Systematics and biogeography of the ant genus *Crematogaster* Lund subgenus *Orthocrema* Santschi in Asia (Hymenoptera: Formicidae)

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The subgenus *Orthocrema* of the ant genus *Crematogaster* is a well defined group and diverse in the tropical Asia. Its systematics has remained poorly understood because of a lack of modern revisionary work. *Crematogaster* (*Orthocrema*) is revised for the Asian region, and 27 species including ten new species are recognized. Five species groups: the *C. baduvi* group (4 spp.); the *C. binghamii* group (3 spp.); the *C. biroi* group (10 spp.); the *C. moatensis* group (1 sp.); the *C. quadriruga* group (9 spp.) are established based on worker caste morphology. A key to Asian species of the subgenus *Orthocrema* based on the worker caste is given. Phylogenetic relationships of Asian *Orthocrema* are analyzed. The analysis revealed that the *C. baduvi*-, *C. binghamii*-, and *C. biroi* groups are monophyletic, and that the allopatric distribution patterns of closely related species imply that Asian *Orthocrema* is composed of relatively young taxa. There have been at least three west-to-east dispersal events across Wallace’s line in the *C. baduvi*-, *C. quadriruga*-, and *C. biroi* groups.


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INTRODUCTION

The genus *Crematogaster* is one of the most diverse ant genera, particularly in the tropics (Hölldobler & Wilson, 1990). The regional-scale taxonomy and systematics of the genus, which includes 487 valid species-level names (Bolton, 2014) in two subgenera (Blaimer, 2012c, d), have received considerable attention in recent years (Longino, 2003; Hosoishi & Ogata, 2009b, 2012; Blaimer, 2010, 2012a, 2013).

The subgenus *Orthocrema* consists of 142 species around the world (Blaimer, 2012c), and of these, 15 species and 4 subspecies are presently known from Asia. In his review of the ants of the former British India, Bingham (1903) listed only one species in *Orthocrema*. A key to *Orthocrema* species from the Indo-Australian region was provided in Menozzi (1935), but the key is of little use now as it has not been updated to include more recently described species and changes in the classification of the subgenus (Blaimer, 2012c).

*Orthocrema* ants have generally been considered to be ground dwellers, and they have frequently been collected by general sampling methods in faunal surveys (e.g., Malsch, Rosciszewski & Maschwitz, 2003; Eguchi et al., 2005; Pfeiffer et al., 2011). Although some specimens have been identified to species level based on distinct morphological characters (e.g., Hosoishi, Yamane & Ogata, 2010), many specimens have not been identified to species.

Workers of the subgenus are roughly distinguished even in the field, by having a yellow-colored body and acrobatic style. The subgenus has been characterized based on the following features: two-segmented antennal club; petiole with subparallel sides; postpetiole without median sulcus (Santschi, 1918; Emery, 1922; Wheeler, 1922). Subsequently Blaimer (2012c) diagnosed the subgenus based on a variety of character combinations on a global scale. The aim of this study is to revise the *Orthocrema* species found in Asia.

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The Winkler extraction method is generally suitable for collecting many of the species in the subgenus, but a fogging machine is better suited for collecting some of the rarer species in the canopies of tropical rainforests. We also collected several species from dead twigs or leaves on trees in Asia. As mentioned by Blaimer (2012b) in her revision of Malagasy taxa, the nesting site of the subgenus is more extensively distributed than expected. It is not known whether each taxon in the subgenus shows a particular nesting behaviour. In this study, our collections comprise a wide range of material, covering subterranean and ground-dwelling ants obtained by Winkler extractions and general collections, hand-collected arboreal ants, and canopy ants with fogging. We consider that nesting site information can reveal interesting phylogenetic relationships.

Generally, workers of the subgenus are monomorphic in size, but morphological intermediate workers of queens and ordinary workers have been found in some species (Heinze et al., 1999; Longino, 2003; Blaimer, 2012b; Peeters et al., 2013). It is reported that the intermediate workers lay unfertilized trophic eggs. In our revision of Asian taxa, we found intermediate workers in five species. Phylogenetic relationships reveal the occurrence patterns of the intermediate workers in Asian fauna.

The goal of the present study is a phylogenetic study and taxonomic revision of the subgenus Orthocrema in Asia, including keys to the species, distribution maps, and discussion of biogeographic patterns. We also discuss the monophyly and systematic position of the species groups based on worker morphology. Nesting behaviour and information of intermediate worker on the phylogeny provide insight into the character evolution.

**MATERIAL AND METHODS**

‘Asia’ in the present paper refers to the Manchurian subregion of the Palearctic Region, Oriental Region, and Australian region excluding Australia, Papua New Guinea, the Solomon Islands, Vanuatu, Fiji and the islands in the Pacific Ocean. We generally followed the geographical terminology of Ward (2001). The term ‘Wallace’s line’ refers to the original definition of the line (Wallace, 1863), that runs east of Bali, Borneo and the lace’s line’ refers to the original definition of the line geographical terminology of Ward (2001). The term ‘Wal-

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Type specimens were examined and/or deposited in the collections listed below. Codes for public institutions generally follow those in Arnett, Samuelson & Nishida (1993). The acronyms and abbreviations of the institutions/collections cited in the text are: ACEG, Ant Collection of Katsuyuki Eguchi, Graduate School of Science and Engineering, Tokyo Metropolitan University, Tokyo, Japan; BMNH, Natural History Museum, London, UK; CASC, California Academy of Sciences, San Francisco, CA, USA; FRIM, Forest Research Institute Malaysia, Kuala Lumpur, Malaysia; HNMH, Hungarian Natural History Museum, Budapest, Hungary; JEBR, Institute of Ecology and Biological Resources, Hanoi, Vietnam; IEGG, Istituto di Entomologia ‘Guido Grandi’, Bologna, Italy; ITTJ, National Institute of Agro-Environmental Sciences, Tsukuba, Japan; KUEC, Institute of Tropical Agriculture, Kyushu University, Fukuoka, Japan; MBBJ, Museum Zoologicum Bogoriense, Cibinong, Java, Indonesia; MCSI, Museo Civico di Storia Naturale ‘Giacomo Doria’, Genoa, Italy; MCZC, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MHNG, Muséum d’Histoire Naturelle, Geneva, Switzerland; MNHA, Museum of Nature and Human Activities, Hyogo, Japan; MPMP, National Museum of the Philippines, Manila, Philippines; NHMB, Naturhistorisches Museum, Basel, Switzerland; NHMW, Naturhistorisches Museum, Wien, Austria; SKYC, Seiki Yamane Collections, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan; THNHM, Thailand Natural History Museum, Technopolis, Khlong Luang, Pathum Thani, Thailand. In the lists of ‘Material examined’ the records for each species are arranged alphabetically by country. Nest series samples are represented as colony code, e. g. ‘SH10-Mal-48’.

Most observations were made under a Leica M205C stereomicroscope. Images were created using a Canon EOS 50D with a Canon MP-E 65 mm ×1–5 macro lens, then processed using CombineZM software.

Measurements were made under the Leica M205C stereomicroscope using micrometres. All measurements are expressed in millimetres, recorded to the second decimal place. Abbreviations used for measurements and indices follow Longino (2003) and Hosoishi (2015). The measurements for petiole and postpetiole generally follow Longino (2003) when applicable, except as follows. head width (HW) (Fig. 1); head length (HL) (Fig. 1); cephalic index (CI): HW/HL × 100; scape length (SL) (Fig. 2); scape index (SI): SL/HW × 100; eye length (EL) (Fig. 1); pronotal width (PW) (Fig. 3); Weber’s length of the mesosoma (WL) (Fig. 4); propodeal spine length (PSL) (Fig. 4); petiole length (PtL) (Fig. 5) (slightly modified from Longino, 2003: fig. 2); petiole width (PtW) (Fig. 6); petiole height (PtH) (Fig. 5) (see Longino, 2003: fig. 2); postpetiole length (PpL) (Fig. 6) (see Longino, 2003: fig. 2); postpetiole width (PpW) (Fig. 6); petiole height index (PtHI): PtH/PtL × 100; petiole width index (PtWI): PtW/PtL × 100; postpetiole width index (PpWI): PpW/PpL × 100; waist index (WI): PpW/PtW × 100.

Chaetotaxy is very important for species identification in some ant genera, such as Lasius (Salata & Borowiec, 2011), Formica (Petrov & Collingwood, 1993; Fedoseeva, 2011; Korochkina, Konopleva & Zryanina, 2014), Polyrhachis (Sorger & Zettel, 2009), Messor
Figures 1–7. 1–6, Measurements of workers. 1, Head width, head length and eye length; 2, Scape length; 3, Pronotal width; 4, Weber’s length and propodeal spine length; 5, Petiole length and petiole height; 6, Petiole width, postpetiole length and postpetiole width. 7, Map of the chaetotaxy of the mesosomal surface of workers of the Asian *Orthocrema* species showing the positions of the setae, cited from Menozzi (1935).

PHYLOGENETIC ANALYSIS

To determine the systematic position of the species groups within the subgenus Orthocrema in Asia, 25 species, including fauna from New Guinea, were examined to code the most informative character states (Table 2). Thirty-three morphological characters were examined from the worker caste and all of the characters including a multistate character were treated as unordered; '?' is given for unknown and inapplicable cases, and the matrix is shown in Table 2. For this analysis, 24 Asian Orthocrema species were selected.

Characters of the queens, males and larvae were not included as it was not represented in our collections. Buren (1958) stated that the differences in the male genitalia are so slight as to be useless for species diagnosis in the genus Crematogaster. As for larvae, Wheeler & Wheeler (1952) examined the former subgenus, Crematogaster, Orthocrema, Physocrema and Sphaerocrema, but they did not find any characters for diagnosing each subgenus because of intra- and interspecific variations. Whereas nest series samples in closely related species collected from Southeast Asia showed the interspecific differences in the male and queen castes (Hosoishi, unpublished data). In the present study, we examine the workers only, but the morphological analysis shown here can contribute to the better understanding of phylogenetic relationships when the male and queen castes are collected in the future.

Cladistic analyses were performed with the TNT 1.1 program (Goloboff, Farris & Nixon, 2008) with outgroup rooting, default consensus options, Tree Bisection and Reconstruction (TBR) branch swapping, and the default ‘traditional search’ mode. The TNT program accepted only one taxon as an outgroup for the analysis, and Crematogaster paradoxa was selected for this purpose as molecular data suggest that C. paradoxa is the sister group of the remaining Orthocrema clades (Blaimer, 2012d). The tree search employed a parsimony ratchet with 10 000 iterations per run. Parsimony analyses were completed under conditions of equal and implied weighting, with k values ranging from 1 to 10. Tree analyses and graphical manipulations were performed with WinClada version 1.00.08 software (Nixon, 2002), and consensus cladograms generated from equally parsimonious trees were generated using the same program.

Table 1. Summary of terms and abbreviations referring to setae important to the systematics of Asian Orthocrema species

<table>
<thead>
<tr>
<th>Term or abbreviation</th>
<th>Definition</th>
<th>Menozzi (1935)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ps1PN</td>
<td>paired setae on pronotal shoulders</td>
<td>A</td>
</tr>
<tr>
<td>ps2PN</td>
<td>paired setae on anteromedian pronotum</td>
<td>B</td>
</tr>
<tr>
<td>psaMN</td>
<td>paired setae on anterior mesonotal ridges</td>
<td>C</td>
</tr>
<tr>
<td>pspMN</td>
<td>paired setae on posterior mesonotal ridges</td>
<td>D</td>
</tr>
<tr>
<td>psPR</td>
<td>paired setae on anterior dorsolateral corners of propodeum</td>
<td>E</td>
</tr>
<tr>
<td>ps1PS</td>
<td>paired setae near base of propodeal spines</td>
<td>F</td>
</tr>
<tr>
<td>ps2PS</td>
<td>paired setae on dorsal surface of propodeal spines</td>
<td>G</td>
</tr>
</tbody>
</table>

(Baroni Urbani, Aktaç & Çamlitepe, 1989) and Technomyrmex (Bolton, 2007), but has not been commonly used in other genera. Different systems of setal nomenclature are used in ant taxonomy. The nomenclature applies only to the head, mesosoma, and legs of closely related species or species groups. Consequently, the nomenclature is typically very limited and not generally applicable on a wide scale. This study did not aim to develop a generally applicable chaetotaxy system for ants; rather, we present a system covering only the Asian Orthocrema fauna.

In his review of Asian Crematogaster ants, Menozzi (1935) also introduced a chaetotaxy system for the dorsal mesosomal surface among members of the subgenus Orthocrema. Our collections suggest that workers of Asian Orthocrema species generally possess a pattern of rows of long erect setae on the body segments (head, mesosoma, petiole, postpetiole and fourth abdominal tergite), and that chaetotaxy in Asian Orthocrema species is informative for both species-level identification and phylogenetic interpretation. We generally follow Menozzi (1935) and redefine each seta on the mesosomal surface. The chaetotaxy system of Asian Orthocrema species proposed in the present study is summarized in Figure 7 (Menozzi, 1935: fig. 1) and the nomenclature is given in Table 1.

As suggested by Sorger & Zettel (2009), although chaetotaxy is important for species identification, counting setae is often difficult in old or damaged specimens. We therefore did not rely on only the number of setae to distinguish between species; careful examination of the specimens in our collection suggests that variations in the relative abundance, length and shape of the setae can be useful additional characters for phylogenetic analysis.

Table 2. The subgenus Orthocrema in Asia: dataset for cladistic analysis. The first taxon is an outgroup. '?' signifies unknown or inapplicable.

| Terminal taxa          | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 |
|------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Crematogaster paradoxa | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. baduvi              | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| C. bandarensis         | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| C. binghamii           | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| C. biroi               | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| C. brevispina          | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| C. brunensis           | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| C. celebensis          | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| C. fritzi              | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| C. longipilosa         | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| C. luzonensis          | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| C. macracantha         | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| C. masukoi             | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| C. moatensis           | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| C. myops               | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| C. ocelata             | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| C. osakensis           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. philippinensis      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| C. quadriruga          | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| C. reticulata          | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| C. schimmeri           | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| C. storki              | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. suehiro             | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| C. sundalandensis      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| C. vieti               | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |

CHARACTER LIST

1. Anterior clypeal margin (0) convex in median portion (Fig. 8); (1) almost straight or weakly concave in median portion (Fig. 9).
2. Clypeus striated with longitudinal rugulae; rugulae (0) not extending to posterior clypeal margin; (1) extending to posterior clypeal margin.
3. Clypeus with erect setae; (0) setae not stout and tapering distally; (1) setae stout and not tapering distally.
4. Scape length in relation to head width (0) longer, SI usually > 100; (1) shorter, SI < 100.
5. Basal flagellar segment (antennal segment III) (0) longer than broad, 1.5 or more × as long as broad (Fig. 10); (1) as long as broad or broader than long (Fig. 11).
6. Apical two flagellar segments (0) not differentiated from other flagellar segments in coloration (Fig. 12); (1) differentiated from other flagellar segments in coloration (Fig. 13).
7. Dorsal surface of head essentially (0) smooth; (1) sculptured.
8. Gena and surrounding region of antennal sockets (0) smooth; (1) striated with rugulae.
9. Head shape in full-face view, (0) rounded (Fig. 14); (1) subquadratic (Fig. 15).
10. Anterior margin of pronotal collar (0) concave in dorsal view (Fig. 16); (1) almost straight in dorsal view (Fig. 17).
11. Pronotum (0) slightly higher than pronotal collar in lateral view (Fig. 18); (1) distinctly higher than pronotal collar in lateral view (Fig. 19).
12. Pronotal shoulders (0) with ridge or rugulae laterally (Fig. 20); (1) without ridge or rugulae laterally (Fig. 21).
13. Posterior portions of mesonotal dorsum (0) not forming short triangular process (Fig. 22); (1) forming short triangular process (Fig. 23).
14. Mesonotal ridges (0) not extending posteriorly to propodeal spines (Fig. 24); (1) extending posteriorly to propodeal spines (Fig. 25).
15. Mesonotal ridges (0) developed (Fig. 26); (1) not developed (Fig. 27).
16. Metepreon (0) sculptured; (1) smooth and shining.
17. Metanotum laterally (0) not margined by lamellate ridges (Fig. 28); (1) margined by lamellate ridges (Fig. 29).
18. Dorsal surface of propodeum (0) generally smooth and shining; (1) mat.
19. Propodeal spines (0) usually developed, longer than diameter of propodeal spiracles; (1) undeveloped (PSL 0) or weakly developed, shorter than diameter of propodeal spiracles.
20. Propodeal spines (0) directed posteriorly (Fig. 30); (1) divergent (Fig. 31).
21. Propodeal spiracles (0) oval, relatively small, as large as or slightly larger than mesothoracic spiracles in diameter (Fig. 32); (1) elliptical, relatively...

Figures 8–15. Characters of head. 8, C. baduvi; arrow indicates convex anterior clypeal margin. 9, C. osakensis; arrow indicates weakly concave anterior clypeal margin. 10, C. brunensis; arrow indicates longer antennal segment III. 11, C. osakensis; arrow indicates broad antennal segment III. 12, C. brevispina. 13, C. baduvi. 14, C. baduvi. 15, C. longippilosa.

Figures 24–31. Characters of mesosoma. 24, C. reticulata; arrow indicates mesonotal ridge. 25, C. baduvi; arrow indicates extending mesonotal ridge. 26, C. brunensis. 27, C. masukoi. 28, C. baduvi. 29, C. fritzi. 30, C. longipilosa; arrow indicates propodeal spine directed posteriorly. 31, C. brunensis; arrow indicates propodeal spines divergent.

large, more than 2 × as large as mesothoracic spiracles in diameter (Fig. 33).
22. Erect setae on mesosoma; (0) tapering distally; (1) stout, not tapering distally.
23. Petiole with (0) anterolateral corners round (Fig. 34); (1) anterolateral corners angulate (Fig. 35).
24. Subpetiolar process (0) undeveloped (Fig. 36); (1) developed, distinctly produced downward (Fig. 37).
25. Petiole (0) relatively long and slender (PtWI usually < 80); (1) relatively short and broad (PtWI usually > 80).
26. Posterior portion of petiole (0) posteriorly raised to form small node (Fig. 38); (1) completely flat (Fig. 39).
27. Posterior portion of petiole (0) with short process; short process higher than posterior end (Fig. 40); (1) without distinct short process; highest at posterior end (Fig. 41). The short process is widely found in Asian Orthocrema species, but the development is variable in some species.
28. Postpetiole (0) not bilobed posteriorly (Fig. 42); (1) weakly bilobed posteriorly, but without longitudinal median sulcus (Fig. 43).
29. Postpetiole in lateral view (0) dorsally not strongly convex, only as high as petiole (Fig. 36); (1) strongly convex, distinctly higher than petiole (Fig. 37).
30. Subpostpetiolar process (0) not developed or venter convex (Fig. 36); (1) developed as process (Fig. 37).

Figures 32–39. Characters of mesosoma, petiole, and postpetiole. 32, *C. storki*; arrow indicates oval and small propodeal spiracle. 33, *C. osakensis*; arrow indicates elliptical and large propodeal spiracle. 34, *C. longipilosa*; arrow indicates petiole with anterolateral corner round. 35, *C. biroi*; arrow indicates petiole with anterolateral corner angulate. 36, *C. brunensis*; arrow indicates undeveloped subpetiolar process (24:0), and undeveloped subpostpetiolar process (30:0). 37, *C. luzonensis*; arrow indicates developed subpetiolar process (24:1), and developed subpostpetiolar process (30:1). 38, *C. paradoxa*; arrow indicates posterior portion of petiole posterior raised to form small node. 39, *C. osakensis*; arrow indicates flat posterior portion of petiole.
31. Subpostpetiolar portion; (0) venter flat in lateral view (Fig. 44); (1) venter convex or developed as process in lateral view (Fig. 45).
32. Fourth abdominal tergite with (0) erect or suberect setae only; (1) erect or suberect setae mixed with decumbent or appressed setae.
33. Standing pilosity on body surface (0) sparse; (1) abundant.

RESULTS

The equal-weighting analysis recovered four equally parsimonious cladograms and the strict consensus cladogram collapsed seven nodes (Fig. 46) with a total number of 55 steps, a consistency index of 60 and a retention index of 85. The inferred species groups consisted of the same species in all trees.

The implied-weighting cladograms with values of \( k = 10 \) produced similar topologies (Fig. 47), with a total number of 53 steps, a consistency index of 62 and a retention index of 87. Although the general topology was consistent among all of the resulting trees, the cladistic relationships varied within the species groups.

Although polytomy was obtained in the strict consensus tree (Fig. 46), this tree did not differ from the equal-weighting tree in terms of the relationships between the species groups.

The three species groups defined here, i.e., \( C. \) baduvi group; \( C. \) binghamii group; and \( C. \) biroi group, were all monophyletic. Although they differed slightly from each other, all of the topologies obtained by implied weighting recovered the \( C. \) quadriruga group as paraphyletic, an unresolved polytomy sister to the \( C. \) biroi group.

In the equal- and implied-weighting parsimony analyses, the clade for the \( C. \) baduvi group was characterized by the following character states: mesopleuron sculptured (character 16: 0), propodeal spines directed laterally (character 20: 1); postpetiolar dorsum highly convex (character 29: 1); the clade for the \( C. \) binghamii group by the following character states: posterior portion of mesonotal dorsum forming a short triangle-shaped process (character 13: 1); standing pilosity long and abundant (character 33: 1); and the clade for the \( C. \) biroi group by the following character states: anterior margin of pronotal collar almost straight (character 10: 1), mesopleuron sculptured (character 16: 0), dorsal surface of propodeum striated with rugulae (character 18: 1), subpostpetiolar process developed as process (character 30: 1). The clade composed of the \( C. \) quadriruga group and \( C. \) biroi group was supported by the following set of synapomorphies: basal flagellar segment (antennal segment III) broader or as long as broad (character 5: 1), weakly bilobed postpetiole (character 28: 1), erect setae mixed with appressed setae on fourth abdominal tergite (character 32: 1).

The \( C. \) baduvi group was consistently placed at a basal position to the rest of the taxa. All analyses recovered \( Crematogaster moatensis \) as the sister taxon to the clade composed of \( [C. \) binghamii group + \( C. \) quadriruga group + \( C. \) biroi group].
DISCUSSION

PHYLOGENETIC RELATIONSHIPS WITHIN THE
ASIAN Orthocrema

In this study, the strict consensus tree obtained by the equal-weighting analysis was used to infer the phylogenetic relationships among the Asian Orthocrema species as the topology of the consensus tree did not differ significantly from the implied-weighting trees. As our primary goal was to clarify the monophyly of the species groups defined, slight variations in tree topology were not considered important.

Blaimer (2012d) used five nuclear genes (3384 bp) to estimate the molecular phylogeny of 124 Crematogaster taxa from around the world. Taxa were selected to cover a broad geographic range in order to clarify the
phylogenetic relationship among species as accurately as possible; her analysis included eight Asian Orthocrema taxa. Although the cladistic analysis presented here based on worker morphology is limited to Asian fauna, it corresponds with her phylogenetic analysis to some extent (Blaimer, 2012d, Fig. 2). Crematogaster reticulata and C. osakensis were placed within the same clade and C. binghamii was a sister to C. longipilosa. However, C. fritzi did not form a clade with C. baduvi in our cladistic analysis. These findings implied that minor

**Figure 47.** Strict consensus tree of $k = 10$ obtained by implied-weighting analysis (length: 53 steps; consistency index 62; retention index: 87). Closed circles represent unique apomorphies and open circles homoplasies. Character numbers are given above each circle.
topological differences might arise between morphological and molecular analyses at higher taxonomic levels. Such topological differences might be due to relatively fewer characters based on worker caste only, and it is also needed to examine queens and males. Whereas Ward (2007) suggests that it is challenging to infer phylogenetic relationships from morphological characters alone due to convergence. Rather, molecular analysis using multiple nuclear genes resolve the differences more clearly (Blaimer, 2012d), but it is beyond the scope of this study to use molecular data due to a lack of fresh material. However this study will facilitate future studies in Asian Orthocrema species, and will provide a starting point for molecular studies to test the monophyly of the species groups defined here and the phylogenetic relationships.

The species groups were defined based on putative apomorphies and discrete morphological boundaries. We defined the species groups by distinct character states even if cladistic analyses did not find any synapomorphic characters. We established the C. quadriruga group as having the following character states: long scape (SI 81–100); basal flagellar segment (antennal segment III) broader than long; subpetiolar process developed; subpostpetiolar portion convex in lateral view. Although these character states can be used to separate the species group from other Asian Orthocrema species, our cladistic analysis did not identify any autapomorphies in the C. quadriruga group.

Despite a lack of synapomorphy, we treat the C. quadriruga group as a distinct species group, although the results were based entirely on morphological analysis inferred by relatively few data. Future studies employing more comprehensive morphological or molecular data therefore need to be undertaken in order to reconstruct the phylogenetic relationships between the members of the C. quadriruga group and other species groups. In addition, such groupings are taxonomically convenient for practical use.

Our cladistic analysis indicated that C. moatensis did not form a monophyletic clade with any other species. The difficulty associated with establishing an accurate position for C. moatensis was due to the character states observed in this species. The clade composed of C. moatensis and the C. binghamii, C. quadriruga and C. biroi groups was supported by the following synapomorphies: relatively short scape length; two apical flagellar segments non-differentiated in coloration; square head shape; pronotum distinctly higher than pronotal collar. Whereas C. moatensis could be separated from the clade for the C. binghamii, C. quadriruga and C. biroi groups by the following character states (non-apomorphies): metanotal groove not covered by lamellate ridges; oval propodeal spiracles; long and slender petiole, therefore C. moatensis was sister to the three species groups. Since C. moatensis did not share any apomorphies with the other species but its position was consistent, we place C. moatensis in the C. moatensis group, which is represented by a single species. Further studies on closely related taxa would clarify the systematic position of the C. moatensis group.

Although we do not estimate the relative divergence time by using morphological differences, their restricted distribution ranges of C. baiduvi group (Sundaic region) and C. moatensis group (Sulawesi) and a few derived character states imply that the two species groups are older taxa than the other three species groups (C. binghamii, C. biroi and C. quadriruga groups).

**Biogeography and Natural History**

The distributions of individual species of Asian Orthocrema species imply several different biogeographic patterns (Figs 49–52). Closely related species appear to be allopatric; in implied-weighted trees (Fig. 47), there are four pairs of sister species, and three of them clearly exhibit allopatric ranges: C. binghamii (Indochina) and C. brevispina (Philippines); C. suehiro (Japan) and C. sundalandensis (Borneo, Sumatra); C. reticulata (W. Malaysia, Borneo, Sumatra) and C. schimmeri (Taiwan). Ward (2001) suggested that the Tetraponera species of Indo-Australian region are relatively old taxa based on sympatric distributions of closely related taxa. However, in contrast with Tetraponera, our observations suggest that the Asian Orthocrema contains relatively young taxa. Recent molecular analyses inferred the divergence time of various ant taxa to be as follows: Crematogaster: 34.7 Mya, with 95% highest posterior density of 28.1–42.4 Mya (Ward et al., 2015); Orthocrema clade: 22.3 to 30.2 Mya (Blaimer, 2012d); Pseudomyrmecinae: 50.5 to 59.2 Mya (Moreau et al., 2006); Tetraponera node: 54 Mya (Ward & Brady, 2003). These estimates support the hypothesis that the Asian Orthocrema fauna appeared relatively recently.

As in the studies on Tetraponera by Ward (2001), the species richness of Asian Orthocrema is highest in Borneo (10 spp.), followed by Sumatra (7 spp.) and Peninsular Malaysia (6 spp.); indeed, it appears that the Sundaic region is the center of diversity for Asian Orthocrema species (Table 3).

The material examined in this study was mainly composed of species from the Oriental biogeographic region, and relatively few species from the Australian biogeographic region were considered. Estimates of phylogenetic relationships imply that the distributions of C. storki, C. celebensis and C. fritzi traverse across Wallace’s line, implying that there have been at least three dispersal events to the Australian region by the C. baiduvi, C. quadriruga and C. biroi groups.
Table 3. Distribution of Orthocrema species in the Asian region

<table>
<thead>
<tr>
<th>Species group</th>
<th>Species</th>
<th>Indian subcontinent</th>
<th>Japan, Taiwan</th>
<th>Indochina, excluding Peninsular Malaysia</th>
<th>Peninsular Malaysia</th>
<th>Sumatra</th>
<th>Java, Bali</th>
<th>Borneo</th>
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Total number of species | 2 | 3 | 4 | 6 | 7 | 5 | 10 | 3 | 4 |
As Briggs (1987) suggested, it seems that the west-to-east dispersal across Wallace’s line is relatively widespread in Asian *Orthocrema* species. The subgenus *Orthocrema* is generally considered to contain ground dwellers that nest in soil, but some species are arboreal and nest in dead twigs on trees (Blaimer, 2012b). Although information on nesting biology of Asian *Orthocrema* species is limited, our collections show that a variety of nesting sites is used. *Crematogaster baduvi* and *C. storki* were collected by using fogging machine, and one nest of *C. baduvi* was found in decayed wood (Yamane, 2013); these species are considered to nest in dead twigs or in leaf litter mats on trees. Conversely, *C. longipilosa*, *C. bandarensis*, *C. biori* and *C. osakensis* are all typical ground dwellers that nest in soil on the ground or in leaf litter. *Crematogaster quadriruga*, *C. suehiro*, *C. fritzi*, *C. reticulata* all nest in dead twigs or in dead leaves on trees. Cladistic analysis also showed that nest site selection is not fixed in each species group, and that variations occur within species groups (Fig. 48).

Hosoishi et al. (2010) revised the subterranean species from the Asian *Orthocrema* fauna. *Crematogaster masukoi* and *C. myops* have reduced compound eyes (approximately 6–10 ommatidia) and depigmented yellowish bodies. The two species are similar in that they have reduced eyes, but they are quite different from each other in other morphological aspects (Hosoishi et al., 2010). Our cladistic analysis showed that *C. masukoi* belongs to the *C. biori* group, whereas *C. myops* belongs to the *C. quadriruga* group, suggesting that their subterranean mode of life evolved independently and is an example of convergence (Fig. 48).

Most *Orthocrema* species are supposed to be general predators. Interestingly, in the subterranean species (*C. masukoi* and *C. myops*), their mandibles show different character states from other species. The basal tooth of the mandibles is arranged away from the third
apical one in those species, although their teeth on masticatory margin are arranged at an equal distance in most species. Little information is known about the biology of those species, but the unique arrangement of the mandibles may be related to their predatory behaviours (Bolton, 1988).

Workers in the subgenus Orthocrema are generally monomorphic in size, but intermediate workers have been found in some species in North America (Heinze et al., 1999), Madagascar (Blaimer, 2012b), Brazil (Longino, 2003; Quinet et al., 2009) and Taiwan (Peeters et al., 2013). These workers are intermediate in size between workers and queens. It is reported that the intermediate workers laid unfertilized trophic eggs for larvae (Heinze et al., 1999; Peeters et al., 2013). Histological studies reveal that the intermediate workers have developed ovaries but lack a spermatheca, it is suggesting that they are a soldier caste with a specialized trophic function (Peeters et al., 2013). In the Neotropical species, *C. smithi*, many of the unfertilized eggs are eaten by the queen and larvae, but some eggs can develop into males (Heinze et al., 2000; Oettler, Dijkstra & Heinze, 2013). In this revision of the Asian taxa, we found intermediate workers in five species, *C. biroi*, *C. reticulata*, *C. schimmeri* (See Peeters et al., 2013), *C. vieti* and *C. quadriruga*. The intermediate workers are clearly separated from ordinary workers by the following features: larger body size, developed ocelli (sometimes vestigial), highly convex mesonotum. The former four belong to the *C. biroi* group, while the last belongs to the *C. quadriruga* group, suggesting that intermediate workers are widely scattered across Asian Orthocrema species (Fig. 48).

The subgenus Orthocrema is abundant among Asian ground ant fauna in the temperate to tropical regions. *Crematogaster osakensis* was one of the most...
abundant species collected by using Winkler extractions in grasslands of temperate regions, Japan (Hosoishi et al., 2015). Several colonies of *C. vieti* and *C. bandarensis* were frequently collected as nest series in northern Vietnam (Eguchi et al., 2005) and Bogor, Indonesia (Ito et al., 2001), respectively.

**SYSTEMATICS**

**SYNOPSIS OF ASIAN SPECIES OF THE SUBGENUS Orthocrema**

The worker caste of the subgenus *Orthocrema* was diagnosed by Blaimer (2012c) on a global scale. For the purpose of taxonomic convenience, we present the following characteristics for Asian fauna:

1. Mandibles with four teeth on the masticatory margin; the teeth located at equal distance each other in most species, but basal tooth located apart from other teeth in subterranean species (Hosoishi et al., 2010).
2. Palp formula 5, 3 (Bolton, 2003).
3. Anterolateral margins of clypeus not protruded anteriorly (Hosoishi & Ogata, 2012).
4. Clypeus usually striated with longitudinal rugulae; the length of rugulae variable in different species.
5. Antenna 11-segmented.

6. Antennal club 2-segmented. Apical two flagellar segments clearly distinguished in coloration from other flagellar segments especially in the *C. baduvi* group.

7. Sensilla basiconica and sensilla trichodea curvata distributed in the apical two flagellar segments (Hosoishi & Ogata, 2009c).

8. Compound eye generally distinct and large, but strongly reduced in subterranean species (Hosoishi et al., 2010).


10. Occipital carina distinct.

11. Mesonotal ridges developed dorsolaterally, but weakly developed in *C. masukoi* and *C. moatensis*.


13. Propodeal spines usually developed, but undeveloped or small tubercles in *C. binghamii*.

14. Petiole usually with subparallel sides.

15. Petiole usually with short process posteriorly.

16. Postpetiole not bilobed. If weakly bilobed, usually without distinct longitudinal median sulcus.

17. Fourth abdominal tergite with erect to suberect setae.

18. Body principally yellow, but sometimes partly brown to black in *C. binghamii* group, *C. biroi* group, *C. moatensis* group and *C. quadriruga* group, but brown in *C. baduvi* group.

Figure 51. Geographical distribution of the species of the *C. biroi* group.
19. Monomorphic in size; intermediate workers occasionally present.
20. Nesting in soil; some species nesting in dead twigs on lower vegetation.

SYNONYMIC LIST OF ASIAN Orthocrema SPECIES

In this study, five species groups are established within the Asian Orthocrema. The species groups were defined based on putative apomorphies and discrete morphological boundaries. The species groups recognized here will provide a possible basis for new monophyletic taxa. The C. baduvi, C. binghamii and C. biroi groups are relatively easily defined, but the C. quadriruga group is probably not monophyletic as currently defined. The C. moatensis group was represented by a single species since the position of C. moatensis in cladograms was always consistent. The taxa should ideally be monophyletic, but also considered as useful units for taxonomic purposes in the case of hyperdiverse genera.

Crematogaster baduvi group
C. baduvi Forel, 1912b.
C. brunensis sp. nov.
C. macracantha Creighton, 1945.
C. storki sp. nov.

Crematogaster binghamii group
C. binghamii Forel, 1904.
C. brevispina sp. nov.
C. longipilosa Forel, 1907.

Crematogaster biroi group
C. biroi Mayr, 1897.
= C. aitkenii Forel, 1902a. syn. nov.
= C. biroi smythiesii Forel, 1902a. syn. nov.

Figure 52. Geographical distribution of the species of the C. quadriruga group.
C. fritzi Emery, 1901.
C. luzonensis sp. nov.
C. ocellata sp. nov.
C. osakensis Forel, 1900.
C. schimmeri Forel, 1912a.
C. udo Forel, 1905.
C. vieti sp. nov.

Crematogaster moatensis group
C. moatensis sp. nov.

Crematogaster quadriruga group
C. bandarensis Forel, 1913. stat. nov.
= C. biroi andelis Santschi, 1928. syn. nov.
C. celebensis sp. nov.
C. gavapiga Menozzi, 1935.
C. myops Forel, 1911a.
C. philippinensis sp. nov.
C. quadriruga Forel, 1911c. stat. nov.
= C. miroku Terayama, 2013. syn. nov.
C. sundalandensis sp. nov.

The species groups of Asian Orthocrema species
Apomorphies of the species groups obtained by cladistic analysis are given in italics.

Crematogaster baduvi group
Relatively long scape (SI 98–118). Basal flagellar segment (antennal segment III) longer than broad. Propodeal spines long and directed laterally. Postpetiolar dorsum highly convex in lateral view; postpetiole distinctly higher than petiole in lateral view.

This species group is easily distinguished by the propodeal spines directed laterally and highly convex postpetiolar dorsum from other Asian Orthocrema species.

Crematogaster binghamii group
Basal flagellar segment (antennal segment III) longer than broad. Posterior margins of mesonotum forming short triangle-shaped process in lateral view. Propodeal spines undeveloped, or developed and directed posteriorly. Standing pilosity abundant on body surface.

This species group is easily distinguished by the short triangle-shaped process on posterior margins of mesonotum and long and abundant standing pilosity from other Asian Orthocrema species.

Crematogaster biroi group
Relatively short scape (SI 70–89). Basal flagellar segment (antennal segment III) broader than long.


This species group is easily distinguished by the subpostpetiolar process developed acutely and sculptured surface of mesosoma from other Asian Orthocrema species.

Crematogaster moatensis group
Two apical flagellar segments not differentiated in coloration. Pronotum distinctly higher than pronotal collar. Metanotal groove not covered by lamellate ridges. Propodeal spiracles oval. Petiole long and slender.

This species group is unique in having the metanotal groove not covered by lamellate ridges, oval-shaped propodeal spiracles and long and slender petiole from other Asian Orthocrema fauna.

Crematogaster quadriruga group

This species group is distinguished by the subpostpetiolar portion wholly convex and smooth and shining surface of mesosoma from other Asian Orthocrema species.

Species accounts

Crematogaster baduvi Forel, 1912b
(Fig. 96)
Crematogaster baduvi Forel, 1912b: 106; one syntype worker, Nusa Kambangan, Java, Indonesia (MHNG, examined).

Crematogaster baduvi; Forel, 1913: 77 [Description of queen].
Crematogaster baduvi; Menozzi, 1935: 104 [Description of male].

Crematogaster baduvi; Blaimer, 2012c: 55 [Combination in C. (Orthocrema)].

Worker measurements (n = 17): HW 0.47–0.57; HL 0.48–0.59; CI 92–100; SL 0.47–0.58; SI 98–108; EL 0.11–0.14; PW 0.26–0.35; WL 0.60–0.72; PSL 0.15–0.21; PtL 0.23–0.28; PtW 0.15–0.20; PtH 0.13–0.16; PpL 0.13–0.16; PpW 0.16–0.20; PtHI 54–67; PtWI 65–83; PpWI 113–146; WI 90–107.

**KEY TO SPECIES BASED ON THE WORKER CASTE (EXCEPT FOR C. GAVAPIGA MENOZZI, C. JAVANICA MENOZZI, AND C. UDO FOREL THAT WERE NOT EXAMINED)**

1. Propodeal spines directed laterally (Fig. 31). Postpetiolar dorsum highly convex in lateral view; postpetiole distinctly higher than petiole in lateral view (Fig. 36) (C. baduvi group) ........................................ 2
   - Propodeal spines directed posteriorly (Fig. 30). Postpetiolar dorsum not highly convex in lateral view; postpetiole as high as petiole in lateral view (Fig. 37) ........................................... 5
2. Transverse distance between tips of propodeal spines distinctly longer than head width in dorsal view (Fig. 53). Mesosoma densely sculptured (Borneo) .................................................. C. macracantha Creighton
   - Transverse distance between tips of propodeal spines shorter than head width in dorsal view (Fig. 54). Mesosoma generally smooth and shining .......................................................... 3
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General description of worker: Workers monomorphic.

Head round in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes exceeding posterolateral corners of head.

Pronotal collar with concave anterior margin in dorsal view, slightly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges laterally. Mesonotal dorsum with lateral ridges that extend posteriorly to tips of propodeal spines; anterior ridges usually as high as posterior ridges. Pronotum and mesonotum in lateral view forming evenly arched, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming shallow concavity that is laterally marginated by ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view strongly divergent.

Petiole in dorsal view with subparallel sides and narrow short peduncle anteriorly, distinctly longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process weakly developed as angulate tubercle. Postpetiolar in lateral view with strongly convex dorsum, distinctly higher than petiole, in dorsal view as wide as petiole, globular, not bilobed. Venter of postpetiolar convex but without distinct process.


Standing pilosity sparse. Dorsal face of head with long erect and short appressed setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pairs of short setae laterally. Scapes with
appressed setae. Mesosoma with two pairs of long erect and stout setae (ps1PN and psaMN) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with one pair of long setae. Postpetiole with one pair of long setae on disc posteriorly. Fourth abdominal tergite with erect setae sparsely, but no decumbent to appressed setae.

Body red-brown. Apical two flagellar segments yellow, contracting with other flagellar segments that are blackish.
Figures 62–70. Key to Orthocrema species in Asia. 62–63, mesosoma sculpture: 62, *C. reticulata*; 63, *C. quadriruga*. 64–65, subpetiolar and subpostpetiolar process: 64, *C. vieti*; left arrow indicates acutely developed subpetiolar process, and right arrow acutely developed subpostpetiolar process. 65, *C. quadriruga*; left arrow indicates developed subpetiolar process, and right arrow undeveloped subpostpetiolar process. 66–68, compound eyes: 66, *C. masukoi*; arrow indicates distinctly reduced compound eye. 67, *C. ocellata*; arrow indicates reduced compound eye. 68, *C. biroi*; arrow indicates developed compound eye. 69–70, dorsal surface of head: 69, *C. reticulata*; 70, *C. osakensis*.
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Comments: In the worker this species can be distinguished from all other members of the *C. baduvi* group by the smooth and shining surfaces of mesosoma, propodeal dorsum (with rugulae), and the very long propodeal spines that are divergent and straight toward tip. This species is similar to *C. brunensis*, but can be distinguished from it by the larger head (HW 0.47–0.57, HL 0.48–0.59 vs. 0.43–0.47 and 0.46–0.49 in the latter), shorter scape (SI 98–108 vs. 113–118) and shorter propodeal spines (PSL 0.15–0.21 vs. 0.20–0.22).

Specimens from Brunei have the anterior mesonotal ridges higher than posterior mesonotal ridges in lateral view.

**Distribution and biology:** This species is known from Malaysia (Peninsula), Brunei and Indonesia (Krakatau, Sumatra, Java) (Fig. 49). Specimens from Endau Rompin National Park, W. Malaysia and Brunei were collected by fogging method.


Specimens from Endau Rompin National Park, W. Malaysia (Peninsula), Brunei and Indonesia (Krakatau, Sumatra, Java) (Fig. 49). Specimens from Endau Rompin National Park, W. Malaysia and Brunei were collected by fogging method.

**CREMATOGASTER BANDARENSIS** Forel, 1913

*Stat. nov.*

(Fig. 97)

*Crematogaster biroi* var. *bandarensis* Forel, 1913: 76; syntype workers, Bandar Baroe, Sumatra, Indonesia (v. Buttel-Reepen) (MHNG, examined). One syntype worker (middle specimen of three on one pin) in MHNG here designated Lectotype.

*Crematogaster biroi* var. *andelis* Santschi 1928: 129. One syntype worker, Ile Varela, Pulu Berhala, Sumatra, Indonesia, 2.i.1919 (Corporaal) (NHMB, examined).

Syn. nov.

*Crematogaster biroi* var. *bandarensis*; Emery, 1922: 132 [Combination in *C. Orthocrema*].

*Crematogaster biroi* var. *andelis*; Stärcke, 1930: 373 [Description of male].

**Worker measurements** (n = 10): HW 0.40–0.47; HL 0.42–0.50; CI 92–98; SL 0.34–0.39; SI 81–86; EL 0.09–0.11; PW 0.26–0.29; WL 0.48–0.54; PSL 0.05–0.08; PtL 0.14–0.17; PtW 0.12–0.15; PtH 0.10–0.12; PpL 0.09–0.11; PPW 0.13–0.16; PtHI 67–82; PtWI 80–88; PpWI 127–150; WI 100–117.

**General description of worker:** Workers monomorphic.

Head subquadricort in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes slightly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Prontal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Prontal dorsum without distinct ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posterior to tips of propodeal spines. Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline; mesonotal dorsum flat. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles elliptical, situated at posterolateral corners of propodeum, touching to metapleural gland bullae. Propodeal spines developed, as long as diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process weakly developed as angulate tubercle. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process undeveloped, but venter of postpetiolar convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth and shining, but with one pair of longitudinal rugulae; rugulae not extending to posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum with rugulae. Mesopleura smooth and shining. Dorsal surface of propodeum smooth and shining, but one pair of rugulae running from metanotal groove to tips of propodeal spines. Dorsal surface of petiole smooth. Lateral surface of petiole generally smooth, but with one longitudinal rugula. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with suberect setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with suberect setae. Mesosoma with five pairs of long erect and stout setae (ps1PN, ps2PN, psaMN, pspMN,
and ps1PS) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with two pairs of long setae. Postpetiole with three pairs of long setae on disc anteriorly, posteriorly and laterally. Fourth abdominal tergite with erect to suberect setae abundantly, and short decumbent setae sparsely.

Body yellow. All flagellar segments yellow.

Comments: In the worker this species can be distinguished from all other members of the C. quadriruga group by the distinct compound eyes, V-shaped metanotal groove in lateral view, large propodeal spira-
cles touching metapleural gland bulla, and short propodeal spines. This species is similar to C. philippinensis and C. sundalandensis, but can be dis-
stinguished from them by the short and stout propodeal spines (PSL 0.05–0.08 vs. 0.08–0.11 and 0.08–0.11 in the latters). This species corresponds to sp. 52 of SKY (Ito et al., 2001; Eguchi & Yamane, 2003).

Distribution and biology: This species is known from S. Thailand, Malaysia (Peninsula and Borneo), Brunei, Indonesia (Bali, Sumatra, Krakatau) (Fig. 52). It in-
habits developed forests, and nests in soil or in leaf litter.


CREMATOGASTER BINGHAMII FOREL, 1904

Worker measurements (n = 10): HW 0.52–0.57; HL 0.52–
0.59; CI 89–100; SL 0.46–0.50; SI 84–92; EL 0.13–
0.16; PW 0.30–0.34; WL 0.64–0.69; PSL 0.0–0.03; PtL 0.18–0.21; PtW 0.16–0.18; PtH 0.12–0.16; PpL 0.13–
0.16; PpW 0.15–0.19; PtH 0.67–0.84; PtWI 0.80–0.94; PpWI 100–138; WI 93–118.

General description of worker: Workers monomorphic.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Ante-
rior clypeal margin convex in medial portion. Com-
pond eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges later-
ally. Mesonotal dorsum with lateral ridges that extend posterioral to anterodorsal corners of propodeal dorsum; the ridges forming pair of small triangular processes (angles) between dorsal and declivity faces of mesonotum (this condition is more easily seen with mesosoma in lateral view). Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline. Metanotal
groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal...
spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines undeveloped.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole without distinct process in lateral view. Subpetiolar process weakly developed as blunt process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpetiolar process undeveloped, but venter of postpetiole convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth and shining, but with one to two distinct pairs of longitudinal rugulae; rugulae not extending to posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum with rugulae. Mesopleura generally smooth and shining. Rugula on higher portion of mesopleura extending to small pit of mesothoracic spiracles. Dorsal surface of propodeum smooth and shining. Lateral surface of propodeum generally smooth, but with one longitudinal rugula. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity abundant. Dorsal face of head with erect to suberect setae abundantly. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with suberect setae. Mesosoma with seven pairs of long erect and stout setae (ps1PN, ps2PN, psaMN, psMN, psPR, ps1PS, and ps2PS) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with three pairs of long setae. Postpetiole with three pairs of long setae on disc anteriorly, posteriorly and laterally. Fourth abdominal tergite with erect to suberect setae abundantly, but no decumbent to appressed setae.

Body yellow. All flagellar segments yellow.

Comments: In the worker this species can be distinguished from all other members of the C. binghamii group by the undeveloped or weakly developed propodeal spines. This species is similar to C. brevispinosa, but can be distinguished from it by the weakly developed propodeal spines (PSL 0–0.03 vs. 0.04–0.07 in the latter); the length smaller than the diameter of propodeal spiracles.

Distribution: This species is known from Nepal, India, Bangladesh, Thailand and Vietnam (Fig. 50).


Crematogaster biroi Mayr, 1897
(Figs 99, 100)

Crematogaster biroi Mayr, 1897: 428; syntype workers, Columbo, Sri Lanka (Biro) (HNHM, examined). One syntype worker (with label of 160) in HNHM from Columbo here designated Lectotype.

Crematogaster biroi var. aitkenii Forel, 1902a: 203; syntype workers, Kanara, India (Aitken) (MHNG, examined). Syn. nov. One syntype worker (top specimen of three on one pin) in MHNG here designated Lectotype.

Crematogaster biroi var. smythiesii Forel, 1902a: 203; syntype workers, Dehra Dun, India (Smythies) (MHNG, examined). Syn. nov. One syntype worker (top specimen of two on one pin) in MHNG here designated Lectotype.


Crematogaster biroi; Bingham, 1903: 138 [Description of intermediate worker].

Crematogaster biroi; Emery, 1922: 131 [Combination in C. (Orthocrema)].

Crematogaster biroi var. aitkenii; Emery, 1922: 132 [Combination in C. (Orthocrema)].

Crematogaster biroi var. smythiesii; Emery, 1922: 132 [Combination in C. (Orthocrema)].

Crematogaster biroi; Imai et al. 1984: 6 [Karyotype].

Crematogaster aitkenii; Wu & Wang, 1992: 1319 [Raised to species].

Crematogaster biroi; Blaimer, 2012c: 55 [Combination in C. (Orthocrema)].

Crematogaster uvrjiae; Blaimer, 2012c: 55 [Combination in C. (Crematogaster)].

Worker measurements (n = 10): HW 0.44–0.55; HL 0.45–0.52; CI 98–106; SL 0.33–0.39; SI 70–75; EL 0.09–0.13; PW 0.30–0.34; WL 0.49–0.58; PSL 0.09–0.12; PtL 0.16–0.19; PtW 0.13–0.17; PtH 0.12–0.15; PpL 0.10–0.13; PpW 0.14–0.17; PtHI 72–82; PtWI 78–89; PpWI 125–141; WI 100–108.

General description of worker: Workers monomorphic, but intermediate worker as large as queen (details below).

Head subquadric in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum with feeble ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriorly to tips of propodeal spines. Pronotum and mesonotum in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriorly.

Petiole in dorsal view with parallel sides and angulate shoulders anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process strongly developed as acute process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as or slightly wider than petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpetiolar process developed as process.

Integument essentially sculptured. Dorsal surface of head generally smooth on central region, but weakly sculptured reticulately laterally. Occipital region near margin weakly sculptured. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth, but with two distinct pairs of longitudinal rugulae and weakly sculptured interspaces; rugulae not extending to posterior clypeal margin. Anterolateral shoulders of pronotum with rugulae. Pronotum and mesonotum with longitudinal rugulae and sculptured interspaces. Lateral surface of pronotum smooth and shining on central portion, but weakly sculptured on surrounding. Mesopleura weakly sculptured, but relatively smooth in central areas. Rugula on higher portion of mesopleura extending to small pit of mesothoracic spiracles. One pair of rugulae running from metanotal groove to tips of propodeal spines (rugulae on mesonotum extending posteriorly to propodeal spines). Dorsal surface of propodeum weakly sculptured. Dorsal and lateral surfaces of petiole sculptured. Dorsal surface of postpetiole smooth and shining. Lateral surface of postpetiole weakly sculptured.

Standing pilosity sparse. Dorsal face of head with several pairs (six to seven) of erect and stout setae, and short and appressed setae abundantly. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with two pairs of long setae medially and some pairs (three to four) of short setae laterally. Scapes with suberect setae. Mesosoma with four pairs of long erect and stout setae (ps1PN, psaMN, pspMN, and ps1PS) that are much longer than other erect setae. Postero lateral tubercles of petiole posteriorly with one pair of stout setae. Postpetiole with one pair of stout setae on disc posteriorly. Fourth abdominal tergite with three or six pairs of erect and stout setae, and short appressed setae abundantly.

Body yellow. All flagellar segments yellow.

Intermediate worker measurements (n = 1): HW 0.82; HL 0.79; CI 104; SL 0.48; SI 59; EL 0.21; PW 0.58; WL 0.98; PSL 0.18; PtL 0.35; PtW 0.28; PtH 0.25; PPL 0.21; PpW 0.32; PpH 71; PtWI 80; PpWI 152; WI 114.

Description of intermediate worker: With worker character conditions, except as follows.

Head subquadric.

Mesonotum highly convex in lateral view. Mesonotal dorsum without lateral ridges. Pronotum forming same dorsal outline with mesonotum in lateral view, but posterior face forming vertical slope to metanotal groove. Propodeal spiracles elliptical.

Subpetiolar area not observable in the specimen examined.

Clypeus with some longitudinal rugulae: rugulae extending to frontal region between frontal carinae.

Dorsal face of head with erect setae sparsely. Clypeus with one pair of long setae around antennal bases; directed upper. Mesosoma without distinct erect setae. Fourth abdominal tergite with short decumbent to appressed setae sparsely.

Comments: In the worker this species is very distinct among the C. biroi group in having the sculptured surface near occipital carinae of head, the strongly developed subpetiolar process, and acutely developed subpostpetiolar process.

Distribution and biology: This species is known from India and Sri Lanka (Fig. 51). Although this species has been reported from China by Wu & Wang (1995) and Zhou (2001), and from Taiwan by Terayama (2009), we have not been able to examine those specimens. This species nests in soil.

Material examined: INDIA: two workers, Chandigarh, Punjab, 10.viii.1978, (H. Imai et al); ten workers,
General description of worker: Workers monomorphic.

Worker measurements (n = 9): HW 0.51–0.62; HL 0.54–0.65; CI 93–98; SL 0.50–0.55; SI 92–96; EL 0.15–0.17; PW 0.34–0.41; WL 0.61–0.72; PSL 0.04–0.07; PtL 0.13–0.15; PpW 0.17–0.21; PtH 0.13–0.17; PpL 0.13–0.15; PtW 0.17–0.21; PtHI 65–70; PtWI 74–90; PpWI 120–140; WI 95–106.

CremaTogastEr brevispina sp. nov.

(FIG. 101)


Paratypes. Eight workers, same data as holotype (BMNH, CASC, KUEC, MHNG, MPMP, THNHM).

Worker measurements (n = 9): HW 0.51–0.62; HL 0.54–0.65; CI 93–98; SL 0.50–0.55; SI 92–96; EL 0.15–0.17; PW 0.34–0.41; WL 0.61–0.72; PSL 0.04–0.07; PtL 0.19–0.25; PtW 0.17–0.21; PtH 0.13–0.17; PpL 0.13–0.15; PpW 0.17–0.21; PtWI 74–90; PpWI 120–140; WI 95–106.

CremaTogastEr brunensis sp. nov.

(FIG. 102)


Paratypes. Five workers, same data as holotype (CASC, ITBC, KUEC, MHNG, THNHM).
Worker measurements (n = 6): HW 0.43–0.47; HL 0.46–0.49; CI 92–100; SL 0.51–0.53; SI 113–118; EL 0.12–0.13; PW 0.26–0.29; WL 0.60–0.63; PSL 0.20–0.22; PpL 0.23–0.26; PtW 0.14–0.17; PtH 0.14–0.15; PpL 0.12–0.13; PpW 0.15–0.17; PtHI 56–61; PtWI 60–67; PpWI 123–133; WI 100–107.

General description of worker: Workers monomorphic.

Head round in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes exceeding posterolateral corners of head.

Pronotal collar with concave anterior margin in dorsal view, slightly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view forming evenly arched, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming shallow concavity that is laterally margined by ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view strongly divergent.

Petiole in dorsal view with subparallel sides and narrow short peduncle anteriorly, distinctly longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process undeveloped. Postpetiole in lateral view with strongly convex dorsum, distinctly higher than petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpetiolar process undeveloped, but venter of postpetiole convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth and shining, but with one pair of longitudinal rugulae; rugulae not extending to the posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum with feeble rugulae. Mesopleura generally sculptured, but sometimes smooth except for their marginal areas in some specimens. Dorsal surface of propodeum generally smooth and shining, but with rugulae dorsolateral areas. Dorsal surface of petiole smooth and shining. Lateral surface of petiole weakly sculptured. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with long erect (three pairs) and short appressed setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pairs of short setae laterally. Scapes with subect to decumbent setae. Mesosoma with three pairs of long erect and stout setae (ps1PN, psaMN, and pspMN) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with one pair of long setae. Postpetiole with two pairs of long setae on disc anteriorly, posteriorly. Fourth abdominal tergite with erect setae sparsely, but no decumbent to appressed setae.

Body red-brown. Apical two flagellar segments light yellow, contracting with other flagellar segments that are yellow.

Comments: In the worker this species can be distinguished from all other members of the C. baduvi group by the smooth and shining surface of mesosoma, smooth surface of propodeal dorsum, and propodeal spines developed straight at the tip. This species is similar to C. baduvi, but can be distinguished from it by the smaller head (HW 0.43–0.47, HL 0.46–0.49 vs. 0.47–0.57 and 0.48–0.59 in the latter) and longer propodeal spines (PSL 0.20–0.22 vs. 0.15–0.21).

Distribution and biology: This species is known only from the type locality in Brunei (Fig. 49). Type specimens were collected by fogging method.

Etymology: The specific name refers to the country of origin, Brunei.

**CREMATOGASTER CELEBENSIS SP. NOV.**

(Fig. 103)


Paratypes. Three workers, same data as holotype (BMNH, CASC, KUEC).

Worker measurements (n = 5): HW 0.49–0.51; HL 0.51–0.53; CI 94–96; SL 0.39–0.42; SI 80–84; EL 0.10–0.11; PW 0.31–0.33; WL 0.56–0.59; PSL 0.09–0.10; PpL 0.19–0.20; PpW 0.15–0.17; PtH 0.13–0.15; PpL 0.11–0.13; PpW 0.16–0.18; PtHI 68–75; PtWI 79–89; PpWI 133–145; WI 100–107.

General description of worker: Workers monomorphic.

Head subquadrate in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes slightly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.
Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges (U-shaped in lateral view). Propodeal spiracles elliptical, situated at posterolateral corners of propodeum, touching to metapleural gland bullae. Propodeal spines developed, as long as diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process undeveloped. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process undeveloped, but venter of postpetiole convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Clypeus generally smooth and shining, but with one distinct pair of longitudinal rugulae; rugulae not extending to posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum with rugulae. Mesopleura smooth and shining. Dorsal surface of propodeum generally smooth and shining, but one pair of rugulae running from metanotal groove to tips of propodeal spines. Dorsal surface of petiole smooth and shining. Lateral surface of petiole generally smooth, but with one longitudinal rugula. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with suberect setae sparsely. Mandibles with feeble rugulae and smooth interspaces. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with suberect setae. Mesosoma with five pairs of long erect and stout setae (ps1PN, ps2PN, psaMN, pspMN, and ps1PS) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with three pairs of stout setae (one pair of shorter setae laterally). Postpetiole with three pairs of long setae on disc anteriorly, posteriorly and laterally. Fourth abdominal tergite with erect to suberect setae abundantly, and short decumbent setae sparsely.

Body yellow. All flagellar segments yellow.

Comments: In the worker this species can be distinguished from all other members of the *C. quadriruga* group by the distinct compound eyes, U-shaped metanotal groove in lateral view, large propodeal spiracles touching metapleural gland bulla, and longer propodeal spines. This species is similar to *C. banadarensis*, but can be distinguished from it by the deep (or U-shaped) metanotal groove in lateral view and long propodeal spines (PSL 0.09–0.10 vs. 0.05–0.08 in the latter).

Distribution: This species is known from Indonesia (Sulawesi) (Fig. 52).

Etymology: The specific name refers to the former name of Sulawesi, Celebes.


*Crematogaster fritzi* Emery, 1901

(Fig. 104)

*Crematogaster fritzi* Emery, 1901: 576, fig. B; syntype workers, Tomohon, Sulawesi, Indonesia (MCSN, examined). One syntype worker (basal specimen of three of top label of one pin) in MCSN here designated Lectotype.

*Crematogaster sordidula* f. *fritzi*: Forel, 1902b: 410 [Race of *sordidula*].

*Crematogaster fritzi*: Emery, 1912: 668 [Revived status as species].

*Crematogaster fritzi*: Emery, 1922: 132 [Combination in *C. (Orthocrema)*].

*Crematogaster fritzi*: Blaimer, 2012c: 55 [Combination in *C. (Orthocrema)*].

Worker measurements (n = 14): HW 0.40–0.48; HL 0.42–0.49; CI 95–100; SL 0.34–0.40; SI 80–89; EL 0.10–0.13; PW 0.24–0.31; WL 0.45–0.54; PSL 0.07–0.1; PtL 0.15–0.18; PtW 0.13–0.16; PH 0.11–0.13; PpL 0.09–0.12; PpW 0.14–0.17; PtHI 69–76; PtWI 82–94; PpWI 127–167; WI 100–108.

General description of worker: Workers monomorphic.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.
Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum with feeble ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posterior to tips of propodeal spines. Pronotum and mesonotum in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spines, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view, with node-like process in lateral view. Subpetiolar process developed as blunt process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view transverse, almost straight in median portion, diverging to tips of propodeal spines. Dorsal surface of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spines, in dorsal view directed posteriad.


Standing pilosity sparse. Dorsal face of head with three pairs of erect and stout setae, and short and appressed setae abundantly. Clypeus with two pairs of long and stout setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pair of short setae laterally. Scapes with appressed setae. Mesosoma with three pairs of long erect and stout setae (ps1PN, psaMN, and pepMN) that are much longer than other erect setae. Posterior petiolar tubercle of petiole posteriorly with one pair of stout setae. Postpetiole with two pairs of stout setae on disc posteriorly. Fourth abdominal tergite with three to four pairs of erect and stout setae, and short appressed setae abundantly. Body yellow. All flagellar segments yellow.

Comments: In the worker this species can be distinguished from all other members of the *C. biroi* group by the scape with appressed setae, distinct compound eyes, generally smooth dorsal surface of head, and sparse erect and stout setae on body. This species is similar to *C. luzonensis*, but can be distinguished from it by the appressed setae on scape, longer setae on anterior mesonotal ridges, sparse erect setae on fourth abdominal tergite.

Distribution and biology: This species is known from Malaysia (Peninsula), Brunei, Indonesia (Sumatra, Sulawesi) (Fig. 51). This species inhabits developed forests, and nests in dead twigs on trees.


**CREMATOGASTER GAVAPIGA** MENOZZI, 1935

*Crematogaster (Orthocrema) gavapiga* Menozzi, 1935: 109, fig. 5; worker, Tjampea, Java, Indonesia (2389) (probably in IEGG, not seen).

*Crematogaster gavapiga*; Blaimer, 2012c: 55 [Combination in *C. (Orthocrema)*].

Comments: We have not been able to examine the types of *C. gavapiga*. From the original description and key provided by Menozzi (1935), this species is close to *C. bandarensis*. He distinguished *C. gavapiga* from *C. bandarensis* by smooth and shining surface of dorsal mesosoma. However, some specimens in our collections of *C. bandarensis* have smooth and shining surface of dorsal mesosoma, suggesting that the character state seen in *C. gavapiga* is within the infraspecific variation of *C. bandarensis*. Taxonomic relationship with *C. bandarensis* will remain uncertain until type material can be examined.

**CREMATOGASTER JAVANICA** MENOZZI, 1935

*Crematogaster (Orthocrema) javanica* Menozzi, 1935: 108, fig. 4; worker, Tjapers, Java, Indonesia (2365) (probably in IEGG, not seen).
Crematogaster javanica; Hosoishi et al. 2010: 346 [Taxonomic remark].
Crematogaster javanica; Blaime, 2012c: 55 [Combination in C. (Orthocrema)].

Comments: This species may be a close relative of C. myops (Hosoishi et al., 2010).

CREMATOGASTER LONGIPILOSA Forel, 1907

(Fig. 105)

Crematogaster longipilosa Forel, 1907: 24; syntype workers, Kuala Lumpur, Malaysia (Biró) (MHNG, examined). One syntype worker (top specimen of two on one pin) in MHNG here designated Lectotype.

Crematogaster longipilosa; Forel, 1911b: 383 [Descriptions of queen and male].

Crematogaster longipilosa; Viehmeyer, 1916: 124 [Description of queen].

Crematogaster longipilosa; Emery, 1922: 132 [Combination in C. (Orthocrema)].

Crematogaster longipilosa; Blaime, 2012c: 55 [Combination in C. (Orthocrema)].

Worker measurements (n = 10): HW 0.60–0.69; HL 0.63–0.71; CI 95–97; SL 0.52–0.58; SI 84–89; EL 0.15–0.18; PW 0.37–0.40; WL 0.71–0.80; PSL 0.13–0.16; PtL 0.25–0.29; PtW 0.20–0.23; PtH 0.16–0.19; PpL 0.16–0.19; PpW 0.20–0.24; PtHI 62–73; PtWI 79–92; PpWI 111–137; WI 95–105.

General description of worker: Workers monomorphic.

Head subquadric in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching postero-lateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriorly to tips of propodeal spines; the ridges forming pair of small triangular processes (angles) between dorsal and declivity faces of mesonotum (this condition is more easily seen with mesosoma in lateral view). Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at postero-lateral corners of propodeum, apart from (or slightly touching) metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriorly.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole without distinct process in lateral view. Subpetiolar process weakly developed as blunt process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpostpetiolar process undeveloped, but venter of postpetiole weakly convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining, but with rugules on surrounding region of antennal sockets. Mandibles with feeble rugules and smooth interspaces. Clypeus generally smooth and shining, but with one to two distinct pairs of longitudinal rugulae; rugulae not extending to posterior clypeal margin. Costulate rugulae present on malar region. Dorsal and lateral surfaces of pronotum smooth and shining; antero-lateral shoulders of pronotum without rugulae. Mesopleura generally smooth and shining. Rugula on higher portion of mesopleura extending to small pit of mesothoracic spiracles. Dorsal surface of propodeum generally smooth and shining, but few longitudinal rugulae on anterior areas. Dorsal surface of petiole smooth and shining. Lateral surface of petiole generally smooth, but with one longitudinal rugula running from spiracles to posterior margin. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity abundant. Dorsal face of head with erect to suberect setae abundantly. Clypeus with three pairs of long setae on anterior portion, one directed upward, one downward, the other laterally below antennal sockets. Anterior clypeal margin with single long setae medially and one pair of long setae laterally, and short setae laterally. Gena (malar space) with some suberect setae near mandibular insertion. Scapes with suberect to decumbent setae; short setae basally and long setae distally. Mesosoma with seven to eight distinct pairs of long erect and stout setae (ps1PN, ps2PN, psaMN, pspMN, psPR, ps1PS, and one to two ps2PS) that are much longer than other erect setae. Postero-lateral tubercles of petiole posteriorly with three pairs of long setae. Postpetiole with four pairs of long setae on disc antero-dorsally, antero-laterally, posteromedially and posteriorly. Fourth abdominal tergite with erect to suberect setae abundantly, but no decumbent to appressed setae.

Body yellow to brown. All flagellar segments yellow.

Comments: In the worker this species is very distinct among the C. binghamii group in having developed propodeal spines (PSL 0.13–0.16 vs. 0–0.07 in the others).

This species corresponds to C. sp. 51 of SKY (Ito et al., 2001).
Distribution and biology: This species is known from S. Thailand, Malaysia (Peninsula) and Indonesia (Kalimantan, Java, Sumatra) (Fig. 50). This species inhabits disturbed to developed forests, and nests in soil.


**CREMATOGASTER LUZONENSIS** sp. nov.  
(FIG. 106)


Paratypes. One worker, same data as holotype (MPMP); three workers, Luzon, PHILIPPINES, 2.v.1992 (PH81 coconut) (M. J. Way) (CAS, KUEC, MHNG).

Worker measurements (n = 5): HW 0.41–0.46; HL 0.42–0.46; CI 96–100; SL 0.36–0.42; SI 88–95; EL 0.11–0.13; PW 0.26–0.29; WL 0.49–0.55; PSL 0.07–0.1; PL 0.15–0.17; PtW 0.13–0.16; PtH 0.11–0.13; PpL 0.09–0.11; PpW 0.15–0.17; PtHI 71–81; PtWI 87–94; PpWI 145–178; WI 100–114.

General description of worker: Workers monomorphic.

Head subquadrate in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Prontal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Prontal dorsum with feebler ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriorly to tips of propodeal spines. Pronotum and mesonotum in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiolar disc in lateral view. Subpetiolar process developed as blunt process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as or slightly wider than petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process developed bluntly.

Integument essentially sculptured. Dorsal surface of head generally smooth, but with rugulae on surrounding region of antennal sockets. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth, but with one distinct pair of longitudinal rugulae and one pair of feeble rugulae; distinct rugulae extending to posterior clypeal margin. Anterolateral shoulders of pronotum with rugulae. Lateral surface of pronotum smooth and shining. Pronotum and mesonotum with longitudinal rugulae and sculptured interspaces. Mesopleura weakly sculptured. Rugula on higher portion of mesopleura weakly developed. Dorsal surface of propodeum generally smooth and shining, but one pair of rugulae running from metanotal groove extending posteriorly and diverging to tips of propodeal spines. Dorsal surface of petiole generally smooth. Lateral surface of petiole scultured. Dorsal and lateral surfaces of postpetiole weakly sculptured.

Standing pilosity sparse. Dorsal face of head with some pairs (c. 8) of erect and stout setae, and short and decumbent setae sparsely. Clypeus with two pairs of long and stout setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pair of short setae laterally. Scapes with decumbent setae. Mesosoma with five pairs of long erect and stout setae (ps1PN, psaMN, pspMN, ps1PS, and ps2PS) that are much longer than other erect setae. Posterolateral...
tubercles of petiote posteriorly with one pair of stout setae. Postpetiote with three pairs of stout setae on disc anterodorsally, anterolaterally and posteriorly. Fourth abdominal tergite with some pairs (> 10) of erect and stout setae, and short appressed setae sparsely.

Body yellow. All flagellar segments yellow.

Comments: In the worker this species can be distinguished from all other members of the C. biroi group by the scape with suberect to decumbent setae, distinct compound eyes, generally smooth dorsal surface of head, and sparse erect and stout setae on body. This species is similar to C. fritzi, but can be distinguished from it by the suberect to decumbent setae on scape, shorter setae on anterior mesonasal ridge, abundant erect setae on fourth abdominal tergite.

Distribution: This species is known from the type locality of the Philippines (Fig. 51).

Etymology: The specific name refers to the island of origin, Luzon.

CREMATOGASTER MACRACANTHA Creighton, 1945
(Fig. 107)
Crematogaster (Rhachiocrema) macracantha Creighton, 1945: 114, pl. 12, figs. 4, 5; worker, Mt. Penrissen, Sarawak, Borneo, Malaysia (E. Mjoberg) (types not seen).
Crematogaster macracantha; Blaimer, 2012c: 55 [Combination in C. (Crematogaster)].

Worker measurements (n = 3): HW 0.57–0.60; HL 0.61–0.63; CI 93–98; SL 0.65–0.68; SI 111–114; EL 0.14–0.15; PW 0.38–0.39; WL 0.84–0.89; PSL 0.50–0.59; PtL 0.37–0.38; PpW 0.21–0.25; PpHI 0.19–0.22; PpL 0.18–0.20; PpW 0.22–0.24; PtWI 50–58; PtWI 57–66; PpWI 118–122; WI 88–105.

General description of worker: Workers monomorphic.

Head round in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes exceeding postpetiolar corners of head.

Pronotal collar with concave anterior margin in dorsal view, slightly lower than pronotum in lateral view. Pronotal dorsum without distinct longitudinal ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view forming evenly arched, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, distinctly longer than diameter of propodeal spiracles, in dorsal view strongly divergent.

Petiote in dorsal view with subparallel sides and narrow short peduncle anteriorly, distinctly longer than wide. Posterior portion of petiote with short process that is slightly higher than posterior margin of petiote disc in lateral view. Subpetiolar process developed as acute tubere. Petiote in lateral view with strongly convex dorsum, distinctly higher than petiote, in dorsal view as wide as petiote, globular, not bilobed. Subpostpetiolar process undeveloped, but venter of postpetiote convex.


Standing pilosity sparse. Dorsal face of head with three pairs of long erect setae and appressed setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pairs of short setae laterally. Scapes with decumbent to appressed setae. Mesosoma with three pairs of long erect and stout setae (ps1PN, ps2PN, and psaMN) that are much longer than other erect setae. Posteriorlateral tubercles of petiote posteriorly with one pair of long setae. Postpetiote with three pairs of long setae on disc anteriorly, posteriorly and laterally. Fourth abdominal tergite with erect setae sparsely, but no decumbent to appressed setae.

Body yellow-brown. Apical two flagellar segments light yellow, contracting with other flagellar segments that are yellow-brown.

Comments: We have not been able to examine the types of C. macracantha, but the original description and figures closely match the specimens examined. In the worker this species can be easily distinguished from the other species of the C. baduwii group by the long propodeal spines (PSL 0.50–0.59 vs. 0.15–0.22 in the others) and sculptured surface of the body.

Blaimer (2012c) assigned C. macracantha in the subgenus Crematogaster in the subgeneric revision, but she did not include the species in molecular phylogenetic
analysis (2012a, 2012c). Although we do not have any sequence data for the species, several morphological features: clearly differentiated two-segmented antennal club; laterally directed propodeal spines; petiole with subparallel sides; node-like process on posterior portion of petiole; highly convex postpetiolar dorsum; subpostpetiolar venter convex, suggest that C. macracantha belongs to the subgenus Orthocrema. Thus we treat C. macracantha as a member of the subgenus Orthocrema.

Distribution: This species is known from Malaysia (Borneo) (Fig. 49).

Material examined: MALAYSIA: one worker, Bt. Entimau (390 m alt.), Sarawak, Borneo, 18.iv.1994, (Mahmud (P1B4); two workers, Poring (600–700 m alt.), Sabah, Borneo, E. Malaysia, 8.i.1998, (F. Yamane).

**CREMATOGASTER MASUKOI** Hosoishi, Yamane & Ogata, 2010
(Fig. 108)


*Crematogaster masukoi*; Blaimer, 2012c: 55 [Combination in *C. (Orthocrema)*].

**Worker measurements** (n = 6): HW 0.46–0.50; HL 0.44–0.48; CI 100–109; SL 0.35–0.37; SI 74–78; EL 0.04–0.06; PW 0.28–0.31; WL 0.53–0.57; PSL 0.08–0.11; PPL 0.16–0.18; PtW 0.16–0.17; PtH 0.11–0.13; PpL 0.10–0.12; PpW 0.15–0.16; PtHI 61–76; PtWI 94–106; PpWI 133–160; WI 88–100.

**General description of worker:** Workers monomorphic.

Head subquadrate in full-face view. Mandibles with four teeth, basal tooth arranged away from the third apical one, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin weakly convex or almost straight in medial portion. Compound eyes not projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges laterally. Mesonotal dorsum without lateral ridges. Pronotum and mesonotum in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by thin lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, touching metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides or weakly convex sides and narrow anteriorly, longer than wide. Posterior portion of petiole without distinct process in lateral view. Subpetiolar process developed, acute apically. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as or slightly narrower than petiole, weakly bilobed posteriorly, but without longitudinal sulcus. Subpostpetiolar process developed as small process.


Standing pilosity sparse. Dorsal face of head with three pairs of long erect and stout setae, and short and appressed setae sparsely. Clypeus with two pairs of long and stout setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one single short seta medially and one pair of long setae laterally, and some pair of short setae laterally. Scapes with suberect to decumbent setae. Mesosoma with five pairs of long erect and stout setae (ps1PN, psaMN, pspMN, ps1PS, and ps2PS) that are much longer than other erect setae. Postpetiole with three pairs of stout setae on disc anterodorsally, anterolaterally, posteriorly. Fourth abdominal tergite with suberect setae sparsely, but no decumbent to appressed setae.

Body yellow to brown. All flagellar segments yellow.

**Comments:** In the worker this species is very distinct among the *C. biroi* group in having reduced com-
pound eyes (with c. 6 ommatidia). It is similar to *C. myops* (*C. quadriruga* group) in having reduced compound eyes, but can be easily distinguished from it by the smooth surface of clypeus, developed subpetiolar process and acutely developed subpostpetiolar process.

**Distribution and biology:** This species is known from Malaysia (Borneo) and Indonesia (Kalimantan) (Fig. 51). This species inhabits developed forests, and nests in soil.


**CREMATOGASTER MOATENSIS SP. NOV.**

(Fig. 109)

**Holotype worker.** nr. Katamobaq (1200 m), Danau Moat, Utara, Sulawesi, INDONESIA, 11.ix.1985 (no collector's name) (BMNH).

**Paratype.** Five workers, same data as holotype (BMNH, CASC, KUEC, MBBJ, THNHM).

**Worker measurements** (*n* = 6): HW 0.46–0.49; HL 0.48–0.53; CI 92–98; SL 0.45–0.47; SI 94–100; EL 0.11–0.12; PW 0.30–0.33; WL 0.60–0.64; PSL 0.12–0.13; PtL 0.19–0.20; PtW 0.14–0.15; PtH 0.13–0.14; PpL 0.10–0.11; PpW 0.15–0.16; PtII 68–70; PtWI 70–79; PpWI 136–160; WI 100–114.

**General description of worker:** Workers monomorphic.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in median portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorum without ridges laterally. Mesonotal dorum without distinct lateral ridges posteriorly. Pronotum and mesonotum in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view.

Subpetiolar process undeveloped. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpostpetiolar process undeveloped.


Standing pilosity sparse. Dorsal face of head with erect to suberect setae sparsely. Clypeus with three pairs of long setae in anterior portion, one directed upward, one downward, the other laterally below antennal sockets. Anterior clypeal margin with single long setae medially and one pair of long setae laterally, and short setae laterally. Gena (malar space) with some suberect setae near mandibular insertion. Scapes with suberect to decumbent setae. Mesosoma with four pairs of long erect and stout setae (ps1PN, psaMN, pspMN, and ps1PS/ps2PS) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with one pair of long setae. Postpetiole with three pairs of long setae on disc anterodorsally, anterolaterally, and posteriorly. Fourth abdominal tergite with erect to suberect setae sparsely, but no decumbent to appressed setae.

Body bicolored, head and gaste with brown, mesosoma with yellow. All flagellar segments yellow.

**Comments:** In the worker this species is very unique among the Asian *Orthocrema* fauna in having the propodeal spines directed posteriad and the metanotal groove laterally not defined by lamellate ridges.

**Distribution:** This species is known only from Indonesia (Sulawesi) (Fig. 49).

**Etymology:** The specific name refers to the type locality, Danau Moat (Lake Moat).

**Material examined:** INDONESIA: three workers, Dumoga-Bone N. P., Utara, Sulawesi, 17.iv.1985 (Clarke' Camp) (lower montane forest, 1140 m) (no collector's name).
Crematogaster myops Forel, 1911a
(Fig. 110)

Crematogaster myops Forel, 1911a: 31; Lectotype and five paralectotype workers, Sarawak, Borneo, Malaysia (Haviland) (MHNG, examined).

Crematogaster myops; Santschi, 1918: 182 [Combination in C. (Orthocrema)].

Crematogaster myops; Emery, 1922: 132 [Combination in C. (Orthocrema)].

Crematogaster myops; Hosoiishi et al. 2010: 347 [Lectotype designation and redescription of type material].

Crematogaster myops; Blaimer, 2012c: 55 [Combination in C. (Orthocrema)].

Worker measurements (n = 7): HW 0.44–0.48; HL 0.45–0.52; CI 92–98; SL 0.40–0.44; SI 90–94; EL 0.05–0.06; PW 0.27–0.31; WL 0.49–0.58; PSL 0.05–0.08; PtL 0.15–0.21; PtW 0.13–0.16; PtH 0.10–0.12; PpL 0.09–0.13; PpW 0.12–0.16; PtHI 55–67; PtWI 75–89; PpWI 115–150; WI 92–100.

General description of worker: Workers monomorphic.

Head subquadrate in full-face view. Mandibles with four teeth, basal tooth arranged away from the third apical one, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes not projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges laterally. Mesonotum with lateral ridges posteriorly. Pronotum and mesonotum in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, touching to metapleural gland bullae. Propodeal spines developed, as long as diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process developed as small acute process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process undeveloped, but venter of postpetiole convex.

Integument essentially smooth and shining. Dorsal surface of head generally smooth and shining, but with rugulae on surrounding region of antennal sockets. Mandibles with feeble rugulae and smooth interspaces. Clypeus weakly sculptured with one distinct pair of longitudinal rugulae; rugulae not extending to posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum without rugulae. Mesopleura smooth and shining. Dorsal surface of propodeum generally smooth and shining, but one pair of rugulae running from metanotal groove to tips of propodeal spines. Dorsal surface of petiole smooth and shining. Lateral surface of petiole generally smooth, but with one longitudinal rugula. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with suberect setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with suberect setae. Mesosoma with four pairs of long erect and stout setae (ps1PN, psaMN, pspMN, and psp1PS) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with one pair of stout setae. Postpetiole with several pairs of long setae on disc anteriorly, posteriorly and laterally. Fourth abdominal tergite with suberect setae abundantly, and short decumbent setae sparsely.

Body yellow. All flagellar segments yellow.

Comments: In the worker this species is very distinct among the C. quadriruga group in having reduced compound eyes (with c. 6 ommatidia). It is similar to C. masukoi (C. biroi group) in having reduced compound eyes, but can be distinguished by the clypeus with rugulae, smooth surface of propodeum, and the lack of subpostpetiolar process.

Distribution and biology: This species is known from Malaysia (Peninsula and Borneo), Singapore and Indonesia (Sumatra) (Fig. 52). This species inhabits developed forests, and nests in soil.

CREMATOGASTER OCELLATA SP. NOV.

(Fig. 111)


Paratypes. Three workers same data as holotype (CASCADE, KUEC, THNHM).

Worker measurements (n = 4): HW 0.50–0.56; HL 0.53–0.59; CI 94–96; SL 0.40–0.45; SI 78–84; EL 0.07–0.08; PW 0.31–0.37; WL 0.58–0.66; PSL 0.08–0.10; PtL 0.18–0.22; PtW 0.16–0.18; PtH 0.12–0.15; PpL 0.12–0.13; PpW 0.17–0.18; PtH 63–78; PtWI 81–85; PpWI 138–142; WI 100–106.

General description of worker. Workers monomorphic.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes not projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum without ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotal in lateral view forming slightly convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, touching metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process weakly developed as blunt process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpostpetiolar process developed as blunt process.

Integument essentially smooth and shining. Dorsal surface of head generally smooth and shining, but with longitudinal rugulae on higher portion extending to mesopleura and lateral sides of propodeum. Mesopleura sculptured. Rugula on higher portion of mesopleura extending to small pit of mesothoracic spiracles. One pair of rugulae running from metanotal groove to tips of propodeal spines. Dorsal surface of propodeum weakly sculptured. Dorsal surface of petiolar smooth and shining. Lateral surface of petiolar smooth and shining. Lateral surface of postpetiole weakly sculptured posteriadly.

Standing pilosity sparse. Dorsal face of head with erect to suberect and stout long setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pairs of short setae laterally. Scapes with suberect setae. Mesosoma with five pairs of long erect and stout setae (ps1PN, ps2PN, psaMN, pspMN, and ps1PS) that are much longer than other erect setae. Posteralateral tubercles of petiole posteriorly with two pairs of stout long setae. Postpetiole with five pairs of long setae on disc anterodorsally, anterolaterally and posteriadly. Fourth abdominal tergite with erect and stout suberect long setae sparsely, and short decumbent setae sparsely.

Body yellow. All flagellar segments yellow.

Comments: In the worker this species is distinct among the C. biroi group in having reduced compound eyes (with c. 12–15 ommatidia). This species corresponds to sp. eg-12 by Eguchi, Bui & Yamane (2011).

Distribution: This species is known from N. Vietnam (Fig. 51).

Etymology: The specific name refers to the small compound eyes.


CREMATOGASTER OSAKENSIS FOREL, 1900

(Fig. 112)

Crematogaster sordidula var. osakensis Forel, 1900: 269; syntype workers, Osaka, Japan (MHNG, examined) (Synonymy under C. japonica by Brown, 1949: 37). One syntype worker in MHNG here designated Lectotype.


37). One syntype worker (top specimen of three on one pin) in MHNG here designated Lectotype.  
Crematogaster sordidula subsp. osakensis; Emery, 1912: 671 [Subspecies of sordidula].  
Crematogaster sordidula subsp. osakensis; Emery, 1922: 131 [Combination in C. (Orthocrema)].  
Crematogaster sordidula var. japonica; Emery, 1922: 131 [Combination in C. (Orthocrema)].  
Crematogaster sordidula subsp. osakensis; Wheeler, 1928: 111 [Subspecies of sordidula; descriptions of queen and male].  
Crematogaster osakensis; Collingwood, 1976: 303 [Raised to species].  
Crematogaster osakensis; Onoyama, 1980: 198 [Subspecies of sordidula].  
Crematogaster osakensis; Kupyanskaya, 1990: 129 [Raised to species].  
Crematogaster osakensis; Bolton, 1995: 159.  
Crematogaster osakensis; Blaimer, 2012c: 55 [Combination in C. (Orthocrema)].

Worker measurements (n = 8): HW 0.47–0.57; HL 0.49–0.59; CI 92–100; SL 0.38–0.44; SI 77–84; EL 0.11–0.13; PW 0.27–0.35; WL 0.54–0.68; PSL 0.08–0.11; PtL 0.16–0.19; PtW 0.15–0.18; PtH 0.12–0.15; PpL 0.11–0.12; PpW 0.14–0.18; PtHI 68–81; PtWI 83–94; PpWI 117–150; WI 88–100.

General description of worker: Workers monomorphic.  
Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin slightly concave in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posteralar corners of head.

Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum with ridges laterally. Mesonotal dorsum with lateral ridges posteriorly that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view forming convex, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally marginated by lamellate ridges. Propodeal spiracles oval, situated at posteralar corners of propodeum, touching metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and weakly angulate shoulders anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process developed as acute process. Subpetiolar in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpetiolar process developed as blunt process.


Standing pilosity sparse. Dorsal face of head with three pairs of erect and stout long setae, and short and appressed setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one single long seta medially and one pairs of long setae laterally, and some pairs (three to four) of short setae laterally. Scapes with suberect to decumbent setae. Mesosoma with three pairs of long erect and stout setae (ps1PN, psaMN, and pspMN) that are much longer than other setae and one pair of shorter setae (ps1P). Posteralar tubercles of petiole posteriorly with one pair of stout long setae. Postpetiolar with three pairs of stout long setae on disc anterodorsally, anterolaterally and posteriorly. Fourth abdominal tergite with suberect to decumbent stout setae sparsely.

Body yellow. All flagellar segments yellow.

Comments: In the worker this species can be distinguished from all other members of the C. biroi group by the distinct compound eyes, generally smooth dorsal surface of head, petiole tapering posteriorly in dorsal view, and erect setae on body tapering distally. This species is similar to C. vieti, but can be distinguished from it by the slender propodeal spines, petiole tapering posteriorly and subpetiolar process angulate.

Distribution and biology: This species is known from Japan (Hokkaido, Honshu, Shikoku, Kyushu, Yakushima Island, Amami Island) (Japanese Ant Database Group 2008, 2008), South Korea (Terayama, Choi & Kim, 1992; Choi, Ogata & Terayama, 1993), North Korea (Collingwood, 1976; Radchenko, 2005) and China (Wu & Wang, 1995; Zhou, 2001) (Fig. 51). It is noted that we have not examined the specimens from South Korea,
North Korea and China in this study. This species inhabits grasslands (Hosoishi et al., 2015) to forests, and nests under stone and in soil or leaf litter. Colonies are polygynous. Reproductive alates fly at evening in September and are attracted to light (Japanese Ant Database Group 2008, 2008). A myrmecophilous beetle, *Triartiger reductus* Nomura (Staphylinidae) are known from the nests in Tsushima Island, Japan (Komatsu & Maruyama, 2008).


**CREMATOGASTER PHILIPPINENSIS SP. NOV.**

(Fig. 113)


*Paratype.* Four workers, same data as holotype (BMNH, CASC, KUEC, SKYC).

Worker measurements (n = 5): HW 0.45–0.46; HL 0.48–0.49; CI 94–96; SL 0.41–0.43; SI 91–93; EL 0.09–0.11; PW 0.28–0.31; WL 0.56–0.59; PSL 0.08–0.11; PtW 0.13–0.14; PtH 0.13–0.14; PpW 0.11–0.12; PpL 0.08–0.11; HW 0.45–0.46; HL 0.48–0.49; CI 94–96; SL 0.41–0.43; SI 91–93; EL 0.09–0.11; PW 0.28–0.31; WL 0.56–0.59; PSL 0.08–0.11; PtL 0.18–0.18; PtW 0.10–0.12; PtH 0.13–0.14; PpL 0.11–0.12; PpW 0.14–0.15; PtHI 72–82; PtWI 76–88; PpWI 117–127; WI 100–108.

**General description of worker:** Workers monomorphic.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorum without distinct ridges laterally. Mesonotal dorum with lateral ridges posteriorly that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline; mesonotal dorum flat. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles elliptical, situated at posterolateral corners of propodeum, touching to metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process undeveloped. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, weakly bilobed posteriorly but without longitudinal suture. Subpostpetiolar process undeveloped, but venter of postpetiole convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth and shining, but with one pair of longitudinal rugulae; rugulae not extending to posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth shining; anterolateral shoulders of pronotum with rugulae. Mesopleura smooth and shining. Dorsal surface of propodeum generally smooth and shining, but one pair of rugulae running from metanotal groove to tips of propodeal spines. Dorsal surface of petiole smooth and shining. Lateral surface of petiole generally smooth, but with one longitudinal rugula. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with suberect setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with suberect setae. Mesosoma with four pairs of long erect and stout setae [ps1PN (two pairs), pslaMN, pspMN, and ps1PS] that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with one pair of stout setae (one pair of short setae laterally). Postpetiole with three pairs of setae on disc anteriorly, posteriorly and laterally. Fourth abdominal tergite with erect to suberect setae abundantly, and short decumbent setae sparsely.

Body yellow. All flagellar segments yellow.

**Comments:** In the worker this species can be distinguished from all other members of the *C. quadriruga* group by the distinct compound eyes, V-shaped metanotal groove in lateral view, large propodeal spiracles touching metapleural gland bulla, long propodeal spines (PSL 0.08–0.11), and yellow-colored body. This species is similar to *C. sundalandensis*, but can be distinguished from it by the scape with suberect setae only and yellow-colored body.

**Distribution:** This species is known from the type locality of the Philippines (Fig. 52).

**Etymology:** The specific name refers to the country of origin, the Philippines.

**CREMATOGASTER QUADRIRUGA** FOREL, 1911c

*Stat. nov.*

(Figs 114, 115)

*CREMATOGASTER BIROI* var. *quadriruga* FOREL, 1911c: 455; syntype workers, Kerr, Thailand (M. Waldo) (MHNG, examined). One syntype worker (top specimen of three on one pin) in MHNG here designated Lectotype.

*CREMATOGASTER BIROI* var. *quadriruga*; Emery, 1922: 132 [Combination in C. (*Orthocrema*)].

Worker measurements (*n* = 8): HW 0.46–0.50; HL 0.48–0.51; CI 94–100; SL 0.44–0.48; SI 94–100; EL 0.11–0.12; PW 0.27–0.31; WL 0.54–0.60; PSL 0.11–0.13; PtL 0.51; PtW 0.25–0.26; PtH 0.23–0.25; PpL 0.21–0.22; PpW 0.15–0.18; PtHI 68–79; PtW 0.14–0.17; PtH 0.13–0.15; PpW 0.28–0.29; PpHI 66–71; PpWI 100–145; WI 100–113.

General description of worker: Workers monomorphic, but intermediate worker as large as queen.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum with ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline; mesonotal dorsum higher anteriorly. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral deep corners of propodeum, apart from metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process developed as acute process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process undeveloped, but venter of postpetiolar convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth and shining, but with one distinct pair of longitudinal longer rugulae and one pair of shorter rugulae laterally; longer rugulae not extending to posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum with longitudinal rugulae. Mesopleura weakly punctuate, but seems smooth and shining. Dorsal surface of propodeum generally smooth and shining, but with longitudinal rugulae anteriorly. Dorsal and lateral surfaces of petiole smooth and shining. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with erect setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with suberect and decumbent setae. Mesosoma with five to six pairs of long erect and stout setae (ps1PN, psaMN, pspMN, ps1PS, and one to two ps2PS) that are much longer than other erect setae. Postero lateral tubercles of petiole posteriorly with one pair of stout long setae and one pair of short setae laterally. Postpetiole with three pairs of setae on disc anterodorsally, anterolaterally and posteriorly. Fourth abdominal tergite with erect setae abundantly, and short appressed setae sparsely.

Body bicolor with head, mesosoma, petiole, postpetiole and first gaster yellow and with the remains of the gaster brown. All flagellar segments yellow.

Intermediate worker measurements (*n* = 2): HW 0.65–0.68; HL 0.66–0.68; CI 98–100; SL 0.60–0.61; SI 90–92; EL 0.17; PW 0.48–0.51; WL 0.89–0.92; PSL 0.15; PtL 0.35; PpW 0.25–0.26; PtH 0.23–0.25; PpL 0.21–0.22; PpW 0.28–0.29; PtHI 66–71; PtWI 71–74; PpWI 131–133; WI 111–112.

Description of intermediate worker: With worker character conditions, except as follows.

Three ocelli present.

Mesonotum strongly convex in lateral view. Posteri or face of mesonotum steeply sloping so that in lateral view dorsal outline of promesonotum not smoothly arched.

Subpetiolar process developed as blunt process.


Postero lateral tubercles of petiole with three to four pairs of stout long setae posteriorly. Fourth
abdominal tergite with erect setae abundantly, and short appressed setae sparsely.

Body usually bicolored with head, mesosoma, petiole, postpetiole and first gater yellow and with remains of gaster brown to black.

Comments: In the worker this species can be distinguished from all other members of the *C. quadriruga* group by the distinct compound eyes, propodeal spiracles small and apart from metapleural gland bulla, and petiole with subparallel sides in dorsal view. This species is similar to *C. suehiro*, but can be distinguished from it by longitudinal rugulae on clypeus not extending to posterior clypeal margin, bicolored body, petiole with subparallel sides in dorsal view.

Specimens from northern part of Thailand (Chiang Mai) differ from other specimens in having the developed rugulae on promesonotum, slightly large propodeal spiracles and slightly broader petiole with sculptured surface. Single specimen from Laos has erect longer setae on pronotal shoulders medially. Some specimens from Bokor National Park, Cambodia differ in having yellow-colored gaster.

Distribution and biology: This species is known from Laos, Cambodia, Thailand and Indonesia (N. Sumatra) (Fig. 52). This species inhabits disturbed to developed forests, and nests in dead twigs on trees.


**CREMATOGASTER RETICULATA** Hosoishi, 2009

(FIGS 116, 117)

Crematogaster (Orthocrema) reticulata Hosoishi, 2009: 261; Holotype worker, Ulu Gombak, Selangor, Malaysia, 27.xi.2005 (SH05-Mal-01) (S. Hosoishi) (KUEC, examined) and ten paratype workers, same data as holotype (BMNH, MCSN, MCZC, MHNG, NHMB, examined).

Crematogaster reticulata; Blaimer, 2012c: 55 [Combination in *C. (Orthocrema)*].

Worker measurements (n = 7): HW 0.40–0.46; HL 0.40–0.46; CI 96–103; SL 0.36–0.42; SI 84–91; EL 0.10–0.11; PW 0.27–0.30; WL 0.46–0.57; PSL 0.09–0.14; PtL 0.15–0.17; PtW 0.12–0.14; PtH 0.11–0.13; PpL 0.09–0.12; PpW 0.14–0.15; PTH 0.76–0.77; PtW 0.75–0.87; PpWI 122–155; WI 107–111.

General description of worker: Workers monomorphic, but intermediate workers as large as queen (see below).

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin weakly convex or almost straight in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum with ridges laterally. Mesonotal dorsum with lateral ridges. Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles elliptical, situated at posterolateral corners of propodeum, apart from metapleural gland bulla. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with parallel sides and angulate shoulders anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process developed as acute process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view slightly wider than...
petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process developed as acute process.


Standing pilosity sparse. Dorsal face of head with several pairs (c. 9) of erect and stout long setae, and short and decumbent setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pairs (three to four) of short setae laterally. Scapes with decumbent to appressed setae. Messosoma with five pairs of long erect and stout setae (ps1PN, ps2PN, psaMN, pspMN, and ps2PS) that are much longer than other setae. Posterolateral tubercles of petiole posteriorly with one pair of ps1PN, ps2PN, psaMN, pspMN, and ps2PS) that are much longer than other setae. Posterolateral tubercles of petiole posteriorly with one pair of erect and stout long setae. Postpetiole with three pairs of stout long setae on disc anterodorsally, anterolaterally and posteriorly. Fourth abdominal tergite sculpture with several pairs (c. 12) of erect and stout setae, and short appressed setae sparsely.

Body yellow-brown. All flagellar segments yellow.

**Intermediate worker measurements** (n = 2): HW 0.66–0.75; HL 0.63–0.69; CI 105–109; SL 0.49–0.54; SI 72–74; EL 0.16–0.18; PW 0.49–0.56; WL 0.80–0.94; PSL 0.16–0.18; PtL 0.28–0.32; PtW 0.23–0.26; PtH 0.18–0.23; PpL 0.17–0.20; PpW 0.27–0.30; PpHI 64–72; PpWI 81–82; PpWI 150–159; WI 115–117.

**Description of intermediate worker:** With worker character conditions, except as follows.

Head subquadratic. Three ocelli present.

Mesonotum highly convex in lateral view. Pronotum not clearly forming same dorsal outline with mesonotum in lateral view, but posterior face forming oblique slope to metanotal groove. Propodeal spiracles oval.

Subpetiolar process developed as small tubercle.

Messosoma with nine to 11 pairs of erect and stout long setae; one ps1PN and one to two ps2PN, five to six pairs on mesonotal ridges, two pairs on propodeal spines. Posterolateral tubercles of petiole with two pairs of stout long setae posteriorly. Postpetiole with four pairs of stout long setae on disc anterodorsally, anterolaterally and posteriorly.

**Comments:** In the worker this species can be distinguished from all other members of the *C. biroi* group by the distinct compound eyes, strongly sculptured dorsal surface of head, and petiole squared without angulate anterolateral corners. This species is very similar to *C. schimmeri*, but can be distinguished from it by the propodeal spiracles apart from metapleural gland bulla, petiole squared without angulate anterolateral corners.

**Distribution and biology:** This species is known from S. Thailand and Malaysia (Peninsula and Borneo) and Brunei (Fig. 51). This species inhabits developed forests, and nests in dead twigs or in dead leaves on trees (SH collections from Ulu Gombak).


**CREMATOGASTER SCHIMMERSI** Forel, 1912a

(Fig. 118)

Crematogaster schimmeri Forel, 1912a: 69; syntype workers, Pilam, Taiwan (H. Sauter) (MHNG, examined). One syntype worker (middle specimen of three on one pin) in MHNG here designated Lectotype.

Crematogaster schimmeri; Emery, 1922: 132 [Combination in *C. (Decacrema)*].

Crematogaster schimmeri; Terayama, 2009: 177 [Combination in *C. (Decacrema)*].

Crematogaster schimmeri; Hosoishi & Ogata, 2009a: 1 [Combination in *C. (Orthocrema)*].

Crematogaster schimmeri; Blaimer, 2012c: 55 [Combination in *C. (Orthocrema)*].

Crematogaster schimmeri; Peeters *et al.*, 2013: 258, figs 2–4 [External and internal morphology of intermediate worker].

**Worker measurements** (n = 5): HW 0.44–0.48; HL 0.45–0.49; CI 96–98; SL 0.38–0.40; SI 79–87; EL 0.12–0.13; PW 0.29–0.32; WL 0.50–0.54; PSL 0.08–0.10; PtL

0.14–0.17; PtW 0.15–0.17; PtH 0.11–0.14; PpL 0.11–0.12; PpW 0.16–0.18; PtHI 75–82; PtWI 88–107; PpWI 142–150; WI 107–113.

**General description of worker:** Workers monomorphic.

Head subquadrate in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin weakly convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum with ridges laterally. Mesonotal dorsum with lateral ridges. Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, touching metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with parallel sides and angulate shoulders anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process developed as blunt process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view slightly wider than petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process developed as acute process.


Standing pilosity sparse. Dorsal face of head with several pairs (c. 9) of erect and stout long setae, and short and decumbent setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pairs (three to four) of short setae laterally. Scapes with decumbent to appressed setae. Mesosoma with five pairs of long erect and stout setae (ps1PN, ps2PN, psaMN, pspMN, and ps2PS) that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with one pair of stout long setae. Postpetiole with three pairs of stout long setae on disc anterodorsally, anterolaterally and posteriorly. Fourth abdominal tergite with several pairs (c. 12) of erect and stout setae, and short appressed setae sparsely.

Body yellow. All flagellar segments yellow.

**Comments:** In the worker this species can be distinguished from all other members of the *C. biroi* group by the distinct compound eyes, sculptured dorsal surface of head, and petiole squared with angulate anterolateral corners. This species is similar to *C. reticulata*, but can be distinguished from it by the propodeal spiracles touching metapleural gland bulla and squared petiole with angulate anterolateral corners.

Terayama (2009) assigned this species to the subgenus *Decarema* by having 10-segmented antennae. However, examinations of the type specimens reveals that the species has 11-segmented antennae and belongs to the subgenus *Orthocrema* (Hosoiishi & Ogata, 2009a).

**Distribution:** This species is known only from the type locality in Taiwan (Fig. 51).

**CREMATOGASTER STORKI SP. NOV.**

*(FIG. 119)*

**Holotype worker.** Dumoga-Bone N. P., Utara, Sulawesi, INDONESIA, Fog. 5, (400 m alt.), 11.ii.1985, BMNH Plot C (N. Stork) (BMNH).

**Paratypes.** Five workers, same data as holotype (CASC, KUEC, MHNG, MBBJ, THNHM).

**Worker measurements (n = 6):** HW 0.47–0.50; HL 0.48–0.52; CI 96–100; SL 0.51–0.54; SI 104–113; EL 0.12–0.13; PW 0.29–0.32; WL 0.60–0.65; PSL 0.17–0.22; PtL 0.24–0.27; PtW 0.16–0.19; PtH 0.14–0.16; PpL 0.13–0.14; PpW 0.18–0.19; PtHI 59–68; PtWI 67–77; PpWI 136–146; WI 100–113.

**General description of worker:** Workers monomorphic.

Head round in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes exceeding posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, slightly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges
laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view forming evenly arched, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming shallow concavity that is laterally margined by ridges. Propodeal spiracles oval, situated at posteolateral corners of propodeum, apart from mepleurall gland bullae. Propodeal spines de- 

developed, longer than diameter of propodeal spiracles, in dorsal view strongly divergent, in lateral view curved upward.

Petiole in dorsal view with subparallel sides and narrow short peduncle anteriorly, distinctly longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process undeveloped. Postpetiole in lateral view with strongly convex dorsum, distinctly higher than petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpetiolar process undeveloped, but venter of postpetiole convex.


Standing pilosity sparse. Dorsal face of head with three pairs of long erect setae and short appressed setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one single long seta medially and one pair of long setae laterally. Scapes with appressed setae. Mesosoma with two pairs of long erect and stout setae (ps1PN, and psaMN) that are much longer than other erect setae and shorter pspMN. Posterolateral tubercles of petiole posteriorly with one pair of stout long setae. Postpetiole with one pair of stout long setae on disc posteriorly. Fourth abdominal tergite with erect setae sparsely (c. 8), but no decem- bument to appressed setae.

Body red-brown. Apical two flagellar segments yellow, contracting with other flagellar segments that are brown.

Comments: In the worker this species can be distin-
guished from all other members of the C. baduvi group by the smooth and shining surface of mesosoma, propodeal dorsum with rugulae, and propodeal spines directed upward at the tip. This species is similar to C. baduvi and C. brunensis, but can be distinguished from them by upward-curved propodeal spines.

Distribution: This species is known only from the type locality in Indonesia (Sulawesi) (Fig. 49).

Etymology: The species name is dedicated to Dr. N. Stork (BMNH), who collected the type material.


Crematogaster suehiro Terayama, 1999

(Fig. 120)

Crematogaster suehiro Terayama, 1999: 726, figs. 1–4; holotype worker and two paratype workers, one paratype queen and one intermediate worker, Ishigaki Island, Japan (MNHA, not examined).

Crematogaster miroku Terayama, 2013: 12, figs 23–25; Holotype worker and six paratype workers, Higashi-

son, Kunigami-gun, Okinawa-jima, Okinawa Pref., Japan, 3.xi.2012 (H. Takamine) (ITLJ, examined; images also examined from Yoshitake et al., 2011). Syn. nov.

Crematogaster suehiro; Blaimer, 2012c: 55 [Combina-

Crematogaster suehiro; Terayama, 1999: 726, figs. 1–4; holotype worker and two paratype workers, one paratype queen and one intermediate worker, Ishigaki Island, Japan (MNHA, not examined).


Worker measurements (n = 6): HW 0.46–0.52; HL 0.47–0.51; CI 96–102; SL 0.46–0.50; SI 94–100; EL 0.12–0.14; PW 0.30–0.33; WL 0.54–0.6; PSL 0.11–0.13; PtL 0.18–0.20; PtW 0.16–0.18; PtH 0.14–0.15; PpL 0.12–0.14; PpW 0.17–0.19; PtHI 74–79; PtWI 85–90; PpWI 123–158; WI 106–112.

General description of worker: Workers monomorphic.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Ante-

crane margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Mesonotal dorsum with lateral ridges. Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, touching mepleurall gland bullae.

Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole without distinct process in lateral view. Subpetiolar process weakly developed as small process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view slightly wider than petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process undeveloped, but venter of postpetiole convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth and shining, but with one distinct pair of longitudinal longer rugulae and one pair of shorter rugulae laterally; longer rugulae extending to posterior or clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum without rugulae. Mesopleura smooth and shining. Dorsal surface of propodeum generally smooth and shining, but with one longitudinal rugulae anteriorly. Dorsal and lateral surfaces of petiole smooth and shining. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with erect setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with suberect setae. Mesosoma with five pairs of long erect and stout setae [ps1PN, ps2PN, psaMN, pspMN (also one pair of short setae medially), and ps1PS] that are much longer than other erect setae. Posterolateral tubercles of petiole posteriorly with two pairs of stout long setae. Postpetiole with four pairs of setae on disc anterodorsally, anterodorsally and posteriorly. Fourth abdominal tergite with erect setae abundantly, and short decumbent setae sparsely.

Body yellow. All flagellar segments yellow.

**Comments:** We have not examined the types of *C. suehiro*, but the original description and figures closely match the specimens examined. In the worker this species can be distinguished from all other members of the *C. quadriruga* group by the distinct compound eyes, propodeal spiracles small and apart from metapleural gland bulla, and petiole tapering anteriorly in dorsal view. This species is similar to *C. quadriruga*, but can be distinguished from it by the
longitudinal rugulae on the clypeus extending to the bottoms between frontal carinae and petiole tapering anteriorly.

In the original description of *C. miroku*, Terayama (2013) separated the species from *C. osakensis* by the carinate dorsolateral corners of mesonotum and smooth and shining mesopleuron. However, the original description and character states mentioned by him match well with *C. suehiro*. Additionally longer scape (SI 96) in holotype of *C. miroku* also suggests the affinity with *C. suehiro* (SI 94–100) rather than *C. osakensis* (SI 77–84). In a key to Japanese *Crematogaster* species (Terayama, Kubota & Eguchi, 2014), *C. miroku* was separated from *C. suehiro* by the petiole with convex sides and slightly broader posteriorly, but he mentioned ‘Petiole... widest at posterior end’ in the original description (Terayama, 2013). Those slight differences are treated as variation within one species, *C. suehiro* until additional characters including molecular data are available.

**Distribution and biology:** This species is known from Southern parts of Japan (Ishigaki Island, Okinawa Island) (Fig. 52). This species inhabits developed forests, and nests in dead twigs on trees.

**Material examined:** JAPAN: six workers, Mt. Omoto, Ishigaki Island, 10.x.2008 (M. Maruyama & T. Komatsu).

**Crematogaster sundalandensis** sp. nov.

(Fig. 121)


*Paratypes.* Seven workers, same data as holotype (BMNH, CASC, KUEC, MHNG, SKYC, THNHM).

**Worker measurements** (*n*=8): HW 0.44–0.53; HL 0.47–0.55; CI 92–100; SL 0.42–0.49; SI 92–96; EL 0.12–0.14; PW 0.29–0.35; WL 0.56–0.64; PSL 0.08–0.11; PtL 0.17–0.21; PtW 0.15–0.16; PtH 0.12–0.15; PpL 0.11–0.13; PpW 0.16–0.19; PtHI 70–78; PtWI 80–88; PpWI 133–146; WI 106–107.

**General description of worker:** Workers monomorphic.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with weakly concave anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum without distinct ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view forming evenly arched, continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles elliptical, situated at posterolateral corners of propodeum, touching to metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with subparallel sides and narrow anteriorly, longer than wide. Posterior portion of petiole without distinct process in lateral view. Subpetiolar process undeveloped. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, weakly bilobed posteriorly but without longitudinal sulcus. Subpostpetiolar process undeveloped, but venter of postpetiole convex.

Integument essentially smooth and shining. Dorsal surface of head smooth and shining. Mandibles with feeble rugulae and smooth interspaces. Clypeus generally smooth and shining, but with one pair of longitudinal rugulae; rugulae not extending to posterior clypeal margin. Dorsal and lateral surfaces of pronotum smooth and shining; anterolateral shoulders of pronotum without rugulae. Mesopleura smooth and shining. Dorsal surface of propodeum generally smooth and shining, but one pair of rugulae running from metanotal groove to tips of propodeal spines. Dorsal surface of petiole smooth and shining. Lateral surface of petiole generally smooth, without longitudinal rugulae. Dorsal and lateral surfaces of postpetiole smooth and shining.

Standing pilosity sparse. Dorsal face of head with subectet setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and short setae laterally. Scapes with subectet setae mixed with two to three long setae. Mesosoma with four pairs of long erect and stout setae (ps1PN, psaMN, pspMN, and ps1PS) that are much longer than other erect setae. Posteriorlateral tubercles of petiole posteriorly with two pairs of stout setae. Postpetiole with three pairs of setae on disc anteriorly, posteriorly, and laterally. Fourth abdominal tergite with erect setae sparsely, and short decumbent setae sparsely.

Body bicolored, head and gaster with brown, mesosoma, petiole and postpetiole with yellow. All flagellar segments yellow.

**Comments:** In the worker this species can be distinguished from all other members of the *C. quadriruga* group by the distinct compound eyes, V-shaped metanotal groove in lateral view, large propodeal spines, and distinctive petiole morphology.
spiracles touching metapleural gland bulla, long propodeal spines (PSL 0.08–0.11), and bicolored body. This species is similar to *C. philippinensis*, but can be distinguished from it by the scape with two to three erect setae and decumbent setae, and bicolored body.

**Distribution:** This species is known from Malaysia (Borneo) and Indonesia (Sumatra) (Fig. 52).

**Etymology:** The specific name refers to the regions which the material is collected.

**Material examined:** INDONESIA: one worker, Ulu Gadut, nr. Padang, W. Sumatra, 27–30.viii.1985 (Sk. Yamane); MALAYSIA: seven workers, Maliau Basin (riparian forest), Sabah, Borneo (300 m alt.), 10.xi.2011 (ex carton cover) (SB11-SKY-38) (Sk. Yamane).

**Crematogaster udo** Forel, 1905

*Crematogaster sordidula* var. *udo* Forel 1905: 20; worker, Tjompea, Java, Indonesia [types not found in MHNG].

*Crematogaster udo*; Emery, 1922: 132 [Raised to species].

*Crematogaster udo*; Emery, 1922: 132 [Combination in *C. (Orthocrema)*].

*Crematogaster udo*; Blaimer, 2012c: 55 [Combination in *C. (Orthocrema)*].

**Comments:** We have not been able to examine the type material of *C. udo*. Forel (1905) referred the affinity with *C. fritzi* Emery in the original description, whereas Menozzi’s key (1935) clearly separated *C. fritzi* from other *Orthocrema* species, including *C. udo*, by having two pairs of hairs on mesosomal dorsum. Taxonomic relationship of *C. udo* with *C. fritzi* will remain unresolved until the type material is examined.

**Crematogaster vieti** sp. nov.  
(Figs 122, 123)

*Holotype worker.* Y Linh Ho, Sa Pa, Lao Cai, VIETNAM, Small fragment of forest (c. 1100 m alt.), 1.v.2002 (Eg02-VN-225) (K. Eguchi) (IEBR).

*Paratypes.* Two workers, same data as holotype (ACEG, KUEC); three workers, Y Linh Ho, Sa Pa, Lao Cai, VIETNAM, Small fragment of forest (c. 1100 m alt.), 1.v.2002 (Eg02-VN-215) (K. Eguchi) (BMNH, CASC, THNHM).

**Worker measurements** (*n* = 9): HW 0.42–0.70; HL 0.45–0.64; CI 92–113; SL 0.37–0.51; SI 72–88; EL 0.10–0.16; PW 0.26–0.39; WL 0.54–0.75; PSL 0.07–0.14; PtL 0.17–0.24; PwW 0.13–0.20; PTh 0.12–0.18; PpL 0.11–0.16; PpW 0.15–0.21; PtTH 74–86; PtWI 77–88; PpWI 120–154; WI 95–111.

**General description of worker:** Workers weakly polymorphic in size.

Head subquadratic in full-face view. Mandibles with four teeth arranged at an equal distance, apical and subapical teeth large, basal two teeth smaller. Anterior clypeal margin weakly convex in medial portion. Compound eyes distinctly projecting beyond lateral margins of head in full-face view. Scapes reaching posterolateral corners of head.

Pronotal collar with almost straight anterior margin in dorsal view, distinctly lower than pronotum in lateral view. Pronotal dorsum with distinct ridges laterally. Mesonotal dorsum with lateral ridges that irregularly extend posteriad to tips of propodeal spines. Pronotum and mesonotum in lateral view not clearly forming continuous dorsal outline. Metanotal groove in dorsal view transverse, almost straight in median portion, forming deep concavity that is laterally margined by lamellate ridges. Propodeal spiracles oval, situated at posterolateral corners of propodeum, apart from or touching metapleural gland bullae. Propodeal spines developed, longer than diameter of propodeal spiracles, in dorsal view directed posteriad.

Petiole in dorsal view with parallel sides and angulate shoulders anteriorly, longer than wide. Posterior portion of petiole with short process that is slightly higher than posterior margin of petiole disc in lateral view. Subpetiolar process developed as acute process. Postpetiole in lateral view with weakly convex dorsum, as high as petiole, in dorsal view as wide as petiole, globular, not bilobed. Subpostpetiolar process developed as acute process.


Standing pilosity sparse. Dorsal face of head with two to three pairs of erect and stout long setae, and short and decumbent setae sparsely. Clypeus with two pairs of long setae in anterior portion, one directed upward and the other downward. Anterior clypeal margin with one pair of long setae medially and some pairs of short setae laterally. Scapes with suberect to
decumbent setae. Mesosoma with four pairs of long erect and stout setae (ps1PN, rsaMN, pspMN, and ps1PS) that are much longer than other erect setae. Posterolateral tubercles of petiolo posteriorly with one pair of stout long setae. Postpetiole with four pairs of stout long setae on disc anterodorsally, anterolaterally and posteriorly. Fourth abdominal tergite with erect and stout setae sparsely, and short decumbent setae sparsely.

Body yellow. All flagellar segments yellow.

**Intermediate worker measurements** (n = 1): HW 0.68; HL 0.70; CI 97; SL 0.54; SI 79; EL 0.19; PW 0.47; WL 0.95; PSL 0.19; PlL 0.32; Ptw 0.25; PhH 0.24; PpL 0.20; PpW 0.28; PtHI 75; PtWI 78; PpWI 140; WI 112.

**Description of intermediate worker:** With worker character conditions, except as follows.

Vestigial lateral ocelli present. Mesonotum highly convex in lateral view. Mesonotal dorum without lateral ridges. Pronotum not clearly forming same dorsal outline with mesonotum in lateral view, but posterior face forming oblique slope to metanotal groove. Propodeal spiracles touching metapleural gland bulla.

Petiole with subparallel sides in dorsal view, tapering anteriorly. Subpetiolar process developed as blunt process.

Dorsal surface of pronotum smooth and shining. Dorsal surface of mesonotum with rugulae anteriorly and laterally. Mesopleura generally smooth, but oblique sulcus running from anterior areas.

Anterodorsal surface of propodeum with rugulae reticulately.

Anterior clypeal margin with one single and one pair of long setae on median portion and some pairs of short setae laterally. Mesosoma with several pairs of long setae on promesonotum, one ps1PS. Posterolateral tubercles of petiolo with two to three pairs of stout long setae posteriorly. Fourth abdominal tergite with suberect to decumbent setae abundantly.

**Comments:** In the worker this species can be distinguished from all other members of the *C. biroi* group by the distinct compound eyes, generally smooth dorsal surface of head, petiolo with subparallel sides in dorsal view, and erect setae on body tapering distally. This species is very similar to *C. osakensis*, but distinguished from it by the thick propodeal spines and petiolo with subparallel sides.

This species corresponds to sp. 36 of SKY (Eguchi et al., 2005) and sp. eg-1, sp. eg-4 by Eguchi et al. (2011).

**Distribution:** This species is known from Vietnam (Fig. 51).

**Etymology:** The species name is dedicated to Dr. Bui T. Viet, who helped with field surveys in Vietnam.

**Material examined:** VIETNAM: one worker, Tam Dao 1000 m alt., Vinh Phuc Prov., N. Vietnam, 8.viii.1998 (Sk. Yamane); one worker, Tam Dao 1000 m alt., Vinh Phuc Prov., N. Vietnam, 9.viii.1998 (Sk. Yamane); two workers, Tam Dao 1000 m alt., Tam Duong Dist., Vinh Prov., 6.xi.2001 (K. Ogata); four workers, Ba Vi 460 m alt., Ba Vi Dist., Ha Tay Prov., 11.xi.2001 (K. Ogata); two workers, Ba Vi 670 m alt., Ba Vi Dist., Ha Tay Prov., 12.xi.2001 (K. Ogata); four workers, Tu Lung, Mai Chau Dist., Hoa Binh Prov., 27.xi.1999 (K. Ogata); three workers, Small fragment of forest (c. 1100 m alt.), Y Linh Ho, Sa Pa, Lao Cai, 1.v.2002 (Eg02-VN-215) (K. Eguchi); three workers, Small fragment of forest (c. 1100 m alt.), Y Linh Ho, Sa Pa, Lao Cai, 1.v.2002 (Eg02-VN-225) (K. Eguchi); four workers, M. Nghe An, Pu Hoat, Lung Khung (640 m alt.), 5.xi.1999 (code-011) (T. V. Bui); one worker, Chua Yen Tu (720–845 m alt.), Quang Ninh, 19.v.2004 (K. Eguchi); two workers and one intermediate worker, near Forestry Station (253 m alt.), Khe Kem, Pu Mat N. P., Nghe An, 15.iii.2006 (Eg15iii06-03) (K. Eguchi).

Species excluded from the subgenus *Orthocrema* in Asia.

**CREMATOGASTER CRASSICORNIS** Emery, 1893

*Crema* catalogus Nej конкурис Emery, 1893: 265, pl. 2, figs 4, 5; syntype workers, Manila, Philippines (M. E. Simon) (MCSN, MHNG, examined).

*Crematogaster crassicornis*; Emery, 1922: 132 [Combination in *C. (Orthocrema)*].

*Crematogaster crassicornis*; Blaimer, 2012c: 55 [Combination in *C. (Orthocrema)*].

**Comments:** Examination of syntype workers in MCSN and MHNG reveals that *C. crassicornis* does not belong to the subgenus *Orthocrema*. Although this species has two-segmented antennal club, characteristic features include: anterolateral margins of clypeus protruded anteriorly; petiolo without node-like process posteriorly in lateral view; postpetiole bilobed with longitudinal median sulcus. These features are characteristic of the subgenus *Crematogaster* and we consider *C. crassicornis* to be referred to that subgenus.

**CREMATOGASTER PAULI** Emery, 1901

*Crematogaster pauli* Emery, 1901: 575, fig. A; syntype workers, Salabanka, Sulawesi, Indonesia (MCSN, MHNG, examined).
Comments: Examination of syntype workers in MCSN and MHNG reveals that *C. pauli* does not belong to the subgenus *Orthocrema*. Although this species has two-segmented antennal club, characteristic features include: anterolateral margins of clypeus protruded anteriorly; petiole without node-like process posteriorly in lateral view. These features are characteristic of the subgenus *Crematogaster* and we consider *C. crassicornis* to be referred to that subgenus.

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REFERENCES


Crawley WC. 1924. Ants from Sumatra. with biological notes. *ZooKeys* 109–118.


