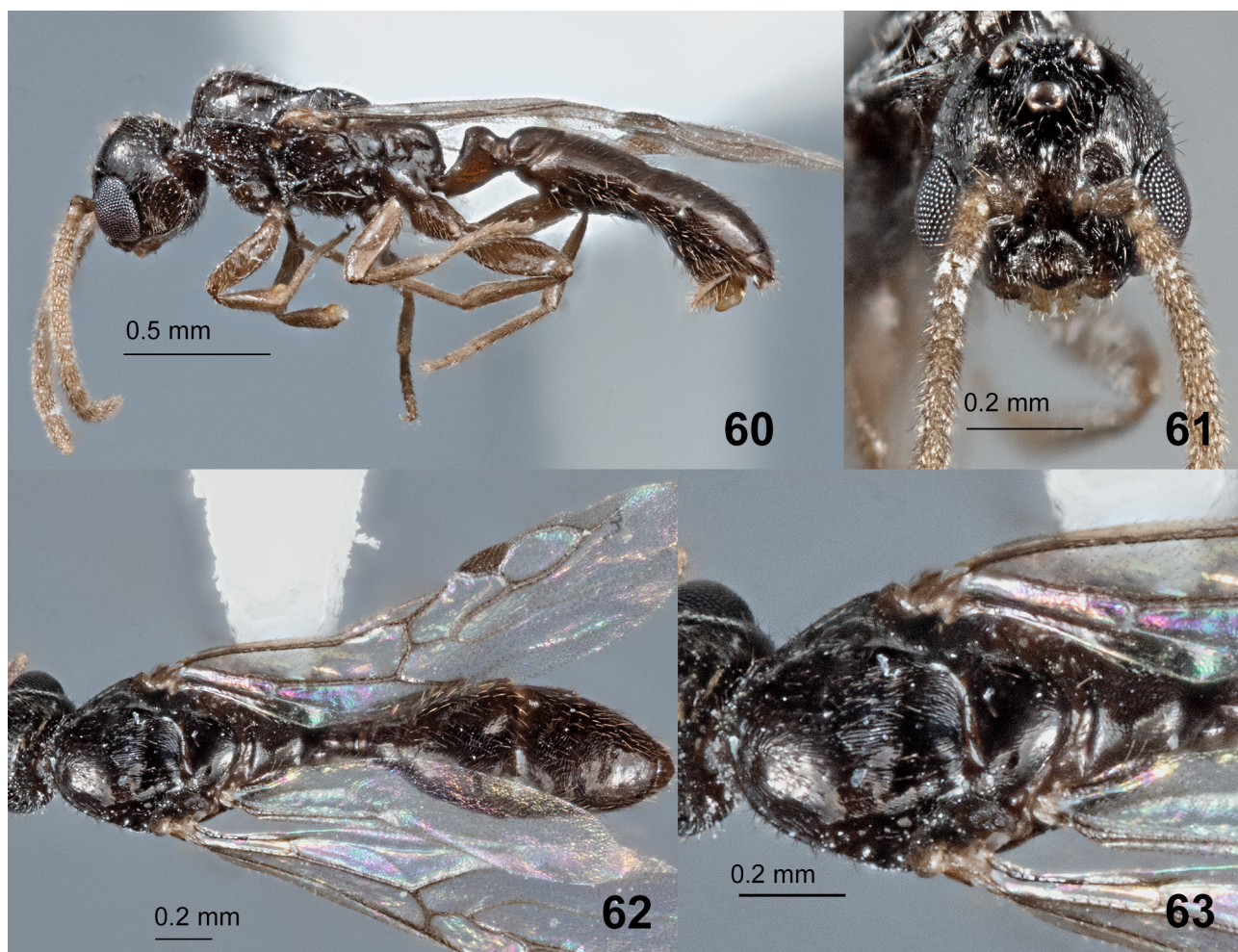
**Distribution.** Singapore.

**Etymology.** The specific name refers to the fine striations on the entire dorsum and lateral head surfaces.

**Habitat.** This species can be found mainly nesting in bark of large native trees, located in either primary or secondary native-dominated forest. A colony usually occupies a large expanse of the tree trunk, with numerous workers. Queens appear to be rare.

**Remarks.** Workers are morphologically similar to *R. johorensis* but can be differentiated by the following characters: for small workers -1) anterior pronotal margin strongly convex, median point almost angulate, whereas in *R. johorensis*, anterior pronotal margin weakly and broadly convex, median point not angulate, 2) head in full face view distinctly longer than wide for both small and large workers, whereas in *R. johorensis*, head in full face view more squarish, almost as wide as long, especially for smaller workers, 3) in profile, outline of median clypeal projection weakly and evenly convex, projecting forward from dorsal margin of head, in *R. johorensis*, clypeal outline generally flat and not evenly convex, 4) posterior margin of subpetiolar process almost straight or slightly concave in profile, for *R. johorensis*, posterior margin of subpetiolar process often weakly convex.

**Non-type material examined.** SINGAPORE: 8 workers, 3 queens, Bukit Timah Nature Reserve (1.35386°N, 103.77988°E), nest in bark of large tree in primary forest, 30 Aug 2017, W.Wang leg., ZRC\_HYM\_0001752 (ZRC); 12 workers, 1 queen, Bukit Timah Nature Reserve (1.34904°N, 103.77892°E), nest in bark of *Endospermum diadenum* (Miq.) Airy Shaw, 27 Sep 2017, colony no.WW-SG17-02,W. Wang leg., ZRC\_HYM\_0001793(ZRC); 7 workers, Mandai Road (1.40824°N, 103.80200°E), bark of tree in native-dominated secondary forest, 21 Dec 2016, G.W. Yong leg., ZRC\_HYM\_0000512 (ZRC).



**FIGURES 60–63.** Paratype male of *R. striata*. 60, habitus in profile; 61, head in full face view; 62, body in dorsal view; 63, closeup of mesosoma in dorsal view.

**DNA Barcoding.** A total of 20 workers from Singapore were successfully barcoded, with representatives from three colonies examined, including that of the holotype (no. of workers per colony in parentheses): ZRC\_HYM\_0000290 (7), ZRC\_HYM\_0001752 (9), ZRC\_HYM\_0000512(4). Based on the combined cluster

dendrogram (Fig. 1), barcode divergences from other species are as follows: *R. glabricephala*, 17 %; *R. johorensis*, 12.5%; *R. murphyi*, 19.2 %; *R. tenebra*, *R. javana*, 13.8%.

***Rhopalomastix tenebra* sp. n.**

(Figs. 64–75)

**Type.** Holotype. Worker. SINGAPORE, Upper Thomson Nature Park (1.38653°N, 103.81938° E), nest in bark of *Durio zibethinus* tree, 24 Oct 2016, G.W. Yong & S.X. Chui leg., colony no. GY-SG16-RhoB, ZRC\_ENT\_00000877 (ZRC).

**Paratypes.** Thirty-six workers (THNHM, ZRC), 3 queens (ZRC), one male (ZRC), same data as holotype, ZRC\_HYM\_0000288.

**Diagnosis. Worker.** Workers medium sized; generally monomorphic with moderate size variation (HL 0.44–0.53, HW 0.4–0.48). In profile view, clypeus evenly and broadly convex, in full face view, posterior margin with deep median concavity; anterior half and vertex of head substrate and shining, posterior half of lateral head surface largely finely reticulate with smooth and shiny interspaces; ventral head surface superficially reticulate with smooth and shiny interspaces; outer faces of femora and first gastral tergite superficially reticulate with smooth and shiny interspaces; anterior rising face of petiole almost straight, superficially reticulate and shiny. Head and dorsum of mesosoma very dark brown, rest of body relatively uniform lighter brown; joints and tarsi lighter and more yellowish in colour. Larger worker generally darker in colour relative to smaller worker.

**Queen.** Medium size (HL 0.5–0.54, HW 0.44–0.47), head more rectangular than that of worker, posterior margin with a relatively deep and broad median concavity; posterior half of head largely smooth and shiny, vertex, occipital lobe and ventral surface superficially reticulate; anterior margin of pronotum strongly convex and angulate at its median point; mesoscutum wider than long; anterior face of petiole weakly concave and almost straight, petiole subtrapezoidal with blunt apex. Head, mesosoma, gaster dark blackish-brown, legs, petiole and postpetiole lighter brown.

**Male.** Medium size (HL 0.44, HW 0.41–0.42). Head in profile view broad-ovate, ventral margin roundly convex; clypeus in profile convex and sub-semicircular, projecting strongly from dorsal margin of head; petiole relatively high and subtrapezoidal; dorsal outline of postpetiole weakly convex, cinctus with gaster distinct; anteroventral extension of subpetiolar process very small and subtriangular. Entire head mostly substrate-reticulate, with smooth and shining interspaces and scattered deep punctures; clypeus weakly reticulate-punctate and shiny; dorsum of mesosoma largely superficially reticulate. Largely uniform grey-brown, head blackish brown; legs and antennae paler in tone, joints of legs pale yellowish brown.

**Worker measurements.** Holotype: TL 2.1; HL 0.5; HW 0.46; SL 0.18; ML 0.64; PronW 0.36; EL 0.1; EW 0.06; CI 92; REL 21.74; SI. 39.13.

Paratype workers (n = 9): TL 1.92–2.36; HL 0.44–0.53; HW 0.4–0.48; SL 0.17–0.21; ML 0.52–0.68; PronW 0.30–0.38; EL 0.08–0.12; EW 0.04–0.07; CI 88–94; REL 18–25; SI 39–46.

**Queen measurements.** Three paratype queens and 1 non-type (n = 4): TL 2.56–2.8; HL 0.50–0.54; HW 0.44–0.47; SL 0.20; ML 0.68–0.70; MsW 0.41–0.42; EL 0.16–0.18; EW 0.10–0.12; CI 85–90; REL 36–39; SI 43–45.

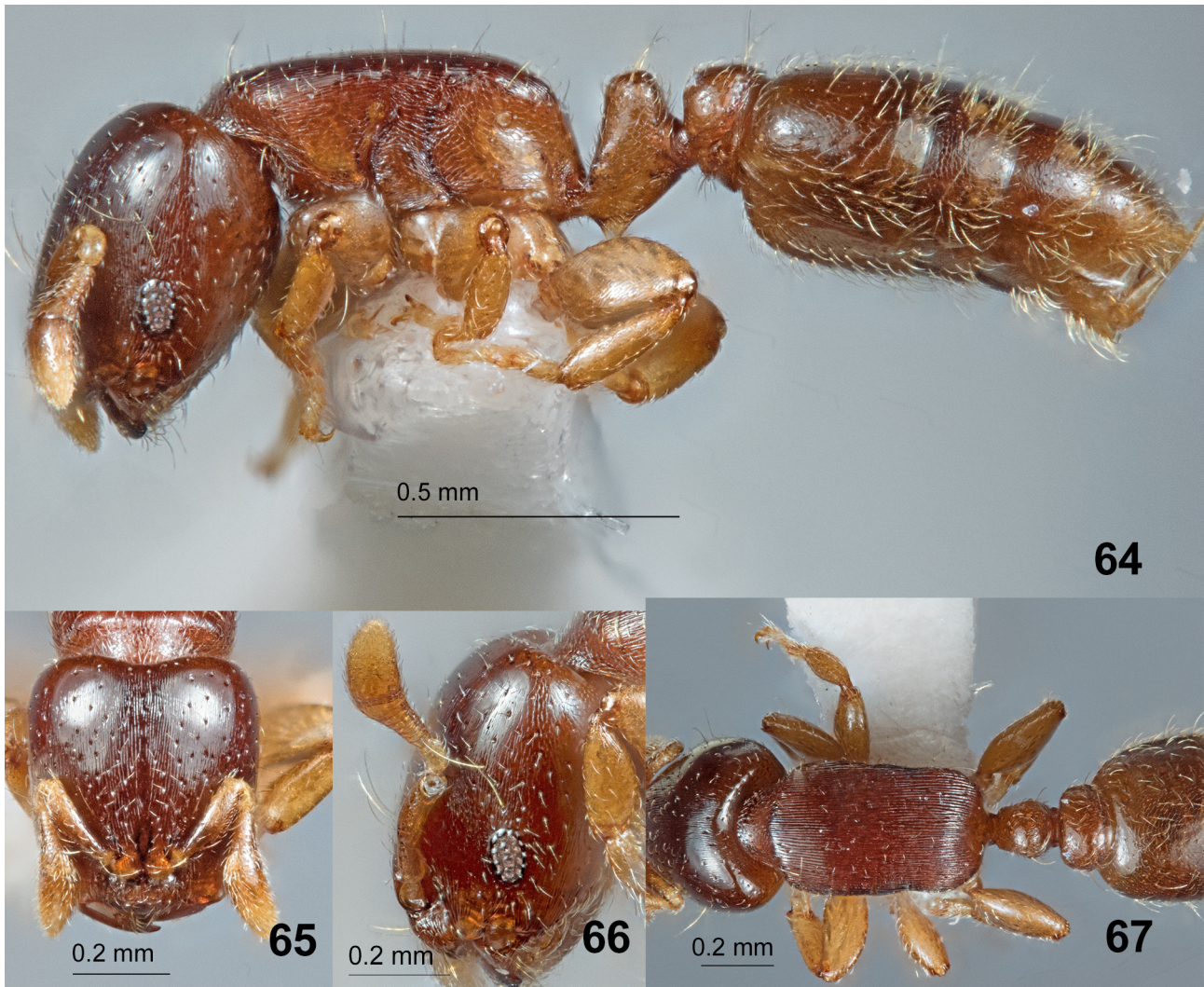
**Male measurements.** Paratype male and one non-type (n = 2): TL 2.17–2.18; HL 0.44; HW 0.41–0.42; SL 0.05–0.06; ML 0.78–0.84; MsW 0.46–0.48; EL 0.22–0.24; EW 0.16–0.20; CI 93–95; REL 54–57; SI 12–15.

**Description. Worker.** Medium sized, generally monomorphic with moderate size variation. Head in full face view subrectangular, slightly longer than wide, posterior margin with a relatively deep and concave median depression, posterolateral corners very smooth and rounded, lateral margins of head broadly convex and almost parallel with each other. Eye with 12–18 ommatidia. In profile, mesosoma subcylindrical, dorsal margin weakly convex, propodeal declivity steep and almost vertical. In dorsal view, mesosoma subrectangular, anterior pronotal margin strongly convex, almost angulate at its median point, humeral angle obtuse but smooth and rounded, lateral margins almost entirely parallel with each other except for a gentle depression where the metanotal groove occurs, dorsolateral sides of propodeum rounded and smooth, posterior propodeal margin weakly concave. In large workers, mesosoma more robust, pronotal width in dorsal view very broad, posterior propodeal margin almost as broad as pronotum. In profile, petiole slightly inclined posteriorly, not much longer than high, anterior rising margin almost entirely straight and steep, petiolar node bell-shaped, apex smooth and rounded, posterior petiolar declivity slightly shorter and steeper than anterior margin. In the same view, petiole slightly higher and much



longer than postpetiole, postpetiole quadrant in shape, dorsal margin broadly convex. In dorsal view, petiole globular, less than twice as broad as long; in small worker, petiole sub-oval, nearly twice as broad as long. Postpetiole globular, larger and wider than petiole, lateral margins rounded, about twice as wide as long.

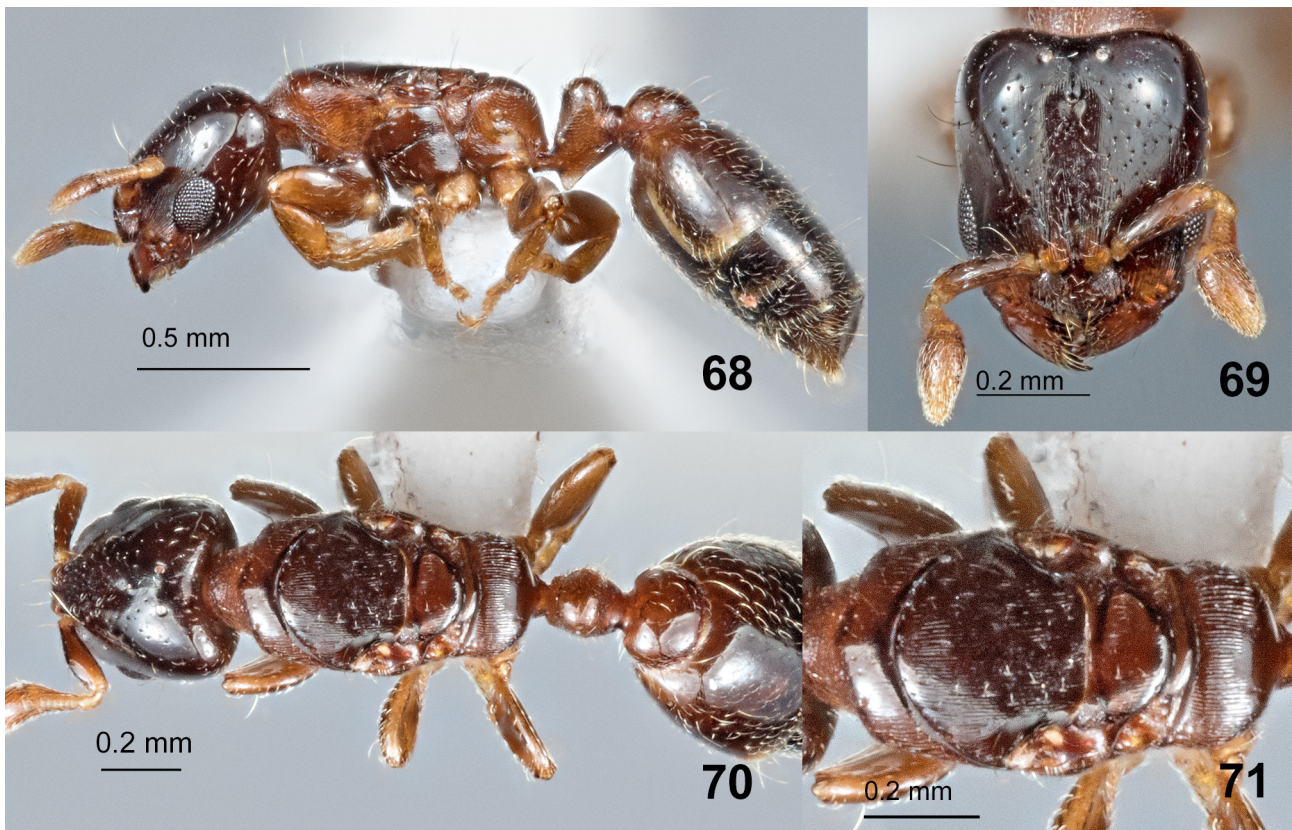
Surfaces of head substriated and shining, clypeus with dense punctures and striae but still weakly shining. Striations on head strong anteriorly but somewhat weaker posteriorly, posterior half of lateral head surface including occipital lobe mostly superficially reticulate with smooth and shiny interspaces; ventral surface of head finely reticulate with smooth and shiny interspaces. Mandible mostly smooth and shining, punctures concentrated to small areas close to masticatory margin and basal insertion. Lateral surface of mesosoma mostly striate-reticulate and shining, upper part of mesopleuron, i.e. anepisternum, rugulose-reticulate and weakly shiny; dorsum of mesosoma striated, dorsolateral margin wholly lamellate and distinct. Lateral and dorsal surfaces of petiole, postpetiole superficially reticulate, weakly punctate, interspaces shining. Gastral tergites mostly smooth and shining, with feeble microreticulate sculpture.



**FIGURES 64–67.** Holotype worker of *R. tenebra* sp. nov. 64, habitus in profile; 65, head in full face view; 66, closeup of head in profile view; 67, body in dorsal view.

Surfaces of head including gena with scattered but abundant short erect hairs, one or two long erect hairs; antennal scape also lined with evenly distributed short standing hairs and sparse longer erect hairs. Mesosoma dorsum with scattered short standing hairs, and sparse longer erect hairs limited to dorsolateral sides. Anterior rising face and posterior declivity of petiole with abundant decumbent hairs, dorsoapical surface of petiole with many uniform short standing hairs and one pair of much longer erect hairs. Dorsum of postpetiole also covered with abundant short erect hairs of uniform length, and one pair of long erect hairs. Gaster pilose, both dorsal and ventral surfaces covered with dense short erect, suberect hairs, interspersed with sparse longer erect hairs.

Head and dorsum of mesosoma very dark brown, rest of body relatively uniform lighter brown; joints and tarsi relatively lighter and more yellowish in colour. Large worker much darker in colour, head, dorsum of mesosoma and gaster almost opaque blackish-brown, rest of body lighter brown, also paler in tone towards distal parts of antennae and legs, i.e. antennal tips and tarsi.



**FIGURES 68–71.** Paratype queen of *R. tenebra*. 68, habitus in profile; 69, head in full-face view; 70, body in dorsal view; 71, closeup of mesosoma in dorsal view.

**Queen.** Medium size. Head in full face view subrectangular, more rectangular than that of worker, posterolateral corners smooth and rounded, lateral margins almost entirely straight and weakly converging anteriorly, posterior margin of head clearly wider than anterior clypeal margin, with a relatively deep and broad median concavity. Posterior margin of eye located roughly at midline of head in full face view. In profile, clypeus very weakly but evenly convex. Scape short, not exceeding midline of head when laid back. In profile, mesosoma subcylindrical, more elongate than that of worker, dorsal outline broadly and weakly convex, propodeal junction rounded and smooth, posterior face of propodeum steep and smoothly flat. In dorsal view, mesosoma sub-elliptical, propodeum distinctly less wide than pronotum, anterior margin of pronotum strongly convex and angulate at its median point; humeral corners more angular than that of worker, mesoscutum wider than long. In profile view, petiole subtrapezoidal, inclined posteriorly, longer than high, anterior face steep and weakly concave, almost entirely straight, apex bluntly rounded, slightly higher than postpetiole; dorsal margin of postpetiole nearly entirely straight. In dorsal view, petiole suboval, less than twice as wide as long, postpetiole globular, much larger and wider than petiole.

Posterior half of head largely smooth and shining; vertex, occipital lobe and ventral surface superficially reticulate; anterior half of head finely striated, interspaces punctate but shiny, median part of clypeus striate-punctate and weakly shining. Mandible mostly smooth and shining, area close to masticatory margin punctate. Lateral surface of mesosoma including pronotum weakly substrate-reticulate, interspaces smooth and shining; dorsum of mesosoma largely finely striate and shining, median section of pronotum superficially reticulate and shiny, with feeble striations; mesoscutellar disc with very weak striations, mostly smooth and shining. Lateral surfaces of petiole, postpetiole reticulate with smooth and shining interspaces, apices superficially reticulate, largely smooth and shining. Gaster superficially reticulate and shining.

Dorsum of head with numerous short erect and suberect hairs with sparse longer erect hairs; antennal scape with scattered short erect hairs. Gena and ventral surface of head with abundant but scattered short appressed hairs. Dorsum of mesosoma with sparse short standing hairs mainly on the mesoscutum and along dorsolateral margin; sparse long erect hairs along dorsolateral margin, one pair on pronotal humerus. Anterior face of petiole with short decumbent hairs, apex posterior declining face abundant short standing hairs, sparse long erect hairs on apex. Dorsum of postpetiole with abundant short suberect hairs and a pair of long erect hairs. Dorsal surface of gaster with abundant suberect and subdecumbent short hairs, ventral surface with many appressed and decumbent short hairs, both surfaces with sparse long erect hairs; hairs denser distally.

Head, mesosoma, gaster dark blackish-brown, petiole and postpetiole lighter brown, legs also lighter brown, paler in tone towards tarsi.

**Male.** Medium size. Head in full face view almost entirely spherical, posterior margin broad and roundly convex; maximum diameter of eye only slightly exceeding midline of head; outline of eye convex and exceeding lateral margin of head. In profile, head broad-ovate, lateral corners smooth and rounded, ventral and posterior margins forming a continuous smooth curve, ventral margin roundly convex; clypeus convex and sub-semicircular, projecting strongly from dorsum of head. In profile, mesosoma sub-oblong, dorsal margin almost straight, propodeal junction rounded and smooth, posterior face of propodeum steep and weakly convex, almost entirely vertical. In dorsal view, mesosoma obovate and narrower posteriorly, notauli absent. In profile view, petiole slightly inclined posteriorly, relatively high and subtrapezoidal, anterior margin weakly concave, apex weakly and broadly convex, forming a continuous convex curve with posterior margin; anteroventral extension of subpetiolar process greatly reduced to a very small, shallow, and subtriangular translucent lamella. Dorsal outline of postpetiole weakly convex, differentiated from gaster by a weak but distinct cinctus.

Entire head mostly substriate-reticulate, with smooth and shining interspaces and scattered deep punctures; clypeus weakly reticulate-punctate and shiny. Lateral surface of mesosoma mostly superficially reticulate with smooth and shining interspaces; dorsum very feebly and superficially striate-reticulate, interspaces smooth and shining, mesoscutum with scattered punctures. Petiole, postpetiole and gaster superficially reticulate with smooth and shiny interspaces.

Dorsum of head with abundant short standing hairs, ventral surface with dense short appressed hairs. Dorsum of mesosoma with numerous but scattered short decumbent and erect hairs, mainly on mesoscutum. Dorsal surfaces of petiole, postpetiole with many uniformly-short erect hairs. Gaster pilose, dorsal surface with abundant decumbent and erect short hairs, ventral surface with numerous appressed and decumbent short hairs, sparse short erect hairs.

Body generally a uniform dark grey-brown, head blackish-brown, legs and antennae lighter in tone; joints of legs pale yellowish brown.

**Distribution.** Singapore.

**Etymology.** The specific name means “darkness” in Latin and alludes to this species’ dark body colours, and observed inclination to hide in dark crevices in tree bark.

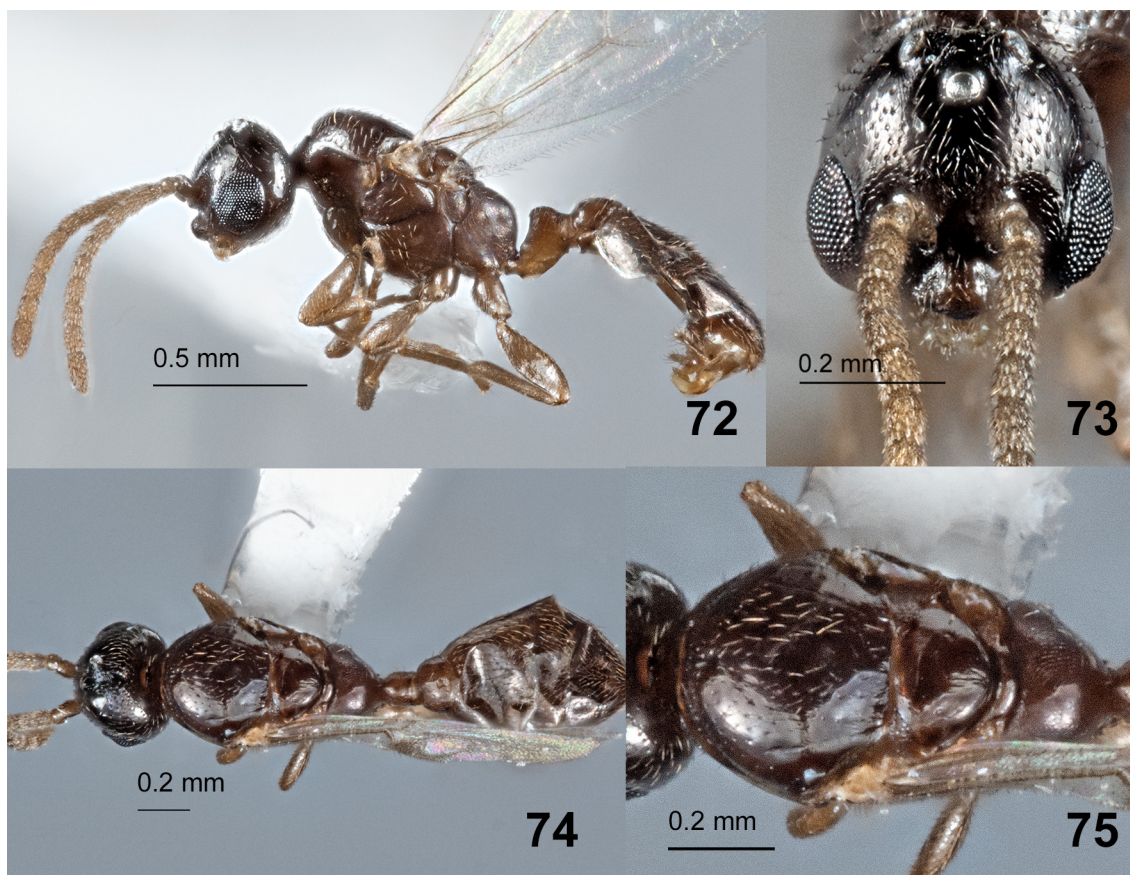
**Habitat.** The type series of *R. tenebra* was found deep within bark of *Durio zibethinus* (durian tree) in an abandoned plantation, just a few metres away from another durian tree colonized by *R. murphyi*. Unlike *R. murphyi*, the colony of *R. tenebra* seemed more dispersed throughout a relatively broad area, workers less numerous; individuals were often obscured or well-hidden under bark layers; few or none were found on the bark surface.

**Remarks.** *Rhopalomastix tenebra* is most similar to *R. javana* in having the posterior half of lateral head surface weakly sculptured (weak striations or striate-reticulate with smooth and shiny interspaces). However, *R. tenebra* can be separated from *R. javana* based on the following characteristics: posterior half of lateral head surface largely superficially reticulate with smooth and shiny interspaces ( finely striate-reticulate and shining in *R. javana*); in full-face view, median depression of posterior margin of head deeply concave (relatively shallow in *R. javana*); in profile, anterior rising margin of petiole almost straight (weakly concave in *R. javana*); larger variation in size, larger worker slightly larger than that of *R. javana*.

**Non-type material examined.** SINGAPORE: 37 workers, 1 male, Upper Thomson Nature Park (1.38653°N, 103.81938°E), 2 Nov 2016, G.W. Yong & C. Peeters leg., colony no. SP021116-2 (THNHM); 2 workers, same locality, date and collector as above, colony no. SP021116-3 (THNHM).

**DNA Barcoding.** Nine individuals from the same colony as the type series (ZRC\_HYM\_0000288) were

successfully barcoded. Based on the combined cluster dendrogram (Fig. 1), barcode divergences from other species are as follows: *R. glabricephala*, 17%; *R. javana*, 7.1%; *R. murphyi*, 19.2%; *R. striata*, *R. johorensis*, 13.8%.



**FIGURES 72–75.** Paratype male of *R. tenebra*. 72, habitus in profile; 73, head in full-face view; 74, body in dorsal view; 75, closeup of mesosoma in dorsal view.

## Discussion

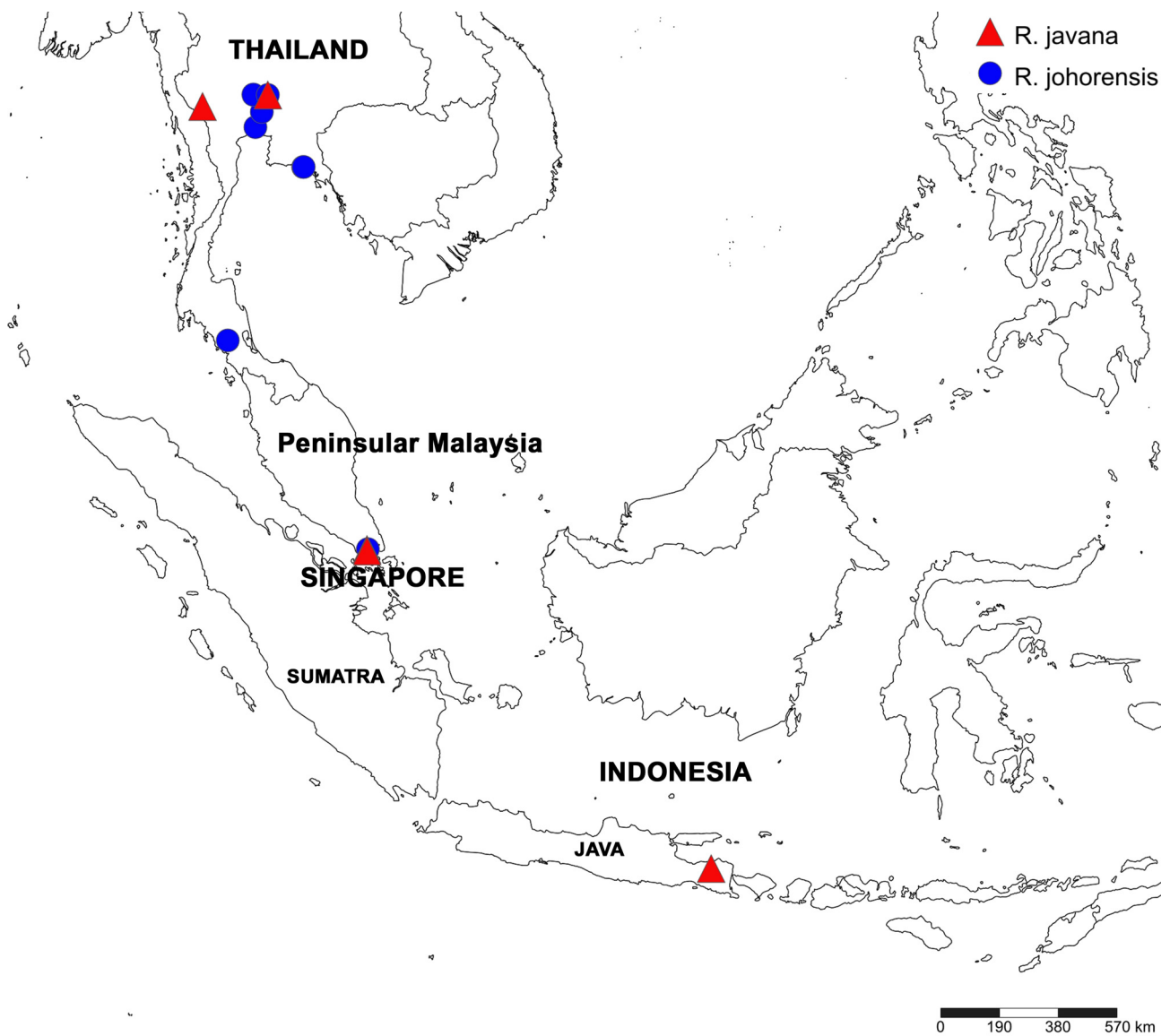
In this study, we used a combination of molecular (DNA barcoding) and morphological techniques to establish six extant species of *Rhopalomastix* in Southeast Asia, four of these new to science. We further note that *Rhopalomastix* species in Southeast Asia can roughly be separated into two broad species groups based on distinct morphological characters: the *R. murphyi* and *R. rothneyi* groups. These groupings are based wholly on morphological similarities; actual phylogenetic relationships may be established in the future when additional genetic markers are available.

*R. murphyi* group—Relatively small size across all castes; workers monomorphic with little intranidal size variation; head, body surfaces, and femora mostly completely smooth and shining, and/or with fine or superficial sculpture. Two novel species from Southeast Asia belong to this group: *R. murphyi* and *R. glabricephala*.

*R. rothneyi* group—Generally larger in size compared to the *murphyi* group across all castes; workers monomorphic, tend to exhibit broad but isometric size variation, with allometric variation in minor characters; head, body surfaces, and femora mostly strongly sculptured, sometimes superficial, few or no surfaces entirely smooth and shining. Four species from Southeast Asia fit these criteria, including two new species: *R. johorensis*, *R. javana*, *R. striata*, and *R. tenebra*.

It is striking that so many species of this rather obscure genus can be found in Singapore, a small country of severely limited land area. The existence of multiple species in Singapore alone implies a strong possibility of many more species of *Rhopalomastix* awaiting discovery across the Southeast Asian region. In our study, we have identified two species in particular—*R. javana* and *R. johorensis*—that comprise genetically distinct but morphologically cryptic populations. The short COI barcodes generated in this study, however, yield insufficient

information to determine if those populations fulfil the operational criteria for delimitation as cryptic species (Ross *et al.* 2009). A combination of nuclear and mitochondrial genetic markers will be needed to reliably resolve deeper evolutionary relationships within and amongst different nominal species. Resolving the phylogeny of *Rhopalomastix* is beyond the scope of this study, but we advocate an integrated approach based on morphology and more comprehensive DNA sequencing for future systematic work on this genus, given the complexities of morphological variation between and within populations. That said, we do not discount the value of short fragment DNA barcodes—these barcodes still serve as useful tools to aid initial species delimitation (Doña *et al.* 2015; Wang *et al.* 2018), but should not constitute the single basis for species inference. Genetic information should always be analysed in conjunction with morphology and/or other forms of biological evidence.



**FIGURE 76.** Distribution of *R. javana* and *R. johorensis* in Southeast Asia.

While we cannot confirm from limited samples in this study that *Rhopalomastix* species are specialized colonists of particular species or families of trees, we observed that trees where *Rhopalomastix* can be found are typically of wide girth, with relatively thick layers of bark, inner layers often succulent and fairly moist. Trees with dry, cracked layers of bark are unlikely to harbour *Rhopalomastix*. It is also notable that many colonies sampled in this study were found living in close association with armored scale insects (diaspidids) (G.W.J. Yong, pers. comm.). It has been surmised that the ants ‘rear’ these scale insects in their nests, and feed on proteins and/or waxy

compounds secreted by the latter to build their protective ‘armour’ or shields (Peeters *et al.* 2017; Yong *et al.* 2018, in press). Mutualistic relationships between ants and diaspidids have been observed and recorded in *Melissotarsus*, the Afrotropical cousin of *Rhopalomastix* from the same tribe (Peeters *et al.* 2017). Much more awaits to be uncovered on the biology, behaviour, and systematics of this unique but poorly-studied bark-dwelling ant genus in Southeast Asia.

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