



RESEARCH ARTICLE - ANTS

Taxonomic Revision of the Obligate Plant-Ants of the Genus *Crematogaster* Lund (Hymenoptera: Formicidae: Myrmicinae), Associated with *Macaranga* Thouars (Euphorbiaceae) on Borneo and the Malay Peninsula

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Abstract

The taxonomy and natural history of ants of the genus *Crematogaster* Lund, 1831 (*Crematogaster borneensis*-group of the former subgenus *Decacrema*) obligately associated with myrmecophytic host-plants of the euphorb genus *Macaranga* are reviewed. Within this group of ants *Crematogaster borneensis* André, 1896 (with five subspecies and four varieties), *Crematogaster captiosa* Forel, 1910 as well as *Crematogaster decamera* Forel, 1910 have previously been described from SE Asia. Here we synonymise *C. borneensis* subsp. *capax* Forel, 1911, *C. borneensis* subsp. *hosei* Forel, 1911, *C. borneensis* subsp. *sembilana* Forel, 1911, and *C. borneensis* var. *macarangae* Viehmeyer, 1916 with *C. borneensis* André, 1896. *Crematogaster borneensis* var. *harpysia* Forel, 1911, *C. borneensis* var. *insulsa* Forel, 1911, *C. borneensis* subsp. *symbia* Forel, 1911, and *C. borneensis* subsp. *novem* Forel, 1911 are synonymised with *C. captiosa* Forel, 1910. In addition we describe five new species: *C. claudiae* sp. nov., *C. hullettii* sp. nov., *C. linsenmairi* sp. nov., *C. maryatii* sp. nov., and *C. roslihashimi* sp. nov.. Seven of these eight species are placed into two informal species subgroups based on queen morphology, life-history characters and a formerly published molecular phylogeny. Keys are provided for the identification of queens and workers, as well as natural history information on the eight ant species. The morphology of these *Macaranga*-associated *Crematogaster* (formerly *Decacrema*) species is compared to the only other three species described for this former subgenus in SE Asia, i.e. *C. angulosa* André, 1896, *C. biformis* André, 1892 and *C. cephalotes* Smith, 1857.

Introduction

The cosmopolitan myrmicine genus *Crematogaster* Lund, 1831 is among the largest genera of ants, with the highest diversity of species found in tropical regions (Bolton, 1995; Longino, 2003; Blaimer, 2012a; Bolton, 2014). Species of this genus often show an arboreal lifestyle, nesting in cavities of woody plants or in carton nests that are usually attached to plant parts (Blaimer, 2010). Aside from extensive associations with trophobionts (Dejean et al., 1996; Seufert & Fiedler, 1999; Blaimer, 2010), numerous species of *Crematogaster*

show mutualistic associations with plants that range from facultative to obligate (Maschwitz & Fiala, 1995; Fiala et al., 1999; Fonseca, 1999; Palmer et al., 2000; Vasconcelos & Davidson, 2000; Kaufmann et al., 2001; Moog et al., 2002; Stanton et al., 2002; Feldhaar et al., 2003a; Gaume et al., 2005). In SE Asia, *Crematogaster* species, mainly from a single clade, are engaged with host plants of the euphorb tree genus *Macaranga* in one of the most species-rich obligate ant-plant symbioses found worldwide. In these mutualistic associations, the ants defend the trees against herbivores and overgrowing vegetation (Fiala et al., 1994; Itioka et al., 2000;



Heil et al., 2001; Federle et al., 2002) in return for nesting space in hollow stems as well as food in the form of food-bodies and extrafloral nectar (Fiala et al., 1989). With one exception (see below), all species belong to one group (formerly subgenus *Decacrema*) that was recently placed into the *Crematogaster borneensis*-group within the subgenus *Crematogaster sensu stricto* after subgeneric revision (Blaimer, 2012a; Blaimer, 2012b).

When the ecology and evolution of this ant-plant symbiosis was initially studied in a few myrmecophytic *Macaranga* species on Peninsula Malaysia, they appeared to be inhabited by a single *Crematogaster* species only, namely *Crematogaster borneensis* André, 1896 (Baker, 1934; Ong, 1978; Tho, 1978). However, it soon became obvious that ants associated with different *Macaranga* species comprised a species complex (Fiala & Maschwitz, 1990). Within the last decade, several research groups have independently classified the *Macaranga*-associated *Crematogaster* species into a total of nine morphospecies (Fiala et al., 1999; Feldhaar et al., 2003a; Feldhaar et al., 2010) or five morphospecies from one site in Sarawak (Itino et al., 2001). However, a key to the morphospecies has not been published to date, preventing a comparison of the results obtained by the different research groups. Quek and her coworkers circumvented the problem by using phylotypes based on mitochondrial DNA sequences in order to uncover the evolutionary history of the *Crematogaster* ants involved in this symbiosis (Quek et al., 2004; Quek et al., 2007). Some lineages are, however, congruent with at least four of our delimited morphospecies (unpubl. results, and Quek et al., 2007). Ueda et al. (2015) identified six distinct lineages in a small region in Sarawak using mitochondrial and nuclear DNA markers. These six lineages were, however, assigned to three morphospecies only, which were formerly published by Itino et al. (2001). A comparison with the morphospecies used in Fiala et al. (1999) and Feldhaar et al. (2003a) was again not possible due to a lack of formal description in all studies. Therefore, the comparability of most ecological studies would be highly facilitated by a taxonomic revision of this group of obligate plant-ants. In addition, a full understanding of evolutionary processes such as speciation or ongoing hybridization among lineages of the involved *Crematogaster* species can only be attained by a combination of morphological and genetic data. Our first molecular phylogenetic analyses over a broad distribution area mostly confirmed the morphospecies; however, some mismatches, possibly due to introgression, were observed particularly in the mtDNA data, whereas the microsatellite data separated most of the species (Feldhaar et al., 2003a; Feldhaar et al., 2008; Feldhaar et al., 2010).

Here we provide a taxonomic revision of the species of the *Crematogaster borneensis*-group obligately associated with *Macaranga*. The *Macaranga*-associated *Crematogaster* are compared with the type material of the three other described former *Decacrema* - species from Peninsula Malaysia and Borneo (*C. angulosa* André, 1896, *C. cephalotes* Smith,

1857, and *C. biformis* André, 1892) that are presumably not associated with *Macaranga*. To facilitate ecological studies on this *Macaranga*-ant-system we provide keys for queens and workers. This study is based mainly on material from Peninsula Malaysia, Sabah, Sarawak and East Kalimantan and may therefore not allow secure identification of ants from a few other parts of Sundaland (such as Sumatra and West Kalimantan) where *Macaranga*-ant associations also occur but have not been widely sampled. In these regions, however, no ecological studies on the system have been conducted thus far; such studies have been mainly concentrated in Peninsular Malaysia, Sabah and eastern Sarawak.

A short overview of the natural history of the *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group) species is given to allow comparison of former ecological studies conducted by different research groups.

Taxonomy of the genus *Crematogaster*

The genus *Crematogaster* Lund, 1831 (Myrmicinae: Crematogastrini) is among the most species rich genera in Bolton's catalogue of the ants of the world (Bolton, 1995). In the latest edition (Bolton, 2014) the genus comprised 486 valid species (52 synonyms, 5 homonyms, 5 unavailable), and 296 valid subspecies (89 synonyms, 5 homonyms, 81 unavailable).

Since the genus *Crematogaster* is such a large, diverse and widespread genus, a modern taxonomic revision is still lacking and a large number of species remain formally undescribed, especially from tropical regions. However, recently regional taxonomic revisions of the genus or subgenera have been conducted (Buren, 1959; Buren, 1968; Longino, 2003; Hosoishi & Ogata, 2009; Blaimer, 2010; Blaimer, 2012b; Blaimer, 2012c; Blaimer, 2012d; Hosoishi & Ogata, 2012; Blaimer & Fisher, 2013; Hosoishi 2015). While the genus itself is morphologically clearly defined by the dorsal attachment of the postpetiole to the first gaster segment (Bolton, 1994; Blaimer, 2012b), the formerly used subgenera were based on vague characters only. Subgeneric classifications of the genus were established by Forel (Forel, 1910; Forel, 1911), Santschi (1918), Mann (1919), Emery (1922) and Wheeler (1922). Until recently the genus was divided into 16 subgenera (Bolton, 2014), although it was doubtful whether all of these subgenera represented monophyletic groups. Blaimer recently revised the subgenera of the genus globally (Blaimer, 2012b) and confirmed the non-monophyly of most historic subgenera, this research being based on molecular phylogenetic analyses (Blaimer, 2012a). For a full listing of generic synonymy see also Bolton (2014).

The diagnostic character for the subgenus *Decacrema* (Forel, 1910) was the normally 10-segmented (sometimes 9-segmented, (Emery, 1922)) antenna of workers and females (Santschi, 1918). Males have 12 antennal segments in African species but only 10 or 11 in the Indo-Malayan region (Emery, 1922). Due to its discontinuous distribution (comprising Africa,

Madagascar and the Indo-Malay region including New Guinea), as well as the differing number of antennal segments in males among regions, Emery (1922; p. 137) had already suggested that the subgenus *Decacrema* may not be monophyletic. Blaimer recognizes three monophyletic clades based on molecular data (Blaimer, 2012a), and recommends grouping the species of this hyperdiverse genus into two subgenera only, since most formerly recognized subgenera are not retrieved as monophyletic groups (Blaimer, 2012a; Blaimer 2012b).

The former subgenus *Crematogaster* (*Decacrema*) is polyphyletic in the molecular phylogeny of Blaimer (2012a), splitting into an Afrotropical (African and Malagasy) and an African clade within the global *Crematogaster* clade, with a second, distinct clade comprising the South-East Asian species. Blaimer recommends grouping the species from Africa and Madagascar into the *Crematogaster hova*-group (Blaimer, 2012b). South-East Asian species comprise *Crematogaster enneamera* Emery, 1900 (New Guinea) and *Crematogaster angulosa* André, 1896, *Crematogaster biformis* André, 1892, *Crematogaster cephalotes* Smith, 1857, *Crematogaster captiosa* Forel, 1910, *Crematogaster borneensis* André, 1896 (with 9 subspecies) and *Crematogaster decamera* Forel, 1910 from the Indo-Malaysian region. Again, due to morphological similarities (such as the 10-segmented antenna) these species may form a monophyletic group. However, in contrast to the *Macaranga*-associated *Crematogaster* species *C. angulosa* André, 1896, *C. biformis* André, 1892, and *C. cephalotes* Smith, 1857, are dimorphic with distinct major and minor worker castes and possess a pronounced metanotal groove.

As only three species obligately associated with *Macaranga* host-plants (*C. borneensis*, *C. decamera* and *C. captiosa*) have been included into the molecular phylogeny, monophyly is only clarified for those species, while the affiliation of the other former *Decacrema* species to this clade remains unknown to date (Blaimer, 2012a; Blaimer, 2012b). Blaimer suggests the name *Crematogaster borneensis*-group for this clade (Blaimer, 2012b). In accordance with Blaimer's suggestions we will refer to the *Macaranga*-associated *Crematogaster* species formerly belonging to the subgenus *Decacrema* as *Crematogaster* (*Crematogaster-borneensis*-group).

The earlier taxonomic literature on *Macaranga*-inhabiting *Crematogaster* (*Crematogaster-borneensis*-group) species contains only very short and rather anecdotal descriptions of various species, subspecies and 'varieties', based only on a few individuals (mainly workers but also several queens). Forel (1911) and Viehmeyer (1916 (1915)) both already suggested that *Crematogaster borneensis* may be very variable or a species complex, which is also reflected in the large number of subspecies and varieties described. For *C. borneensis* var. *macarangae* Viehmeyer, 1916 as well as two varieties and two subspecies of *Crematogaster borneensis* collected by Haviland and determined by Forel (1911) it is mentioned that the ants were collected "from a tree called *Macaranga*" (Forel, 1911).

Natural history of the *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group) ants

As extensive work on this ant-plant symbiotic system has been conducted over the last decades, we here summarize only some important aspects (for a detailed compilation see e.g. Feldhaar et al., 2010 and references therein). All associations between *Crematogaster* (*Crematogaster borneensis*-group) and *Macaranga* begin by newly mated foundress queens swarming and searching for a suitable host for colonization. Mating flights are presumably nocturnal and occur all year round (personal observation, B. Fiala and H. Feldhaar). After localization of a host-plant, probably by chemical cues (Inui et al., 2001; Jürgens et al., 2006), single queens enter the plant by chewing an entrance hole into an internode. The hole is sealed from the inside and colony founding is claustral. The first emerging workers open up the internode from inside and start foraging for food provided by the plant, i.e. food bodies (Beccarian bodies) and extrafloral nectar as well on honeydew from specific coccids living in the interior of the stem (Fiala & Maschwitz, 1991; Fiala & Maschwitz, 1992). Whereas several colonies may be founded simultaneously on a seedling, only a single colony dominates each host due to competitive replacement. Ant colonies grow as available nesting space and food provisioning increases with the growth of the host-plant. Workers are never found leaving their host for foraging.

The eight species of *Crematogaster* (*Crematogaster borneensis*-group) associated with *Macaranga* can be subdivided into two subgroups based on the morphology of queens and life history characters, which are largely supported in phylogenetic analyses (Feldhaar et al., 2003a; Quek et al. 2004, Quek et al. 2007). They were named *C. decamera*-subgroup and *C. captiosa*-subgroup after one member of the respective subgroup corresponding to an already described species (Feldhaar et al., 2003a). Ants belonging to the *decamera*-subgroup, as well as *C. maryatii* which, based on mitochondrial DNA sequences, does not cluster with either subgroup (Feldhaar et al., 2003a), have distinctly smaller queens than ants of the *captiosa*-subgroup and share life-history characters such as an earlier onset of reproduction than the latter (Feldhaar et al., 2003b). This late onset of reproduction may preclude species of the *captiosa*-subgroup from reproducing on slow-growing *Macaranga* hosts specialized to grow in primary forest habitats (e.g. *M. angulata* or *M. havilandii*).

The *Crematogaster* (*Crematogaster borneensis*-group) associated with *Macaranga* are generally monogynous and monandrous (Feldhaar et al., 2005; Feldhaar et al., 2010). There are exceptions, though, with *C. decamera* and *C. captiosa* regularly turning secondarily polygynous (Feldhaar et al., 2000). Furthermore, associations of unrelated foundresses may lead directly to polygynous colonies in *C. linsenmairi* in habitat patches with strong nest site limitation (Feldhaar et al., 2005).

All obligately *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group) colonize host species belonging to the sections *Pachystemon* and *Pruinosae* within the genus *Macaranga* (Blattner et al., 2001; Davies et al., 2001). The section *Winklerianae* that is endemic to Borneo is exclusively colonized by a species that we had named *Crematogaster* morphospecies 8 in former publications by our group (Fiala et al., 1999). This species belongs to a different subclade of the genus *Crematogaster* and was never found on *Macaranga* species of sections *Pachystemon* or *Pruinosae*. Since its placement within the genus *Crematogaster* is still unclear we have not included this species in the present study. Three *Macaranga* species (*M. puncticulata*, and, in part of their range, *M. lamellata* and *M. griffithiana*) were found to be specifically inhabited by different species of the genus *Camponotus*, subfamily Formicinae (Maschwitz et al., 1996; Federle et al., 1998a; Federle et al., 1998b; Maschwitz et al., 2004).

The associations of ants and plants are not strictly species-specific, as each of the eight species of *Crematogaster* (*Crematogaster borneensis*-group) inhabits between two to seven different *Macaranga* hosts over their whole distributional range. From the plants' point of view, each species of *Macaranga* is obligately associated with up to three different *Crematogaster* (*Crematogaster borneensis*-group) species (with exception of *M. winkleri* and *M. winkleriella* that are always colonized only by *C. msp. 8*) (Fiala et al., 1999; Feldhaar et al., 2003a; Feldhaar et al., 2003b). Nonetheless, non-random recurring association patterns between the two groups are stable over a wide geographic range (Fiala et al., 1999; Feldhaar et al., 2003a; Feldhaar et al., 2003b; Quek et al., 2004; Quek et al., 2007). *Macaranga* hosts generally show a smaller geographic distribution in comparison to the ants, and a higher degree of endemism. In contrast, four out of the eight species of *Crematogaster* (*Crematogaster borneensis*-group) occur over the whole distributional range of this ant-plant association comprising Malaya, Sumatra and Borneo and some smaller islands in the Sunda-region (Fiala et al., 1999; Quek et al., 2007). These widespread species of *Crematogaster* (*Crematogaster borneensis*-group) often inhabit different *Macaranga* species in different regions and may also colonize more than one host plant species within a region (Fiala et al., 1999; Feldhaar et al., 2003a; Feldhaar et al., 2003b; Quek et al., 2004; Quek et al., 2007). However, at most three *Macaranga* species per site are inhabited by a particular ant species. The *Crematogaster* (*Crematogaster borneensis*-group) each colonize a non-random subset of *Macaranga*-species that shares specific morphological traits (Fiala et al., 1999; Quek et al., 2004; Feldhaar et al., 2010). *Macaranga*-hosts form two distinct groups with host plants whose stems are covered with an epicuticular wax-bloom and non-waxy hosts lacking such coating, with the exception of a few hosts that have only

a slight wax-cover (*M. glandibracteolata*) or produce wax-blooms only as large trees (*M. indistincta*) (Blattner et al., 2001). Only “wax-runners” are able to walk on the slippery, waxy plant surfaces, whereas workers of the other species will either drop off the plant or can only move very slowly on such host stems (Federle & Brüning, 2005; Federle et al., 1997). Wax-running ability is a species-specific trait facilitated by a combination of morphological, locomotory and behavioural adaptations (Federle & Brüning, 2005). A second trait influencing ant colonization involves stems that need to be actively excavated, versus naturally hollow stems (Feldhaar et al., 2010). In the former, energy expenditure during colonization may be higher for the ant partner. Thus, host species with stems that need to be actively excavated tend to be colonized by species of the *captiosa*-subgroup with larger queens. As a consequence, hosts of the solid-stemmed section *Pruinosae* are solely colonized by queens of the *captiosa*-subgroup. These hosts can only be colonized when seedlings are taller than approximately 50 cm. Hosts are then more strongly lignified in comparison to the small and relatively thin-tissued seedlings *Macaranga* species of the section *Pachystemon* that develop swollen internodes for ant colonization. The larger size of queens, their presumably stronger mandibles and their greater energy reserves enable queens of the *captiosa*-subgroup to also found colonies in tips of branches of large, abandoned *Macaranga* hosts. This behaviour was never observed for queens of the *decamera*-subgroup and *C. maryatii* (Feldhaar et al., 2003b).

Materials and Methods

All measurements were taken at 6.5x to 40x magnification with a stereomicroscope (Leica M3C). Measurements (Fig 1) were made with a micrometer stage with digital output in increments of 0.001mm. All measurements are presented in mm.

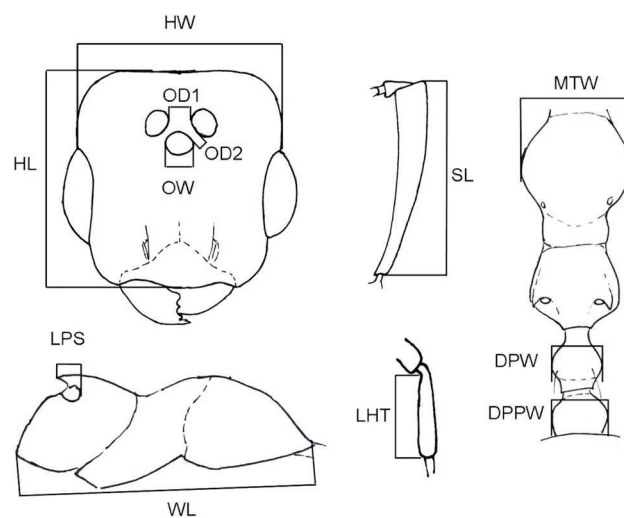


Fig 1. Standard measurements of *Crematogaster* workers and queens. See text for definitions.

The following measurements were taken:

CI	Cephalic index: HW/HL
DPPW	Dorsal postpetiole width: maximum width of post-petiole, measured in dorsal view.
DPW	Dorsal petiole width: maximum width of the petiole, measured in dorsal view.
EL	Eye length: measured along maximum diameter.
HL	Head length: perpendicular distance from line tangent to rearmost points of vertex margin to midpoint of the anterior clypeal margin at full-face view.
HW	Head width: maximum width of the head in full-face view excluding the eyes.
LHT	Metatibia length: length of hind tibia, excluding the proximomedial part of the articulation that is received into the distal end of the metafemur. The measurement is taken with the extensor surface of the tibia in full view, so that the line of view corresponds with the plane of tibial flexion.
LPS	Length of propodeal spines (workers only), measured as the greatest distance from anterior margin of propodeal spiracle to the tip of the spine. This measurement is only given in species where spines are present.
MTW	Metapleural width: maximum distance between metapleura, measured in dorsal view.
OD1	Ocellar distance 1: Distance between the lateral ocelli measured from their inner margin (measured in queens).
OD2	Ocellar distance 2: Distance between one lateral and the medial ocellus from their inner margin (measured in queens).
OW	Ocellar width: Maximal width of the medial ocellus.
PI	Petiole index: DPW/DPPW
REL	Relative eye length: EL/HL
RLEG	Relative leg length: LHT/WL
ROD	Relative ocellar distance: OD1/HW
ROD2	Relative ocellar distance 2: OD2/HW
SI	Scape index: SL/HW
SL	Scape length: length of scape shaft from apex to basal flange, not including basal condyle and neck.
TL	Total length: The total length of the outstretched individual, from the anterior clypeal margin to the gastral apex. This measurement is only taken to give an idea of the size of individuals but is subject to large variation, as total length of the body will strongly depend on nutritional status (e.g. fat content of the gaster).
WL	Weber's length: viewing mesosoma in lateral profile, distance from approximate inflection point, where downward sloping pronotum curves into anteriorly projecting neck to posteroventral propodeal lobes.
ROD2	Relative ocellar distance 2: OD2/HW
SI	Scape index: SL/HW
SL	Scape length: length of scape shaft from apex to basal flange, not including basal condyle and neck.
TL	Total length: The total length of the outstretched individual, from the anterior clypeal margin to the gastral apex. This measurement is only taken to give an idea of the size of individuals but is subject to large variation, as total length of the body will strongly depend on nutritional status (e.g. fat content of the gaster).
WL	Weber's length: viewing mesosoma in lateral profile, distance from approximate inflection point, where downward sloping pronotum curves into anteriorly projecting neck to posteroventral propodeal lobes.

Sampling localities of specimens examined

For an overview of collection sites see Fig 2 (adjacent sites have been comprised under one sampling site number). Additional material not included in the measurements has been collected and identified according to our keys from many more sites in all regions and has supported our species concept.

Peninsula Malaysia:

- Bukit Rengit (Fig 2, site 1): lowland, secondary forest, swampy; 4°41'N 103°26'E
- Gombak (Fig 2, site 1): lowland, secondary forest; 3°18'N 101°47'E
- Genting Highlands (Fig 2, site 1): highland, primary forest, and roadsides, elevation approximately 500-to 1000m; 3°24'N 101°47'E
- Fraser's Hills (Fig 2, site 2): highland, primary forest, elevation approximately 1000m; 3°43'N 101°40'E
- Cukai (Fig 2, site 3): lowland, secondary forest; 4°14'N 103°25'E
- Kuantan (Fig 2, site 3): lowland, secondary forest; 3°48'N 103°22'E
- Maran (Fig 2, site 3): lowland, secondary forest; 3°34'N 102°47'E
- Kuala Rompin (Fig 2, site 4): lowland, secondary forest; 2°47'N 103°30'E
- Belum Forest (Fig 2, site 5): lowland, primary forest, 5°33'5"N 101°20'50" near Gerik, 05°50'N 101°15'E

Sabah:

- Crocker Range, road Kota Kinabalu to Rafflesia Center (Fig 2, site 6): lowland secondary forest up to 900 m; 5°51'N 116° 17'E
- Crocker Range, near Keningau (Fig 2, site 6), lowland secondary forest up to 900 m, 5° 27'N 116°3' E
- Poring Hot Spring (Fig 2, site 6): lowland forest, up to 900m, secondary and primary forest; 6°3'N 116°43'E
- Bukit Taviu (Fig 2, site 7): lowland, secondary forest; 5°37'N 116°55'E
- Danum Valley Conservation Area (Fig 2, site 7): lowland, secondary and primary forest; 4°58'N 117°48'E
- Deramakot (Fig 2, site 7): lowland, secondary forest; 5°24'N 117°28'E
- Telupid (Fig 2, site 7): lowland, secondary forest; 5°38'N 117°7'E
- Kampung Madai (Fig 2, site 8): lowland, secondary forest; 4°43'N 118°10'E
- Tawau (Fig 2, site 8): lowland, secondary forest; 4°25'N 118°01'E

Sarawak:

- Bau (Fig 2, site 9): lowland, secondary forest; 1°24'N 110°9'E
- Matang (Fig 2, site 9): lowland, 1°35'N 110°13'E
- Santubong (Fig 2, site 9): lowland, secondary forest; 1°40'N 110°20'E
- Sibul (Fig 2, site 10): lowland, secondary forest; 4°2'N 113°53'E
- Lambir National Park (surroundings) (Fig 2, site 11): lowland, secondary and primary forest; 4°12'N 113°59'E

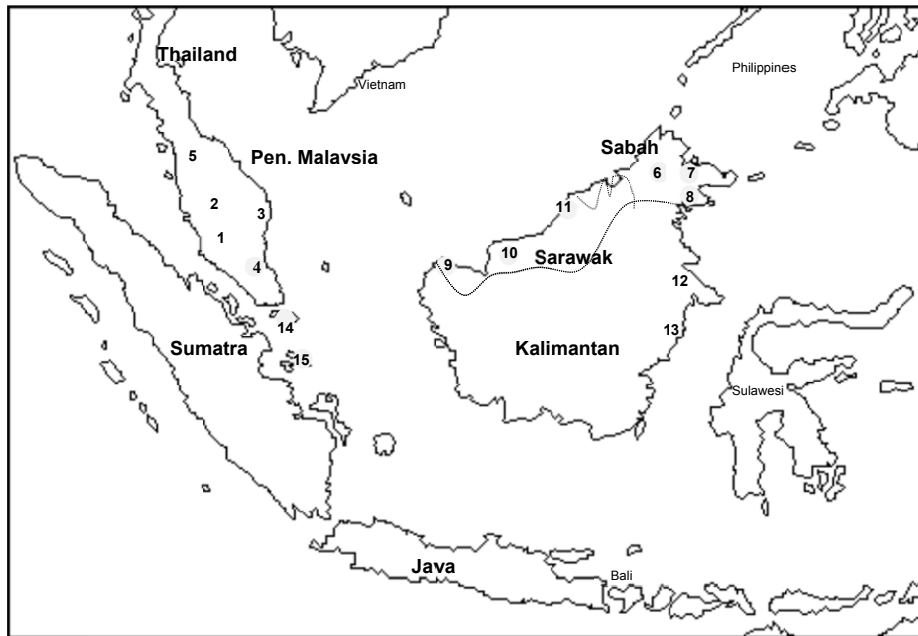


Fig 2. Main sampling sites of specimens included this revision (Site numbers refer to a sampling radius of about 100 km with may contain several sampling sites). **Peninsula Malaysia:** (1) Bukit Rengit, Genting Highlands, Gombak Valley, (2) Fraser's Hill, (3) Cukai, Kuantan, Maran, (4) Kuala Rompin, (5) Belum. **Borneo:** **Sabah:** (6) Crocker Range, Poring Hot Springs, (7) Bukit Taviu, Danum Valley, Deramakot, Telupid, Tawai, (8) Kampung Madai, Tawau. **Sarawak:** (9) Bau, Matang, Santubong, (10) Sibul, (11) Lambir, Mulu, Niah. **Indonesia:** (12) Berau, (13) Wanariset, (14) Pulau Bintang, (15) Pulau Lingga.

- Mulu National Park (surroundings) (Fig 2, site 11): lowland, secondary and primary forest; 4°0'N 114°50'E
- Niah (Fig 2, site 11): lowland, secondary forest; 3°47'N 113°46'E

Indonesia:

- Berau East Kalimantan (Borneo) (Fig 2, site 12): lowland, secondary forest; 1°56'N 117°14'E
- Wanariset: East Kalimantan (Borneo) (Fig 2, site 13): lowland, primary forest; 0°59'S 116°56'E
- Pulau Bintang: Island approximately 30 km south of Singapore (Fig 2, site 14): secondary forest; 1°0'N 104°30'E
- Pulau Lingga: Island approximately 150 km south of - Singapore (Fig 2, site 15): secondary forest; 0°2'N 104°29'E

Abbreviations of museums

MHNG – Muséum d'Histoire Naturelle, Geneva, Switzerland
 MNHN – Muséum National d'Histoire Naturelle, Paris, France
 OXUM – Hope Entomological Collections, University Museum, Oxford, UK

SMNK – Staatliches Museum für Naturkunde Karlsruhe, Germany
 ZMBH – Museum für Naturkunde an der Humboldt-Universität, Berlin, Germany

Key to *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group) species: Queens

1a Queens light to medium-brown; compound eyes oval and > 0.5 mm diameter (longest distance) when head is in lateral view (e.g. Fig S1.1A and S1.1B). **2**

1b Queens medium- to dark brown (nearly black); compound eyes round to slightly oval and < 0.5 mm in diameter (longest distance) when head is in lateral view (e.g. Fig S1.3A and S1.3B). **4**

2a Distance between lateral ocelli always greater than diameter of anterior ocellus (OD1 > OW) (Fig 3.1; Fig S1.1A and S1.1B). Head (in full-face view) always longer (measured from anterior clypeal margin to posterior margin of head)

than wide (measured at the widest point; head capsule only, compound eyes not included) (CI < 0.95). **C. borneensis 2b** Anterior ocellus as wide as or wider in diameter than distance between lateral ocelli (Fig 3.2 and 3.3), or, if the anterior ocellus is not as wide as the distance between the two lateral ocelli, then CI > 0.95. **3**

3a Length of scape > 0.75 mm. Diameter of compound eyes (EL) rarely < 0.65 mm (Fig 3.2). LHT rarely < 1.1 mm. Species colonizes predominantly waxy hosts of the section *Pruinosae* (*M. hosei*, *M. pearsonii*, *M. pruinosa*) (Fig S1.2A and S1.2B).

C. linsenmairi 3b Length of scape usually < 0.75 mm. Diameter of compound eyes (EL) between 0.55 and 0.65 mm, usually around 0.6 mm (Fig 3.3). LHT rarely > 1.1 mm (specimens with LHT between 1.1 and 1.8 were rarely found in Sarawak only). Widespread

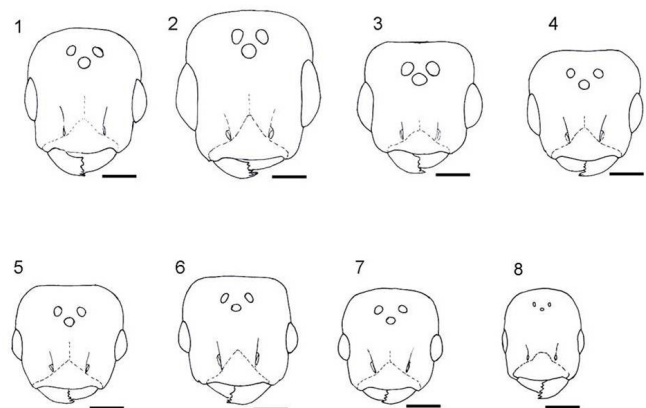


Fig 3. Queens of *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group) species in full-face view. 3.1: *Crematogaster borneensis*; 3.2: *Crematogaster linsenmairi*; 3.3: *Crematogaster captiosa*; 3.4: *Crematogaster claudiae*; 3.5: *Crematogaster hullettii*; 3.6: *Crematogaster decamera*; 3.7: *Crematogaster maryatii*; 3.8: *Crematogaster roslihashimi*. Scale bar corresponds to 0.4 mm.

on non-waxy host species of the section *Pachystemon* (*M. bancana*, *M. indistincta*, *M. angulata*, *M. trachyphylla*, *M. petanostyla*, *M. hullettii*, *M. calcicola*, *M. kingii*) (Fig S1.4A and S1.4B).
C. captiosa

4a Small queens with elongated head (CI < 0.9) and small compound eyes (EL 0.3 – 0.32; Legs in comparison to alitrunk length relatively short (REL < 0.28), HW 0.95 to 1.02 (Fig 3.8; Fig S1.8A and S1.8B). Postpetiole always wider than petiole (or at most as wide) (PI ≤ 1.0). Species endemic to east of Peninsula Malaysia and colonizing waxy hosts of the section *Pachystemon* (*M. constricta* and *M. hypoleuca*).

C. roslhashimi

4b Head of queens less elongated (CI > 0.9) and small to medium sized compound eyes (EL between 0.34 and 0.5 mm). **5**

5a Scape length (SL) > 0.7 mm. Postpetiole always wider than petiole (PI < 1.0). HL between 1.21 and 1.42, head usually as wide as or wider than long (Fig 3.6; Fig S1.5A and S1.5B), rarely longer than wide (CI usually > 1.0). Widespread species, occurring over the whole geographical range of the symbiosis that colonizes waxy hosts of the section *Pachystemon* (*M. beccariana*, *M. havilandii*, *M. hypoleuca*). **C. decamera**

5b Scape length (SL) < 0.7 mm. Petiole usually as wide as or wider than postpetiole (PI > 1.0). **6**

6a Eye length (EL) between 0.34 to 0.38 mm. HL < 1.22, HW 1.01 – 1.2 mm. Compound eyes relatively small in relation to head length in lateral view (REL 0.28 – 0.34; Fig 3.7; Fig S1.6A and S1.6B). The first three segments (distal) of the flagellum of the antenna form a distinct club. Species found on Borneo (Sabah, Sarawak, East Kalimantan), mostly on waxy host plants of the section *Pachystemon* (*M. havilandii*, *M. hypoleuca*, *M. motleyana*) and rarely on the non-waxy *M. angulata* and *M. indistincta* (in primary forest or at higher elevation). **C. maryatii**

6b Eye length (EL) between 0.39 and 0.5 mm, HL > 0.18. Flagellum not with distinct club (may look slightly like 3- or 4-segmented club) **7**

7a Compound eyes relatively large (EL 0.45 to 0.5 mm). Head as wide as or wider than long (CI > 1.0) and petiole usually wider than postpetiole in dorsal view (PI > 1.0). ROD between 0.13 and 0.17 (Fig 3.4; Fig S1.7A and S1.7B). Species endemic to Borneo, mainly found in Sabah, occurring mostly on non-waxy host plants of the section *Pachystemon* (e.g., *M. angulata*, *M. indistincta*) and on the slightly wax covered *M. glandibracteolata*. **C. claudiae**

7b Compound eyes rarely larger than 0.45 mm (EL 0.39 – 0.47 mm). Cephalic index (CI) between 0.96 and 1.07. Postpetiole usually as wide as or wider than petiole in dorsal view (PI < 1.0). ROD between 0.09 and 0.13 (Fig 3.5; Fig S1.3A and S1.3B). Petiole flat and rounded when in dorsal view. Species colonizes non-waxy hosts of the section *Pachystemon* (*M. bancana*, *M. hullettii*, *M. kingii*, *M. trachyphylla*, *M. umbrosa*); on Peninsula Malaysia found at higher elevation only (approximately > 500m); not found in Sabah. **C. hullettii**

Key to Macaranga-associated *Crematogaster* (*Crematogaster borneensis*-group) species: Workers

1a Propodeal spines present, sometimes only short but always protruding beyond the posterior margin of the propodeal spiracle (see Supplementary S1.2C for long propodeal spines; S1.3C for short propodeal spines, Fig S2.4A and S2.4B;) **2**

1b Propodeal spines absent. Propodeum only slightly and bulb-like elevated above the propodeal spiracle (see Fig S1.5C and Fig S1.6C). **7**

2a Scape relatively short in relation to head width. Scape index (SI) < 0.65 **3**

2b Scape relatively long in relation to head width. Scape index (SI) > 0.65 **5**

3a Petiole always distinctly wider than postpetiole with PI > 1.15. Propodeal spines very short only with tip of spine barely protruding beyond margin of propodeal spiracle (Fig S1.7C and S1.7D). Species endemic to Borneo, mainly found in Sabah, occurring mostly on non-waxy host plants of the section *Pachystemon* (*M. angulata*, *M. indistincta*) and on the slightly wax covered *M. glandibracteolata*. **C. claudiae**

3b Petiole wider than postpetiole with PI ranging from 1.0 to 1.15, but PI rarely > 1.10. Propodeal spines either very short with tip of spine barely protruding beyond margin of propodeal spiracle or distinctly longer. **4**

4a Legs in comparison to alitrunk length relatively short (RLEG between 0.58 and 0.62). Head usually as wide as long (CI around 1.0). Propodeal spines present but short, with the tip barely protruding beyond the posterior margin of the propodeal spiracle (LPS/WL ranging from 0.09 to 0.12) (see Supplementary Fig S2.4A and S2.4B; Fig S1.3C and S1.3D). Specimens from Peninsula Malaysia always have CI > 1.0, whereas specimens from Sarawak have more slender heads with CI ≤ 1.0. Species colonizes non-waxy hosts of the section *Pachystemon* (*M. bancana*, *M. hullettii*, *M. kingii*, *M. trachyphylla*, *M. umbrosa*); on Peninsula Malaysia found at higher elevation only (approximately > 500m). **C. hullettii**

4b Legs in comparison to alitrunk relatively longer (RLEG between 0.61 and 0.69). Propodeal spines always prominent and acute, with the tip of the spine distinctly exceeding the posterior margin of the propodeal spiracle (LPS/WL ranging from 0.12 to 0.17). Head always longer than wide (CI < 0.98) (Fig S1.4C and S1.4D). Widespread on non-waxy host species of the section *Pachystemon* (*M. angulata*, *M. bancana*, *M. calcicola*, *M. hullettii*, *M. indistincta*, *M. kingii*, *M. trachyphylla*, *M. petanostyla*) **C. captiosa**

5a Propodeal spines very short only, with the tip barely exceeding the posterior margin of the propodeal spiracle (LPS/WL ranging from 0.07 to 0.08). RLEG 0.67-0.72. CI > 0.94 (Fig S1.6C and Fig S1.6D). Species found on Borneo (Sabah, Sarawak, East Kalimantan), mostly on waxy host plants of the section *Pachystemon* (*M. havilandii*, *M.*

hypoleuca, *M. motleyana*) and rarely on the non-waxy *M. indistincta* and *M. angulata* (in primary forest or at higher elevation).

C. maryatii

5b Propodeal spines long and acute (LPS/WL ranging from 0.1 to 0.17). **6**

6a CI ranges from 0.92 to 0.97, but most workers have a CI < 0.95. RLEG ranges from 0.62 to 0.71 and RLEG is rarely > 0.7. Petiole always wider than postpetiole (PI > 1.0; ranging from 1.01 to 1.14) (Fig S1.1C and S1.1D; Fig S2.4A). Species colonizes a large variety of waxy hosts from both section *Pachystemon* as well as *Pruinosae* (main host species: *M. griffithiana*, *M. motleyana*, *M. hypoleuca* (on the latter mainly on large trees), and *M. pearsonii*, *M. pruinosa*, and *M. hosei*, respectively).

C. borneensis

6b CI ranges from 0.94 to 0.97, most workers have a CI > 0.95. Legs in comparison to alitrunk length relatively long (RLEG ranges from 0.68 to 0.79 and is rarely < 0.7) (Fig S1.2C and S1.2D). Petiole approximately as wide as postpetiole (PI ranging from 0.93 to 1.07 but rarely < 0.99). Species colonizes predominantly waxy hosts of the section *Pruinosae* (*M. hosei*, *M. pearsonii*, *M. pruinosa*).

C. linsenmairi

7a Legs and scape relatively short with RLEG < 0.69 and SI < 0.65. Petiole always distinctly wider than postpetiole with PI > 1.15. Propodeal spines absent (Fig S1.7C and S1.7D). Species endemic to Borneo, mainly found in Sabah, occurring mostly on non-waxy host plants of the section *Pachystemon* (*M. angulata*, *M. indistincta*) and on the slightly wax covered *M. glandibracteolata*.

C. claudiae

7b Legs and scape relatively longer with RLEG > 0.65 (usually > 0.7) and SI > 0.7, rarely below. Petiole may be wider than postpetiole, but PI always < 1.1. **8**

8a Head distinctly longer than wide, CI: 0.91. Propodeal spines absent. Species endemic to east of Peninsula Malaysia. Legs in comparison to alitrunk length relatively short and colonizing waxy hosts of the section *Pachystemon* (*M. constricta* and *M. hypoleuca*).

C. roslhashimi

8b Head only slightly longer than wide (CI 0.94 to 1.02). **9**

9a Propodeal spines always absent, with a sometimes nodiform elevation above propodeal spiracle present (Fig S1.5C and Fig S1.5D). Postpetiole always wider than petiole, PI < 1.0. Petiole only slightly nodiform in dorsal view, rather elongate. Legs relatively long with RLEG 0.71 to 0.85. Widespread species occurring over the whole distributional range of the symbiosis that colonizes waxy hosts of the section *Pachystemon* (*M. beccariana*, *M. havilandii* and *M. hypoleuca*)

C. decamera

9b Propodeum with nodiform elevation above propodeal spiracle or with very short propodeal spines (Fig S1.6C and Fig S1.6D). Petiole nodiform in dorsal view and as wide as or slightly wider than postpetiole, PI ranging from 0.98 to 1.07, PI rarely < 1.0. RLEG ranging from 0.67 to 0.72, in most workers RLEG < 0.7. Endemic to host species found

on Borneo (Sabah, Sarawak, East Kalimantan), mostly on waxy host plants of the section *Pachystemon* (see queen key above)

C. maryatii

Synonymic list of *Crematogaster* (*Crematogaster borneensis*-group) species from Borneo and the Malay Peninsula obligately associated with *Macaranga*

In this study eight species of *Crematogaster* (*Crematogaster borneensis*-group) are recognized (including five new species), belonging to three species subgroups. Species subgroups were designated based on morphological characters of the queen caste, i.e. queens of the *decamera*-subgroup are smaller (WL ranging from 1.7 to 2.3 mm) and have relatively smaller compound eyes (EL < 0.5 mm) than queens of the *captiosa*-subgroup (WL ranging from 2.2 to 2.9 mm and EL > 0.5 mm) (Feldhaar et al., 2003a; Feldhaar et al., 2010) (see Table S.1 for comparison of morphospecies designations used by our group and synonymized or new species names).

All workers of *Crematogaster* (*Crematogaster borneensis*-group) workers including those associated with *Macaranga* have ten antennal segments. The workers of the *Macaranga*-associated *Crematogaster* species are all monomorphic. This is in contrast to the other three described species belonging to the former *Decacrema* from SE-Asia (*C. angulosa*, *C. biformis* and *C. cephalotes*) that all have dimorphic workers (see Supplementary Fig S2.1A to S2.3B). Body size may vary strongly within species although this is dependent on colony size (e.g. TL ranges from ~ 2.1 mm to 3.3 mm in *Crematogaster captiosa* workers). Thus, especially in workers relative measures (e.g. SI or RLEG) are more important characters than absolute measurements (e.g. SL or LHT) (see overview of most important distinguishing characters of workers in Table 1). Workers collected from small colonies are also lighter in colour. In queens shade of body coloration is a useful character, as are absolute measures. If possible, queens should be used for determination as worker characteristics are sometimes less distinctive (see overview of most important characters distinguishing queens in Table 1).

Most of the diversity of the species is apportioned between the *decamera*-subgroup and the *captiosa*-subgroup. The placement of *C. maryatii* is unclear. In the molecular phylogeny based on mitochondrial DNA this species does not cluster with either group and came out most basal. Based on nuclear DNA (elongation factor 1 α) (Feldhaar et al., 2010) this species is not separated from species of the *captiosa*-group. However, queen morphology and life-history characters resemble that of the *decamera*-group. Small size of queens and workers and early onset of reproduction may be a convergent trait though as this seems to enable usage of less productive and slow growing host plants (Feldhaar et al. 2010). Therefore, we currently do not place *C. maryatii* in either group.

Table 1. Overview of most distinct morphological characters of the *Macaranga*-associated *Creinatogaster* (*borneensis*-group) species.

Species	Worker characters	Queen characters
<i>C. borneensis</i>	Propodeal spines present Scape index (SI) > 0.65 RLEG < 0.7, rarely above	EL > 0.5 mm (to 0.6mm) REL 0.36 - 0.43 OD1 > OW Head longer than wide (CI < 0.95)
<i>C. linsenmairi</i>	Propodeal spines present Scape index (SI) > 0.65 RLEG > 0.7, rarely below	EL rarely < 0.65mm REL 0.39 - 0.48 OD1 < OW Scape length > 0.75 mm
<i>C. hullettii</i>	Propodeal spines present Scape index (SI) < 0.65 Head as wide as long (CI ~ 1.0) Legs relatively short, RLEG 0.58 to 0.62	EL 0.39 – 0.47 mm (rarely > 0.45) REL 0.32-0.4 OD1 > OW ROD between 0.09 - 0.13
<i>C. captiosa</i>	Propodeal spines present Scape index (SI) < 0.65 RLEG 0.61 to 0.69	EL ~ 0.6mm REL 0.38 - 0.48 OD1 < OW Scape length usually < 0.75 mm
<i>C. decamera</i>	Propodeal spines absent Legs relatively long (RLEG 0.71 - 0.85) Head slightly longer than wide (CI 0.94 - 1.02) Postpetiole always wider than petiole (PI < 1.0)	EL 0.39 - 0.45mm REL 0.29 - 0.35 OD1 > OW SL > 0.7 mm CI usually > 1.0 PI < 1.0
<i>C. maryatii</i>	Very short propodeal spines, sometimes absent Scape index (SI) > 0.65 Head slightly longer than wide (CI 0.94 - 1.02) Petiole as wide or wider than postpetiole, PI > 0.98 RLEG usually < 0.7	EL 0.34 - 0.38mm REL 0.28-0.34 OD1 > OW PI usually > 1.0 (to 1.12)
<i>C. roslihashimi</i>	Propodeal spines absent Scape index (SI) > 0.7 Head distinctly longer than wide (CI: 0.91) Legs relatively long (RLEG 0.71-0.73)	EL 0.3 – 0.32; REL < 0.28 OD1 > OW Elongated head (CI < 0.9) PI ≤ 1.0
<i>C. claudiae</i>	Propodeal spines usually absent, when present very short Petiole distinctly wider than postpetiole (PI > 1.15) Legs and scapi short, RLEG < 0.69 and SI < 0.65	EL 0.45 - 0.5 mm (REL 0.36-0.39) OD1 > OW PI > 1.0 ROD between 0.13 - 0.17

Creinatogaster maryatii* sp. nov.**C. decamera*-subgroup***Creinatogaster decamera* Forel, 1910*Creinatogaster hullettii* sp. nov.*Creinatogaster roslihashimi* sp. nov.***C. captiosa*-subgroup***Creinatogaster borneensis* André, 1896= *C. borneensis* subsp. *capax* Forel, 1911 syn. nov.= *C. borneensis* subsp. *hosei* Forel, 1911 syn. nov.= *C. borneensis* subsp. *sembilana* Forel, 1911 syn. nov.= *C. borneensis* var. *macarangae* Viehmeyer, 1916 syn. nov.*Creinatogaster captiosa* Forel, 1910= *C. borneensis* var. *harpyia* Forel, 1911 syn. nov.= *C. borneensis* var. *insulsa* Forel, 1911 syn. nov.= *C. borneensis* subsp. *symbia* Forel, 1911 syn. nov.= *C. borneensis* subsp. *novem* Forel, 1911 syn. nov.*Creinatogaster linsenmairi* sp. nov.*Creinatogaster claudiae* sp. nov.**Species accounts*****Creinatogaster maryatii* sp. nov.**

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Holotype

Queen (to be deposited in SMNK, provisional specimen number DG06-263-Q).

Tawau Forest Reserve, secondary forest (B. Fiala)
Queen from *Macaranga hypoleuca*; 29.8.2006.

CI 0.95, DPPW 0.37, DPW 0.38, EL 0.37, HL 1.17, HW 1.11, LHT 0.82, MTW 0.89, OD1 0.15, OD2 0.06, OW 0.11, PI 1.01, REL 0.31, RLEG 0.41, ROD 0.13, ROD2 0.05, SI 0.6, SL 0.67, (TL 5.5), WL 2.0

Paratype

Worker from same colony as holotype queen (to be deposited in SMNK, provisional specimen number DG06-263-W).

CI 1.0, DPPW 0.14, DPW 0.14, EL 0.08, HL 0.54, HW 0.52, LHT 0.41, LPS 0.055, MTW 0.3, PI 1.01, REL 0.15, RLEG 0.69, SI 0.71, SL 0.37, (TL 2.1), WL 0.59

Additional material examined

Sabah (Borneo): Poring Hot Spring (H. Feldhaar, B. Fiala, H.P. Heckroth, R. Kern), Telupid (H. Feldhaar), Kampung Madai (H. Feldhaar), Tawau (B. Fiala). **East Kalimantan (Borneo):** Berau (F. Slik), Wanariset (F. Slik)

Worker measurements (n=7)

CI 0.94-1.02, DPPW 0.14-0.2, DPW 0.14-0.21, EL 0.08-0.12, HL 0.54-0.65, HW 0.52-0.63, LHT 0.41-0.54, LPS 0.047-0.063, MTW 0.3-0.38, PI 0.98-1.07, REL 0.15-0.18, RLEG 0.67-0.72, SI 0.65-0.79, SL 0.37-0.47, (TL 2.1-3.0), WL 0.59-0.73

Worker description

Colour medium to dark brown with head and gaster a slightly darker shade than alitrunk. Workers monomorphic in size. Total body length of workers ranges from 2.3 mm to 3.0 mm. Head and gaster shiny with smooth surface, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole. Head subquadratic but slightly elongated, usually longer than wide and only slightly rounded on sides. Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Occipital margin slightly concavely rounded, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from most proximate to most distal denticle. Surface of mandibles smooth, covered with short pubescent hairs. Antennae relatively long in comparison to head width (SI 0.65-0.79; usually > 0.7) and covered in short pubescent hair. Terminal three funicular segments form a club, sometimes only the terminal two segments.

Compound eyes elliptically shaped and not protruding over margin of head in full-face view. Pronotum and mesonotum form a convex dome in profile that is flattened dorsally. Anterodorsal surface of pronotum sloping downwards as steep as posterodorsal surface of mesonotum. Metanotal groove slightly notched and clearly developed; promesonotal suture is visible but not prominent (Fig S1.6C and S1.6D).

Propodeal spines very short or nearly absent, but dorsum of the propodeal spiracle with a nodiform elevation. Slope of posterior face of propodeum similar to posterior slope of mesonotum and approximately 45°.

In dorsal view postpetiole always wider than petiole (PI: 0.98-1.07) (Fig S1.6C and S1.6D). Both petiole and postpetiole round in dorsal view and nodiform in lateral

view. Subpetiolar process usually absent. (See Table 1 for comparative overview of worker characters.)

Queen measurements (n=15)

CI 0.90-1.04, DPPW 0.36-0.44, DPW 0.38-0.49, EL 0.34-0.38, HL 1.09-1.22, HW 1.01-1.2, LHT 0.72-0.95, MTW 0.78-1.21, OD1 0.15-0.2, OD2 0.06-0.09, OW 0.09-0.11, PI 0.97-1.12, REL 0.28-0.34, RLEG 0.39-0.47, ROD 0.13-0.18, ROD2 0.05-0.08, SI 0.51-0.6, SL 0.59-0.68, (TL 5.4-6.6), WL 1.74-2.2

Queen description

Queens small, from 5.4 to 6.6 mm in total body length and uniformly dark brown in colour. Surface of head and gaster smooth and shiny, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior present on the clypeus. Mandibles relatively short, capable of closing tightly against the clypeus.

Head usually longer than wide (CI: 0.90-1.04; mean 0.97). Sides of the head straight and head narrower anterior than posterior. Occipital margin of the head straight. Occipital lobes rounded. Anterior clypeal margin slightly convex. Terminal 3 segments of funiculus forming a distinct antennal club. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes only slightly oval-shaped from lateral view and maximum head width with compound eyes slightly wider than HW (see Fig 3.7, Fig S1.6A and S1.6D). Compound eyes small relative to head length spanning one third or less of HL. Maximum diameter of compound eyes from 0.34 to 0.38 mm. Ocelli relatively small in diameter. The two lateral ocelli widely spaced and the median ocellus always smaller in diameter than the distance between the two lateral ocelli.

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and drops off steeply posterior of the propodeal spiracle. Mesoscutum relatively short, stretching out over approximately a third of the alitrunk in lateral view. In dorsal view, posterior margin of the propodeum forms a straight line and mesonotum is broadly triangular. Propodeum not armed with spines.

Petiole in dorsal view rounded and node approximately as wide as long. Petiole approximately as wide as postpetiolar node (PI 0.97-1.12). In lateral view the petiole anterodorsally flattened and sloping downwards, and slightly longer than the postpetiole. Postpetiole rounded in lateral view without distinct nodes and subquadratic in dorsal view. (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster maryatii is endemic to Borneo and is associated with hosts of the section *Pachystemon* only (*M. havilandii*, *M. hypoleuca*, *M. motleyana*, locally *M. angulata*, rarely *M. indistincta*). The species colonizes waxy as well as non-waxy hosts, but the latter mostly in primary forest habitats, such as *M. indistincta* (Danum Valley) or *M. angulata* (Poring Hot Spring at higher elevation). Due to the small-sized queen, small workers and early onset of reproduction (when colonies comprise approximately 500 workers) such hosts in relatively dark primary forest habitats may still sustain colonies of *C. maryatii* and enable them to reach the reproductive phase. In secondary forest the small queens may be able to colonize small saplings earlier than the larger queens of the *captiosa*-group (e.g. in *M. hypoleuca*). Thus, the queens are usually found in the very first internodes developed by saplings (Feldhaar, pers. obs.). In previous publications by our group this species was referred to as *Crematogaster* msp. 7 (Fiala et al., 1999; Feldhaar et al., 2003b; Feldhaar et al., 2010).

Crematogaster decamera*-group**C. decamera* Forel, 1910*****C. roslihashimi* sp. nov.*****C. hullettii* sp. nov.****Diagnosis**

Species of the *Crematogaster decamera*-group typically have relatively small workers and queens that are dark brown in colour. The compound eyes are smaller than 0.5 mm in diameter (EL) and eye length usually comprises less than one third of head length (REL < 0.35). Diameter of the median ocellus of queens always smaller than the distance between the two lateral ocelli (OW < OD1). Propodeal spines of workers are absent in *C. decamera* and *C. roslihashimi* and only very short in *C. hullettii*. Species only colonize *Macaranga* hosts of the section *Pachystemon*.

Crematogaster decamera* ForelCrematogaster decamera* Forel, 1910*Type material examined*

Crematogaster decamera (Forel, 1910) Syntypes, 1 worker, 1 queen, Sarawak (Borneo), Malaysia (Haviland) (MHNG).

Lectotype

Queen of syntype series (upper individual on pin, designated as lectotype in collection by a blue cardboard label on pin)

CI 1.03, DPPW 0.42, DPW 0.38, EL 0.39, HL 1.32, HW 1.36, LHT 1.07, MTW 1.05, OD1 0.2, OD2 0.1, OW 0.14, PI 0.90, REL 0.30, RLEG 0.47, ROD 0.154, ROD2 0.082, SI 0.53, SL 0.71, (TL 7.8), WL 2.27

Paralectotype

Worker (upper individual on pin, designated as paralectotype in collection by a blue cardboard label on pin)

CI 0.96, DPPW 0.22, DPW 0.19, EL 0.13, HL 0.75, HW 0.72, LHT 0.66, (LPS not measured, no spines), MTW 0.44, PI 0.86, REL 0.18, RLEG 0.71, SI 0.71, SL 0.51, (TL 3.5), WL 0.94

Other material examined

Peninsula Malaysia: Belum (B. Fiala), Gombak (H. Feldhaar), Frasers Hills (B. Fiala). **Sabah (Borneo):** Poring Hot Spring (H. Feldhaar, B. Fiala). **Sarawak (Borneo):** near Lambir Hills National Park (B. Fiala, U. Moog), Matang (B. Fiala), near Mulu National Park (B. Fiala)

Worker measurements (n= 12)

CI 0.95-1.0, DPPW 0.15-0.22, DPW 0.15-0.21, EL 0.09-0.13, HL 0.51-0.75, HW 0.5-0.74, LHT 0.44-0.77, (LPS not measured, no spines), MTW 0.31-0.44, PI 0.861-1.0, REL 0.15-0.2, RLEG 0.71-0.85, SI 0.68-0.76, SL 0.36-0.51, (TL 2.4-3.6), WL 0.62-0.94

Worker description

Colour medium to dark brown with head and gaster a slightly darker shade than the alitrunk. Workers monomorphic in size. Total body length of workers 2.4 mm to 3.6 mm. Head and gaster shiny with smooth surface, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head, gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole. Head subquadratic but slightly elongated (CI ≤ 1.0), usually longer than wide and only slightly rounded on sides. Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Occipital margin straight, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from most proximate to most distal denticle. Surface of mandibles smooth, covered with short pubescent hairs. Antennae are relatively long in comparison with head width (SI 0.68-0.78; mean 0.72) and covered in short, pubescent hair. Terminal two funicular segments form a club, sometimes the terminal three segments are clubbed.

Compound eyes elliptically shaped and not protruding over margin of head in full-face view. Pronotum and mesonotum form a convex dome in profile. Anterodorsal surface of pronotum sloping downwards less steep than posterodorsal surface of mesonotum. Metanotal groove slightly notched and clearly developed, whereas promesonotal suture visible but not prominent.

Propodeal spines always absent (Fig S1.5C and S1.5D). A nodiform elevation may be present above the propodeal spiracle, albeit not very prominent. Slope of the posterior face of the propodeum similar to posterior slope of mesonotum and

approximately 45°. Legs are relatively long in comparison to alitrunk length (RLEG: 0.71-0.85). Node of petiole in dorsal view rounded and distinctly longer than wide, postpetiolar node also rounded, distinctly shorter and usually wider than node of petiole (PI 0.86-1.0). Subpetiolar process usually absent. (See Table 1 for comparative overview of worker characters.)

Queen measurements (n=14)

CI 0.96-1.05, DPPW 0.39-0.46, DPW 0.37-0.44, EL 0.39-0.45, HL 1.21-1.42, HW 1.16-1.41, LHT 0.83-1.08, MTW 0.9-1.06, OD1 0.15-0.2, OD2 0.08-0.1, OW 0.11-0.14, PI 0.88-1.0, REL 0.29-0.35, RLEG 0.4-0.47, ROD 0.119-0.155, ROD2 0.056-0.082, SI 0.48-0.57, SL 0.7-0.75, (TL 6.5-7.8), WL 2.08-2.37

Queen description

Queens relatively small with total body length from a 6.5 to 7.8 mm and uniformly dark brown in colour. Surface of head and gaster smooth and shiny, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior present on the clypeus. Mandibles relatively short, capable of closing tightly against the clypeus.

Head subquadratic, usually approximately as wide as long (CI: 0.96-1.05; mean 1.01). Sides of the head only very slightly convex, occipital margin of the head slightly concave. Occipital lobes rounded. Anterior clypeal margin slightly convex. Terminal four segments of funiculus continuously increasing in size forming an indistinct antennal club. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes small (ranging from 0.39-0.45 mm) and usually span less than one third of HL (REL 0.29-0.35). Compound eyes round to oval-shaped from lateral view and convex from dorsal view (see Fig 3.6; Fig S1.5A and S1.5B) with margins of compound eyes protruding over margin of head. Ocelli relatively small in diameter. Diameter of the median ocellus smaller than the distance between the lateral ocelli.

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and then drops off at an angle of approximately 45° posterior of the propodeal spiracle. Mesoscutum stretches out over less than half of the alitrunk in lateral view. In dorsal view, the posterior margin of the propodeum forms a straight line and the mesonotum is broadly triangular. Propodeum not armed with spines.

Petiole in dorsal view elongate and not concavely rounded on sides and always less wide than postpetiole (PI: 0.88-1.0). Petiole anterodorsally flattened in lateral view and sloping downwards and distinctly longer than the postpetiole. Postpetiole round in dorsal view. (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster decamera Forel has a large distributional range and occurs in all geographic regions of the *Macaranga-Crematogaster* association (Peninsula Malaysia, Sumatra, Borneo). Queens of *Crematogaster decamera* only colonize saplings, and colonies have an early onset of reproduction. On Peninsula Malaysia several colonies were found that had turned secondarily polygynous or at least contained several mated queens.

This species colonizes glaucous hosts of the section *Pachystemon* only (*M. beccariana*, *M. constricta*, *M. havilandii*, *M. hypoleuca*, *M. motleyana*). It can be distinguished from all other species based on workers only by the complete lack of propodeal spines. Queens from Peninsula Malaysia tend to be smaller than from Borneo, with the largest individuals observed in Sarawak (e.g. mean HW: 1.22 in Peninsula Malaysia (n=6) and 1.35 in Sarawak (n=4)). In earlier publications by our group this species was referred to as *Crematogaster* morphospecies 6 (Fiala et al., 1999).

Crematogaster hullettii sp. nov.

urn:lsid:zoobank.org:act:D18396CF-27F4-4981-A463-1B308F723E2B

Holotype

Queen (to be deposited in SMNK, provisional specimen number HF99-Mhull1-Q) (H. Feldhaar) on 6.7.1999 in Genting Highlands (Bunga Buah) from *Macaranga hullettii* (deposited in SMNK).

CI 1.01, DPPW 0.45, DPW 0.43, EL 0.42, HL 1.28, HW 1.29, LHT 0.95, MTW 1.13, OD1 0.15, OD2 0.06, OW 0.13, PI 0.95, REL 0.33, RLEG 0.41, ROD 0.12, ROD2 0.049, SI 0.51, SL 0.66, (TL 6.5), WL 2.35

Paratype

Worker collected from the same colony (to be deposited in SMNK, provisional specimen number HF99-Mhull1-W)

CI 1.0, DPPW 0.18, DPW 0.19, EL 0.11, HL 0.65, HW 0.65, LHT 0.43, LPS 0.082, MTW 0.39, PI 1.04, REL 0.17, RLEG 0.59, SI 0.59, SL 0.39, (TL 2.5), WL 0.73

Additional material examined

Peninsula Malaysia: Fraser's Hill (R. Kern, B. Fiala), Genting Highlands (H. Feldhaar, B. Fiala), **Sarawak (Borneo):** near Lambir Hills National Park (B. Fiala), near Mulu National Park (B. Fiala), Niah (U. Maschwitz), Sibul (B. Fiala)

Worker measurements (n=9)

CI 0.96-1.03, DPPW 0.16-0.21, DPW 0.17-0.21, EL 0.11-0.13, HL 0.57-0.7, HW 0.58-0.69, LHT 0.39-0.47, LPS 0.062-0.09, MTW 0.34-0.41, PI 1.0-1.15, REL 0.17-0.19, RLEG 0.58-0.62, SI 0.57-0.62, SL 0.35-0.4, (TL 2.4-3.0), WL 0.66-0.8

Worker description

Colour medium to dark brown with head and gaster being a slightly darker shade than the alitrunk. Workers monomorphic in size. Total body length of workers 2.4 mm to 3.0 mm. Head, alitrunk and gaster shiny with smooth surface, only mesonotum slightly less shiny. All body parts bear appressed pubescent hairs. Long flexuous setae present on head, gaster and abdomen: on head only few in frons, on gaster more on the posterior margins of tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole. Head subquadratic and approximately as wide as long (CI 0.96-1.03) usually being only slightly rounded on sides. Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Occipital margin slightly concave, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from most proximate to most distal denticle. Surface of mandibles smooth, covered with short pubescent hairs. Antennae relatively short in comparison to head width (SI 0.57-0.62; mean SI: 0.6) and covered in short pubescent hair. Segments of the funiculus continuously increasing in size, with the terminal three funicular segments forming a club.

Compound eyes elliptically-shaped and not protruding over margin of head in full-face view. Pronotum and mesonotum form a convex dome in profile. Anterodorsal surface of pronotum sloping downwards less steep than posterodorsal surface of mesonotum. Metanotal groove slightly notched and clearly developed, whereas the promesonotal suture is visible but not prominent.

Propodeal spines are present but short. The tip of the spine protrudes only slightly over the posterior margin of the propodeal spiracle (Fig S1.3C and S1.3D). Slope of the posterior face of the propodeum similar to posterior slope of mesonotum and approximately 45°. Legs relatively short in comparison to alitrunk length (RLEG: 0.58-0.62). Node of petiole and postpetiole in dorsal view rounded. Petiole only slightly longer and always as wide as or wider than postpetiole (PI 1.0-1.15). Subpetiolar process usually absent. (See Table 1 for comparative overview of worker characters.)

Queen measurements (n=16)

CI 0.96-1.07, DPPW 0.41-0.48, DPW 0.39-0.47, EL 0.39-0.47, HL 1.18-1.29, HW 1.15-1.29, LHT 0.84-1.04, MTW 0.88-1.23, OD1 0.12-0.17, OD2 0.06-0.09, OW 0.11-0.13, PI 0.95-1.03, REL 0.32-0.4, RLEG 0.39-0.46, ROD 0.09-0.13, ROD2 0.049-0.08, SI 0.51-0.55, SL 0.63-0.68, (TL 6.2-7.0), WL 1.92-2.36

Queen description

Queens relatively small with total body length 6.2 to 7.0 mm and uniformly dark brown in colour. Surface of head and gaster smooth and shiny, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent

hairs. Long, flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior are present on the clypeus. Mandibles relatively short, capable of closing tightly against the clypeus.

Head usually approximately as wide as or wider than long (CI: 0.96-1.07; mean 1.01). Head wider behind the compound eyes than anterior closer to the clypeus. Sides of the head straight, occipital margin of the head slightly concave. Occipital lobes rounded. Anterior clypeal margin slightly convex. Terminal four segments of funiculus continuously increasing in size forming an antennal club. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes small (0.39-0.47 mm) and usually span approximately one third of HL (REL 0.32-0.4). Compound eyes oval in shape from lateral view and convex from dorsal view (see Fig 3.5; Fig S1.3A and S1.3B) with margins of compound eyes protruding over margin of head. Ocelli relatively small in diameter. Diameter of the median ocellus smaller than the distance between the lateral ocelli.

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and then drops off at an angle of approximately 45° posterior of the propodeal spiracle. Mesoscutum stretches out over less than half of the alitrunk in lateral view. In dorsal view, the posterior margin of the propodeum forms a straight line and the mesonotum is broadly triangular. Propodeum not armed with spines.

Petiole in dorsal view broadly rounded on sides and approximately as wide as postpetiole (PI: 0.95-1.03). In lateral view the petiole anterodorsally flattened and sloping downwards and slightly longer than the postpetiole. Postpetiole round in dorsal view. (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster hullettii occurs on Peninsula Malaysia and in Sarawak. On Peninsula Malaysia the species seems to be restricted to higher elevation sites, e.g. Genting Highlands or Fraser's Hill above approximately 500m where it mainly inhabits *M. hullettii* as well as *M. bancana*, which ceases to occur with increasing elevation. In Sarawak (Borneo) it was mainly found in lowland sites (but higher elevational regions were little sampled there). Queens on Borneo also colonize only seedlings of non-waxy host species of the section *Pachystemon* (*M. angulata*, *M. bancana*, *M. hullettii*, *M. petanostyla*, *M. umbrosa*). In Quek et al. (2007) the lineages from the two regions are sister groups, i.e. monophyletic but with some genetic differentiation. Two samples contained in the phylogeny based on mitochondrial DNA and collected in eastern Sarawak cluster with samples of *C. claudiae* from Sabah and thus surprisingly with the *Crematogaster captiosa*-subgroup (Feldhaar et al., 2010). However, based on morphological measurements these samples clearly fall within *C. hullettii*. As hybridization events or introgression of mitochondrial

DNA seem to occur in this species complex (2.5% hybrid individuals were found among two species of the *C. captiosa*-subgroup in one area; Feldhaar et al. 2008), we place a stronger emphasis on the morphological data. In former publications by our group this species was referred to as *Crematogaster* msp. 3 (Fiala et al., 1999; Feldhaar et al., 2003a; Feldhaar et al., 2010).

***Crematogaster roslihashimi* sp. nov.**

urn:lsid:zoobank.org:act:96E181ED-FEC7-4D83-973E-E34EFBBE3735

Holotype

Queen (to be deposited in SMNK, provisional specimen number 22UM-Q) (U. Maschwitz) on 2.12.1996 in Kuantan from *Macaranga constricta*

CI 0.84, DPPW 0.45, DPW 0.45, EL 0.3, HL 1.13, HW 0.95, LHT 0.81, MTW 0.83, OD1 0.11, OD2 0.05, OW 0.07, PI 1.0, REL 0.27, RLEG 0.43, ROD 0.12, ROD2 0.05, SI 0.6, SL 0.57, (TL 5.8), WL 1.9

Paratype

Worker collected from the same colony (to be deposited in SMNK, provisional specimen number 22UM-W).

CI 0.90, DPPW 0.18, DPW 0.19, EL 0.09, HL 0.61, HW 0.55, LHT 0.51, (LPS not measured, no spines), MTW 0.34, PI 1.06, REL 0.14, RLEG 0.72, SI 0.74, SL 0.41, (TL 2.8), WL 0.71

Additional material examined

Peninsula Malaysia: Kuantan (U. Maschwitz) [2 samples: one sample with a single queen only and in the second sample a series of workers and queens]

Worker measurements (n=3)

CI 0.90-0.91, DPPW 0.18-0.19, DPW 0.19-0.20, EL 0.09-0.1, HL 0.61-0.65, HW 0.55-0.59, LHT 0.5-0.52, (LPS not measured, no spines), MTW 0.34-0.36, PI 1.02-1.07, REL 0.14-0.15, RLEG 0.71-0.73, SI 0.69-0.74, SL 0.41, (TL 2.8-2.9), WL 0.69-0.73

Description of worker

Colour uniformly light to medium brown. Workers monomorphic in size. Total body length of workers 2.8 mm to 2.9 mm, but this is a measurement from a single mature colony only. Workers from incipient colonies are expected to be smaller. Head and gaster shiny with smooth surface, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole. Head distinctly longer than wide and only slightly rounded on sides (CI: 0.90-0.91). Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Clypeus with a small median node. Occipital margin slightly concavely

rounded, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from most proximate to most distal denticle. Surface of mandibles smooth, covered with short pubescent hairs. Antennae relatively long in comparison to head width (SI 0.69-0.74) and densely covered in short pubescent hair. Terminal two funicular segments forming a club.

Compound eyes elliptically-shaped and not protruding over margin of head in full-face view. Pronotum and mesonotum form a convex dome in profile. Anterodorsal surface of pronotum sloping downwards as steep as posterodorsal surface of mesonotum. Metanotal groove slightly notched and clearly developed, whereas the promesonotal suture barely visible and not prominent.

Propodeal spines always absent. A nodiform elevation may be present above the propodeal spiracle, albeit not very prominent. Slope of the posterior face of the propodeum similar to posterior slope of mesonotum and approximately 45°.

In dorsal view petiole and postpetiole approximately the same width or petiole slightly broader. Anterodorsal surface of petiole broadly flattened. Both petiole and postpetiole round in dorsal view. Subpetiolar process usually absent. Petiole and postpetiole wide in comparison to MTW (MTW/DPW: <1.8; in all other species >1.8 and usually larger than 1.9). (See Table 1 for comparative overview of worker characters.)

Queen measurements (n=4)

CI 0.84-0.89, DPPW 0.46-0.5, DPW 0.45-0.48, EL 0.3-0.32, HL 1.10-1.15, HW 0.95-1.02, LHT 0.81, MTW 0.8-0.87, OD1 0.11-0.16, OD2 0.05-0.08, OW 0.07-0.09, PI 0.96-1.0, REL 0.27-0.28, RLEG 0.43-0.46, ROD 0.12-0.17, ROD2 0.05-0.08, SI 0.57-0.64, SL 0.57-0.61, (TL 5.8-6.1), WL 1.73-1.9

Description of queen

Queens small, 5.8 to 6.1 mm in total body length and uniformly medium to dark brown in colour. Surface of head, gaster and alitrunk not structured but densely covered in pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior present on the clypeus. Mandibles relatively short, capable of closing tightly against the clypeus.

Head distinctly longer than wide (CI: 0.84-0.89). Sides of the head straight and not becoming narrow towards the clypeus. Occipital margin of the head convex. Occipital lobes rounded. Anterior clypeal margin slightly convex. Terminal four segments of funiculus forming a distinct antennal club. Funiculus covered densely in pubescent hair so that borders between antennal segments barely visible. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes only slightly oval-shaped from lateral view and maximum head width with compound eyes only slightly wider than HW (see Fig 3.8; Fig S1.8A and S1.8B).

Compound eyes small relative to head length spanning one third or less of HL (REL 0.27-0.28). Maximum diameter of compound eyes 0.3 to 0.32 mm. Ocelli relatively small in diameter. The two lateral ocelli widely spaced and the median ocellus always smaller in diameter than the distance between the two lateral ocelli.

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and then drops off steeply posterior of the propodeal spiracle. Mesoscutum relatively short, stretching out over approximately a third of the alitrunk in lateral view. In dorsal view, the posterior margin of the propodeum forms a straight line and the mesonotum is broadly triangular. Propodeum not armed with spines.

Petiole in dorsal view rounded and node approximately as wide as long. Petiole slightly less wide than postpetiole ($PI \leq 1.0$). In lateral view the petiole and postpetiole nodiform. Petiole and postpetiole broad in relation to MTW (MTW/DPW 1.69-1.78; in all other *Macaranga*-associated *Decacrema* MTW/DPW rarely < 2.0). (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster roslihashimi is a very rare species endemic to a small region on the East coast of Peninsula Malaysia (near Kuantan) and is was found on only two wax-covered hosts of the section *Pachystemon* (*M. constricta*, *M. hypoleuca*). The species is closely related to *Crematogaster decamera* based on mitochondrial DNA as well as nuclear DNA (EF-1a) (Feldhaar et al., 2003b; Feldhaar et al., 2010). The species was formerly called *Crematogaster* msp. 9 in publications by our group (Fiala et al., 1999).

Crematogaster (Decacrema) captiosa-group

C. borneensis André, 1896

C. linsenmairi sp. nov.

C. captiosa Forel, 1911

C. claudiae sp. nov.

Diagnosis

Species of the *Crematogaster (Decacrema) captiosa*-subgroup have relatively large queens with large compound eyes with EL > 0.5 mm (except for *C. claudiae* (EL 0.45 – 0.5 mm) whose queens are generally smaller than the queens of the other species within this group). Queens are medium to light brown in colour. Workers of *C. borneensis*, *C. linsenmairi* and *C. captiosa* possess long and acute propodeal spines.

Crematogaster claudiae has an intermediate morphology of species belonging to the *captiosa* and the *decamera*-group. Queens are intermediate in size (HW, HL, WL and EL) and workers possess none or only very short propodeal spines in contrast to the long and acute propodeal spines of workers of the other three species in the *captiosa*-group. As it clusters with species of the *captiosa* group in molecular phylogenies based on

mitochondrial DNA (Feldhaar et al., 2003a, Feldhaar et al., 2010) and is known to hybridize with *C. captiosa* locally (Feldhaar et al., 2010, we have placed this species into this group.

Crematogaster borneensis André 1896

= *Crematogaster borneensis* subsp. *capax* Forel, 1911

= *Crematogaster borneensis* subsp. *hosei* Forel, 1911

= *Crematogaster borneensis* subsp. *sembilana* Forel, 1911

= *Crematogaster borneensis* var. *macarangae* Viehmeyer, 1916

Type material examined

C. borneensis André. *Lectotype* and *Paralectotype*, 2 workers (1 worker designated as *lectotype* with label on pin), Borneo (André) (MNHN).

Lectotype worker

CI 0.96, DPPW 0.19, DPW 0.19, EL 0.13, HL 0.67, HW 0.64, LHT 0.49, LPS 0.101, MTW 0.4, PI 1.0, REL 0.2, RLEG 0.63, SI 0.71, SL 0.45, (TL 2.8), WL 0.77

Crematogaster borneensis subsp. *capax* Forel, 1911, 1 worker 1 alate queen, Borneo (Sarawak) (Haviland) (MHNG)

Crematogaster borneensis subsp. *hosei* Forel, 1911, 1 worker 1 alate queen, Borneo (Hose) (MHNG)

Crematogaster borneensis subsp. *sembilana* Forel, 1911, 2 alate queens, Negri Sembilan Malacca, Peninsula Malaysia (R. Martin) (MHNG); 1 alate queen Negri Sembilan, Malacca, Peninsula Malaysia (R. Martin) from collection Viehmeyer (ZMBH). [Dealate queen from the same series is definitely a different species; posterior margin of the head strongly concavely indented; queen of *Crematogaster cephalotes*?]

[*Crematogaster borneensis* var. *macarangae* Viehmeyer, 1916, Singapore, worker described; Type material lost? Included in catalogue of ZMBH but not found in collection.]

Additional material examined

Peninsula Malaysia: Cukai (U. Maschwitz), Gombak (H. Feldhaar), Kuantan (U. Maschwitz), Maran (U. Maschwitz), Mersing (B. Fiala), Rawang (H. Feldhaar); **Sabah (Borneo):** Bukit Taviu (H. Feldhaar), Deramakot (B. Fiala), Poring Hot Spring (H. Feldhaar), Tawau (H. Feldhaar), Telupid (H. Feldhaar), **Sarawak (Borneo):** Lambir Hills (B. Fiala), Santubong (A. Jakob).

Worker measurements (n=11)

CI 0.92-0.97, DPPW 0.18-0.25, DPW 0.19-0.25, EL 0.12-0.17, HL 0.67-0.97, HW 0.63-0.92, LHT 0.5-0.72, LPS 0.104-0.169, MTW 0.39-0.51, PI 1.01-1.14, REL 0.17-0.2, RLEG 0.62-0.71, SI 0.64-0.74, SL 0.46-0.6, (TL 2.8-3.9), WL 0.82-1.03

Description of worker

Colour light to reddish brown (large workers) with head and gaster being a slightly darker shade than the alitrunk. Workers monomorphic in size. Total body length of workers 2.5 mm to 3.2 mm. Head and gaster shiny with smooth

surface, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole.

Head subquadratic but slightly elongated, always being longer than wide (CI<0.97) and only slightly rounded on sides. Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Occipital margin slightly concavely rounded, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from most proximate to most distal denticle. Surface of mandibles smooth, covered with short pubescent hairs.

Antennae relatively long in comparison to head width (SI 0.64-0.74; mean 0.68) and covered in short pubescent hair. Terminal three funicular segments form a club, sometimes only the terminal two segments.

Compound eyes elliptically shaped and not protruding over margin of head in full-face view. Pronotum and mesonotum form a convex dome in profile, sometimes slightly flattened dorsally. Anterodorsal surface of pronotum sloping downwards slightly steeper than or as steep as posterodorsal surface of mesonotum. Metanotal groove slightly notched and clearly developed, whereas the promesonotal suture visible but not prominent.

Propodeal spines in lateral view strong and acute. Tip of the spines always protruding over posterior margin of the propodeal spiracle and diverging very slightly. Dorsal face of the propodeum confluent with the horizontal spines or spines bent slightly upwards. Slope of the posterior face of the propodeum similar to posterior slope of mesonotum (Fig S1.1C and S1.1D).

In dorsal view petiole always wider than postpetiole (PI: 1.01-1.14). Node of petiole in dorsal view longer than wide and considerably rounded, dorsal surface flat. In profile the anterior face of the petiolar node shorter than the posterior so that the dorsal surface slopes downwards anteriorly. Dorsal surface of the postpetiolar node in profile rounded. Subpetiolar process usually absent. (See Table 1 for comparative overview of worker characters.)

In the original description of the worker of *C. borneensis* by André (1896) he described the worker as having propodeal spines twice as long as their base. Forel (1911) writes that he has had personal contact with M. André and has been told that this was indeed an error made in the original description as spines are shorter (see above).

Queen measurements (n=27)

CI 0.88-0.96, DPPW 0.49-0.61, DPW 0.44-0.57, EL 0.50-0.60, HL 1.31-1.50, HW 1.18-1.42, LHT 1.01-1.18, MTW 0.96-1.21, OD1 0.17-0.23, OD2 0.07-0.10, OW 0.13-0.17, PI 0.87-1.0, REL 0.36-0.43, RLEG 0.42-0.49, ROD 0.13-0.17, ROD2 0.054-0.077, SI 0.53-0.6, SL 0.7-0.77, (TL 7.0-8.5), WL 2.23-2.7

Description of queen

Queens large, 7.0 to 8.5 mm in total body length and uniformly light to medium brown in colour. Surface of head and gaster smooth and shiny, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior present on the clypeus. Mandibles relatively short, capable of closing tightly against the clypeus.

Head elongate, always longer than wide (CI: 0.88-0.96; mean 0.91). Sides of the head only very slightly convex, occipital margin of the head straight to slightly convex. Occipital lobes strongly rounded. Anterior clypeal margin slightly convex. Terminal three segments of funiculus continuously increasing in size forming an antennal club that is not very distinct. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes oval-shaped from lateral view and only slightly convex from dorsal view (see Fig 3.1; Fig S1.1A and S1.1B). Compound eyes large relative to head length spanning more than one third of HL. Maximum diameter of compound eyes 0.5 to 0.6 mm. Maximum width of head including compound eyes maximally 10% wider than HW. Ocelli relatively small in diameter. The two lateral ocelli widely spaced and the median ocellus always smaller in diameter than the distance between the two lateral ocelli.

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and then drops off steeply posterior of the propodeal spiracle. Mesoscutum long, stretching out over approximately half of the alitrunk in lateral view. In dorsal view, the posterior margin of the propodeum forms a straight line and the mesonotum broadly triangular. Propodeum not armed with spines.

Node of petiole in dorsal view roughly rectangular, anterior side broader than posterior one. Petiolar node quadrangular in shape in dorsal view and not as wide as postpetiolar node (PI<1.0). In lateral view the petiole is anterodorsally flattened and sloping downwards and is slightly longer than the postpetiole. Postpetiole round in dorsal and lateral view without distinct nodes. (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster borneensis André has a large range and occurs in all geographic regions of the *Macaranga-Crematogaster* association (Malay Peninsula, Sumatra, and Borneo). It is the most generalised species with respect to host plant use. Queens colonize mostly waxy hosts. However, hosts that develop a slight wax-coating only as mature trees will also be colonized secondarily by this species after having been abandoned due to death of the original colony (e.g. *M. indistincta*). In this case queens of *C. borneensis*

are found in the tip of branches of abandoned mature hosts. *Crematogaster borneensis* is frequently found on hosts of the section *Pachystemon* (*M. aetheadenia*, *M. glandibracteolata*, *M. griffithiana*, *M. lamellata*, *M. motleyana*, *M. hypoleuca*, *M. indistincta*, (in the latter two mainly in larger trees, rarely in saplings) as well as the section *Pruinosae* (*M. hosei*, *M. pearsonii*, *M. puberula*, *M. pruinosa*). Virgin alate queens have been found to be parasitized by the phorid fly *Trucidophora feldhaarae* while still inside the nest within the hollow stem of their host plant on Peninsula Malaysia (Maschwitz et al., 2006).

In former publications we have referred to this species as *Crematogaster* msp. 1 (Fiala et al. 1999).

Crematogaster linsenmairi sp. nov.

urn:lsid:zoobank.org:act:A2B1ED89-6A3A-468A-8081-4C6ECB0CCEBE

Crematogaster borneensis subsp. *hosei* var. *tubuli* (Viehmeyer, 1916), Syntypes, 2 workers, Singapore (Overbeck) (ZMBH) [unavailable name]

Type material examined

Syntype worker measurements (n=2)

CI 0.94-0.97, DPPW 0.19, DPW 0.2-0.21, EL 0.15, HL 0.69-0.72, HW 0.68, SL 0.49, MTW – (not fully visible), LHT 0.53-0.76, SI 0.71, LPS 0.13, PI 1.05-1.08, REL 0.2-0.21, RLEG 0.71, (TL 2.8) WL 0.82-0.83

Additional material examined

Peninsula Malaysia: Belum (B. Fiala), Gombak (H. Feldhaar), Perak (B. Fiala), Maran (U. Maschwitz), Pulau Lingga (R. Kern), **Sabah (Borneo):** Danum Valley (H. Feldhaar), Deramakot (B. Fiala), Poring Hot Spring (B. Fiala, H. Feldhaar). **Sarawak (Borneo):** Bau (B. Fiala), near Lambir Hills National Park (B. Fiala), Sibul (B. Fiala)

Worker measurements (n=13)

CI 0.94-1.02, DPPW 0.16-0.24, DPW 0.17-0.25, EL 0.13-0.17, HL 0.66-0.86, HW 0.63-0.86, LHT 0.53-0.76, LPS 0.81-1.181, MTW 0.38-0.53, PI 0.93-1.08, REL 0.17-0.21, RLEG 0.68-0.79, SI 0.68-0.76, SL 0.47-0.59, (TL 2.7-3.8), WL 0.82-1.07

Description of worker

Workers brown in colour (large workers) with head and gaster a slightly darker shade than the alitrunk. Workers monomorphic in size. Total body length of workers 2.7 to 3.8 mm. Head and gaster shiny with smooth surface, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more

on the posterior margins of tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole.

Head subquadratic but slightly elongated, usually being longer than wide (mean CI: 0.97) and only slightly convex on sides. Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Occipital margin slightly concavely rounded, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from most proximate to most distal denticle. Surface of mandibles smooth, covered with short pubescent hairs.

Antennae are relatively long in comparison to head width (SI 0.68-0.76; mean 0.72) and covered in short pubescent hair. Terminal three funicular segments form a club, sometimes only the terminal two segments.

Compound eyes elliptically shaped and not protruding over margin of head in full-face view. Pronotum and mesonotum form a convex dome in profile, sometimes slightly flattened dorsally. Anterodorsal surface of pronotum sloping downwards slightly steeper than or as steep as posterodorsal surface of mesonotum. The metanotal groove is slightly notched and clearly developed, whereas the promesonotal suture is visible but not prominent.

Propodeal spines in lateral view strong and acute. Tip of the spines always protruding over posterior margin of the propodeal spiracle and are diverging very slightly. Dorsal face of the propodeum confluent with the horizontal spines or spines bent slightly upwards. Slope of the posterior face of the propodeum similar to posterior slope of mesonotum (Fig S1.2c and S1.2D).

In dorsal view petiole approximately as wide as postpetiole (PI: 0.96-1.08). Node of petiole in dorsal view longer than wide and considerably rounded, dorsal surface flat. In profile the anterior face of the petiolar node shorter than the posterior so that the dorsal surface slopes downwards anteriorly. Dorsal surface of the postpetiolar node in profile rounded. Subpetiolar process usually absent. (See Table 1 for comparative overview of worker characters.)

Queen measurements (n=28)

CI 0.93-1.04, DPPW 0.48-0.62, DPW 0.46-0.59, EL 0.58-0.71, HL 1.34-1.61, HW 1.30-1.62, LHT 1.06-1.37, MTW 1.13-1.34, OD1 0.11-0.2, OD2 0.02-0.08, OW 0.16-0.21, PI 0.89-1.04, REL 0.39-0.48, RLEG 0.42-0.49, ROD 0.07-0.14, ROD2 0.018-0.057, SI 0.54-0.61, SL 0.74-0.88, (TL 6.8-9.3), WL 2.45-2.9

Description of queen

Queens are the largest of all *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group); with total body length ranging from approximately 6.8 to 9.3 mm and uniformly medium brown in colour. Surface of head and gaster smooth and shiny, alitrunk is slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs.

Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior are present on the clypeus. Mandibles relatively short, capable of closing tightly against the clypeus.

Head subquadratic, being usually approximately as wide as long (CI: 0.93-1.04; mean 0.99). Sides of the head only very slightly convex, occipital margin of the head slightly concave. Occipital lobes rounded. Anterior clypeal margin slightly convex. Terminal 3 segments of funiculus continuously increasing in size forming an indistinct antennal club. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes large (rarely below 0.6 mm) and span more than one third of HL. Compound eyes oval-shaped from lateral view and convex from dorsal view (see Fig 3.2; Fig S1.2A and S1.2B) with margins of compound eyes protruding distinctly over margin of head. Maximum width of head including compound eyes between 8 to 16% wider than HW. Ocelli relatively large in diameter. Diameter of median ocellus larger than distance between the lateral ocelli.

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and then drops off at an angle of approximately 45° posterior of the propodeal spiracle. Mesoscutum long, stretching out over approximately half of the alitrunk in lateral view. In dorsal view, the posterior margin of the propodeum forms a straight line and the mesonotum is broadly triangular. Propodeum not armed with spines.

Node of petiole in dorsal view roughly rectangular, anterior side broader than posterior one. Petiolar node round in shape in dorsal view and often, but not always not as wide as postpetiolar node. In lateral view the petiole anterodorsally flattened and sloping downwards and slightly longer than the postpetiole. Postpetiole trapezoid-shaped in dorsal view and broader anterior than posterior. Petiole and postpetiole do not have distinct nodes. (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster linsenmairi is the largest species of the *Macaranga*-associated *Crematogaster* (*Crematogaster captiosa*-subgroup) species and is found over the whole distributional range of the association. It colonizes mainly hosts of the section *Pruinosae* whose stems need to be actively excavated and have a waxy cover (*M. hosei*, *M. pearsonii*, *M. pruinosa* but also on non-waxy *M. puberula*). It is also found very rarely on hosts of the section *Pachystemon* (e.g., *M. aetheadenia*, *M. kingii*, *M. lamellata*, and *M. motleyana*) in areas where the usual host species are absent (Fiala et al., 1999).

In parts of Borneo (Sabah) foundress association of unrelated individuals of this species have been found in areas with strong nest site limitation. These colonies stay polygynous even after emergence of workers and several queens may

produce offspring (Feldhaar et al., 2005). Virgin alate queens have been found to be parasitized by the phorid fly *Trucidophora feldhaarae* while still inside the nest within the hollow stem of their host plant on Peninsula Malaysia (Maschwitz et al., 2006). In former publications by our group this species has been referred to as *Crematogaster* msp. 2 (Fiala et al., 1999; Feldhaar et al., 2003a; Feldhaar et al., 2005; Feldhaar et al., 2010).

Crematogaster captiosa Forel, 1911

- = *Crematogaster borneensis* var. *harpypia* Forel, 1911
- = *Crematogaster borneensis* var. *insulsa* Forel, 1911
- = *Crematogaster borneensis* subsp. *sylvania* Forel, 1911
- = *Crematogaster borneensis* subsp. *novem* Forel, 1911

Type material examined

Crematogaster captiosa Forel. Holotype, 1 worker Sarawak (Borneo), Malaysia (Haviland) (MHNG). [In addition 1 queen; however in the original description of Forel (1911) only 1 worker is mentioned but no queen; collection data given on the same label.]

Crematogaster borneensis var. *harpypia* Forel, 1911. Syntypes, 1 queen, 1 worker; Sarawak, Borneo (Haviland; from unspecified *Macaranga*) (MHNG); 1 alate queen, 1 worker, Borneo (Haviland; from unspecified *Macaranga*) (ZMBH)

Crematogaster borneensis var. *insulsa* Forel, 1911. Syntypes, 1 alate queen, 1 worker, Borneo (Hose) (MHNG); 1 worker, Borneo (Hose) (ZMBH).

Crematogaster borneensis subsp. *sylvania* Forel, 1911. Syntypes, 1 queen, 1 worker, Sarawak, Borneo (Haviland; from unspecified *Macaranga*) (MHNG); 1 worker, Sarawak, Borneo (Haviland) (ZMBH).

Crematogaster borneensis subsp. *novem* Forel, 1911. Syntypes, 1 worker, 2 alate queens, Sarawak, Borneo (Haviland; from unspecified *Macaranga*) (MHNG).

Holotype worker

CI 0.97, DPPW 0.19, DPW 0.2, EL 0.1-0.15, HL 0.61, HW 0.6, LHT 0.4, LPS 0.095, MTW 0.35, PI 1.07, REL 0.18, RLEG 0.59, SI 0.55, SL 0.33, (TL 2.5), WL 0.68

Additional material examined

Peninsula Malaysia: Belum (B. Fiala), Fraser's Hill (B. Fiala), Gombak (H. Feldhaar, U. Maschwitz), Kuantan (U. Maschwitz), Pulau Lingga (R. Kern), Pulau Bintang (R. Kern), **Sabah (Borneo):** Crocker Range (B. Fiala), Danum Valley (H. Feldhaar, B. Fiala), Deramakot (B. Fiala), Poring Hot Spring (H. Feldhaar, A. Meenken), **Sarawak (Borneo):** Bau (B. Fiala), near Lambir Hills National Park (B. Fiala), Sibul (B. Fiala)

Worker measurements (n=16)

CI 0.92-0.98, DPPW 0.15-0.22, DPW 0.16-0.23, EL 0.1-0.15, HL 0.53-0.73, HW 0.51-0.7, LHT 0.36-0.57, LPS 0.05-1.08, MTW 0.3-0.45, PI 1.02-1.13, REL 0.17-0.21, RLEG 0.61-0.69, SI 0.57-0.62, SL 0.31-0.45, (TL 2.3-3.3), WL 0.57-0.82

Description of worker

Colour light to reddish brown (large workers) with head and gaster being a slightly darker shade than the alitrunk. Workers monomorphic in size. Total body length of workers 2.3 to 3.3 mm. Head and gaster shiny with smooth surface, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head, gaster and abdomen: on head especially in frons on gaster more on the posterior margins of tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole.

Head subquadratic but slightly elongated, always being longer than wide (CI<0.98) and only slightly convex on sides. Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Occipital margin slightly concavely rounded, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from posterior (close to clypeus) to anterior. Surface of mandibles smooth, covered with short pubescent hairs.

Antennae relatively short in comparison to head width (SI 0.55-0.62; mean 0.61) and covered in short pubescent hair. Terminal three funicular segments form a club.

Compound eyes elliptically shaped and not protruding over margin of head in full-face view.

Pronotum and mesonotum form a convex dome in profile. Anterodorsal surface of pronotum sloping downwards as steep as posterodorsal surface of mesonotum. Metanotal groove slightly notched and clearly developed, whereas the promesonotal suture visible but not prominent.

Propodeal spines in lateral view usually strong and acute. Tip of the spines always protruding over posterior margin of the propodeal spiracle. Dorsal face of the propodeum confluent with the horizontal spines or spines bent slightly upwards. Slope of the posterior face of the propodeum similar to posterior slope of mesonotum and approximately 45° or slightly less steep (Fig S1.4C and S1.4D).

In dorsal view petiole always wider than postpetiole (PI: 1.02-1.13). Node of petiole in dorsal view longer than wide and considerably rounded, dorsal surface flat. In profile the anterior face of the petiolar node flattened and sloping downwards anteriorly and petiole longer than postpetiole. Dorsal surface of the postpetiolar node in profile rounded, lateral nodes visible. Subpetiolar process usually absent. (See Table 1 for comparative overview of worker characters.)

Queen measurements (n=32)

CI 0.90-1.02, DPPW 0.44-0.58, DPW 0.41-0.55, EL 0.55-0.65, HL 1.23-1.47, HW 1.21-1.47, LHT 0.82-1.18, MTW 0.86-1.21, OD1 0.11-0.21, OD2 0.03-0.08, OW 0.16-0.22, PI 0.92-1.10, REL 0.38-0.48, RLEG 0.42-0.49, ROD 0.1-0.17, ROD2 0.024-0.061, SI 0.52-0.59, SL 0.66-0.81, (TL 6.9-8.0), WL 2.17-2.68

Description of queen

Queens are large, 6.9 to 8.0 mm in total body length and uniformly light to medium brown in colour. Surface of head and gaster smooth and shiny, alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior are present on the clypeus. Mandibles relatively short, capable of closing tightly against the clypeus.

Head subquadratic, always slightly longer than wide (CI: 0.90-1.02; mean 0.96). Sides of the head straight and head behind compound eyes as wide as in front of compound eyes. Occipital margin of the head slightly concave. Occipital lobes strongly rounded. Anterior clypeal margin slightly convex. Terminal four segments of funiculus continuously increasing in size forming an indistinct antennal club. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes oval-shaped from lateral view and convex from dorsal view, with the margin of the compound eyes protruding from the sides of the head (see Fig 3.3; Fig S1.4A and S1.4B). Compound eyes large relative to head length spanning more than one third of HL (REL 0.38-0.48). Maximum diameter of compound eyes usually from 0.55 to 0.65 mm (mean EL: 0.6 mm). Maximum width of head including compound eyes usually at least 10% wider than HW (mean 13%). Ocelli relatively large in diameter. Diameter of median ocellus (OW) always larger than distance between lateral ocelli (OD1).

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and then drops off at an angle of approximately 45° posterior of the propodeal spiracle. Mesoscutum long, stretching out over approximately half of the alitrunk in lateral view. In dorsal view, the posterior margin of the propodeum forms a straight line and the mesonotum broadly triangular. Propodeum not armed with spines.

Node of petiole and postpetiole in dorsal view rounded and approximately the same width (mean PI: 0.98), but variable (PI range: 0.93-1.10). In lateral view the petiole anterodorsally flattened and sloping downwards and slightly longer than the postpetiole. Postpetiole round in dorsal and lateral view without distinct nodes. (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster captiosa Forel is a very widespread species occurring over the whole distributional range of the *Crematogaster-Macaranga* association (Peninsula Malaysia, Sumatra, and Borneo). The species has a wide host-range but is usually restricted to non-waxy hosts of the section *Pachystemon* (*M. angulata*, *M. bancana*, *M. calcicola*, *M.*

glandibracteolata, *M. hullettii*, *M. indistincta*, *M. petanostyla*, *M. trachyphylla*, *M. umbrosa*, the non-waxy form of *M. aetheadenia*, and the thinly wax-covered *M. glandibracteolata* as an exception of a glaucous host species).

Queens colonize seedlings as well as the tips of mature hosts that have been abandoned due to the loss of the original colony. On Peninsula Malaysia secondarily polygynous colonies that contained several queens have been found locally in the Gombak area.

In former publications by our group this species was referred to as *Crematogaster* msp. 4 (Fiala et al., 1999; Feldhaar et al., 2003a; Feldhaar et al., 2003b).

Crematogaster claudiae sp. nov.

urn:lsid:zoobank.org:act:3DD21EFA-093D-4CFF-AD78-BBDFB4664676

Holotype

Queen (to be deposited in SMNK, provisional specimen number HF00-Mind.10-Q) (H. FELDHAAR) on 18.10.2000 in Poring Hot Spring from *Macaranga indistincta*

CI 1.0, DPPW 0.44, DPW 0.46, EL 0.46, HL 1.28, HW 1.28, LHT 0.96, MTW 1.07, OD1 0.18, OD2 0.06, OW 0.15, PI 1.05, REL 0.36, RLEG 0.43, ROD 0.139, ROD2 0.049, SI 0.52, SL 0.66, (TL 6.8), WL 2.24

Paratype

Worker collected from the same colony (to be deposited in SMNK, provisional specimen number HF00-Mind.10-W)

CI 0.97, DPPW 0.18, DPW 0.21, EL 0.1, HL 0.72, HW 0.7, LHT 0.53, (LPS only nodiform elevation; distance from anterior to posterior margin of propodeal spiracle 0.068), MTW 0.42, PI 1.13, REL 0.16, RLEG 0.61, SI 0.64, SL 0.45, (TL 3.0), WL 0.87

Material examined

Sabah (Borneo): Poring Hot Spring (H. Feldhaar, B. Fiala, A. Meenken), Tawau (H. Feldhaar)

Worker measurements (n=8)

CI 0.96-1.0, DPPW 0.16-0.19, DPW 0.19-0.23, EL 0.1-0.14, HL 0.65-0.75, HW 0.61-0.72, LHT 0.46-0.56, LPS 0.053-0.094 (in part only nodiform elevation above propodeal spiracle), MTW 0.39-0.45, PI 1.13-1.29, REL 0.16-0.19, RLEG 0.58-0.69, SI 0.61-0.65, SL 0.39-0.45, (TL 2.5-3.4), WL 0.7-0.94

Description of worker

Colour uniformly medium brown. Workers monomorphic in size. Total body length of workers from 2.5 to 3.4 mm. Head, gaster and alitrunk shiny with smooth surface. All body parts bear appressed pubescent hairs. Long flexuous setae present on head, gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of

tergites and sternites. Only few setae on alitrunk and one pair each on petiole and postpetiole.

Head subquadratic but slightly elongated, always being longer than wide or as long as wide ($CI \leq 1.0$) and only slightly convex on sides. Anterior clypeal margin slightly convex and with a row of long erect setae projecting anteriorly. Occipital margin slightly convexly rounded, occipital lobes rounded. Mandibles relatively short and with four denticles, capable of closing tightly against the clypeus. Denticles increasing continuously in size from posterior (close to clypeus) to anterior. Surface of mandibles smooth, covered with short pubescent hairs.

Antennae relatively short in comparison to head width (SI 0.61-0.65; mean 0.63) and covered in short pubescent hair. Terminal three funicular segments form a club.

Compound eyes elliptically shaped and not protruding over margin of head in full-face view. Pronotum and mesonotum form a convex dome in profile. Anterodorsal surface of pronotum sloping downwards less steep than posterodorsal surface of mesonotum. Metanotal groove slightly notched. Promesonotal suture visible and dorsally slightly notched.

Propodeal spines very short or nearly absent, but then dorsally of the propodeal spiracle nodiform elevation. When short spines are present, the tip of the spines protrudes only slightly over posterior margin of the propodeal spiracle (Fig S1.7C and S1.7D). Slope of the posterior face of the propodeum similar to posterior slope of mesonotum and approximately 45°.

In dorsal view petiole and postpetiole round in shape. Petiole always distinctly wider than the postpetiole (PI: 1.13-1.29). In lateral view the anterior face of the petiolar node flattened and sloping downwards anteriorly and petiole longer than postpetiole. Dorsal surface of the postpetiolar node in profile rounded, lateral nodes visible. Subpetiolar process usually absent. (See Table 1 for comparative overview of worker characters.)

Queen measurements (n=11)

CI 1.0-1.05, DPPW 0.41-0.48, DPW 0.44-0.52, EL 0.45-0.5, HL 1.23-1.29, HW 1.23-1.30, LHT 0.90-0.96, MTW 0.99-1.21, OD1 0.17-0.22, OD2 0.06-0.09, OW 0.13-0.16, PI 0.97-1.1, REL 0.36-0.39, RLEG 0.42-0.49, ROD 0.131-0.167, ROD2 0.049-0.071, SI 0.51-0.52, SL 0.64-0.67, (TL 6.5-7.2), WL 2.13-2.31

Description of queen

Queens medium in size, from 6.5 to 7.2 mm in total body length and uniformly medium brown in colour. Surface of head and gaster smooth and shiny alitrunk slightly less shiny and faintly shagreened. All body parts bear appressed pubescent hairs. Long flexuous setae present on head gaster and abdomen: on head especially in frons, on gaster more on the posterior margins of tergites and sternites. A row of long erect setae pointing anterior present on the clypeus. Mandibles

relatively short, capable of closing tightly against the clypeus.

Head approximately as wide as long (CI: 0.99-1.05; mean 1.01). Sides of the head straight and head narrowing slightly from posterior towards clypeus. Occipital margin of the head slightly concave. Occipital lobes strongly rounded. Anterior clypeal margin slightly convex. Terminal four segments of funiculus continuously increasing in size forming an indistinct antennal club. Antennal scrobes strongly developed, with an acute and marked dorsal margin; the frontal carinae short.

Compound eyes oval-shaped from lateral view and convex from dorsal view, with the margin of the compound eyes protruding from the sides of the head (see Fig 3.4; Fig S1.7A and S1.7B). Diameter of the compound eyes spans slightly over one third of HL (REL 0.36-0.39). Maximum diameter of compound eyes ranges from 0.45 to 0.5 mm. Ocelli relatively small in diameter. Diameter of median ocellus (OW) always smaller than distance between lateral ocelli (OD1).

Mesoscutum convexly rounded anterodorsally. Mesoscutellum nearly in horizontal plane in lateral view. Propodeum flattened dorsally and then drops off at an angle of approximately 45° posterior of the propodeal spiracle. Mesoscutum relatively short, stretching out over less than half of the alitrunk in lateral view. In dorsal view, the posterior margin of the propodeum slightly convexly rounded and the mesonotum broadly triangular. Propodeum not armed with spines.

Node of petiole and postpetiole in dorsal view rounded. Petiole as wide as or wider than the postpetiole (mean PI: 1.05). In lateral view petiole anterodorsally flattened and sloping downwards and slightly longer than the postpetiole. Postpetiole round in dorsal and lateral view without distinct nodes. (See Table 1 for comparative overview of queen characters.)

Distribution and biology

Crematogaster claudiae is endemic to Borneo, possibly even to Sabah (see below). The species had mainly been found on two different species of the section *Pachystemon* (*M. glandibracteolata* and *M. indistincta*). We have evidence that this species may hybridize (at least locally) with *Crematogaster captiosa* (in Poring Hot Spring) and presumably fertile offspring (queens) can be produced by rare hybrid queens (Feldhaar et al., 2008; Feldhaar et al., 2010).

In comparison to all other species of the *captiosa*-subgroup the queens have relatively small compound eyes (smaller than 0.5 mm) and an earlier onset of reproduction, when colonies comprise approximately 500 workers. Unlike the queens of other *captiosa*-subgroup species, queens of *C. claudiae* only colonize saplings. Two samples contained in the phylogeny based on mitochondrial DNA (Feldhaar et al., 2010) collected in Sarawak cluster with samples of *C. claudiae* from Sabah (see above in distribution and biology of *C. hullettii*). Thus, we can currently not exclude that *C. claudiae* has a wider distributional range than Sabah only. In former publications by our group this species was referred to as *Crematogaster* msp. 10 (Feldhaar et al., 2008; Feldhaar et al., 2010).

Non-*Macaranga* associated *Crematogaster* (formerly *Decacrema*) from Borneo and Peninsula Malaysia

Three further species of the former subgenus *Decacrema* have been collected and described from the distributional range of the *Crematogaster-Macaranga* association: *C. angulosa* André, *C. biformis* André and *C. cephalotes* Smith. As only geographic regions of sampling locality were given but no other information we examined the type material (see supplementary material). We found no match with our specimens from *Macaranga*. Propodeal spines of *Crematogaster angulosa* and *C. cephalotes* are considerably stronger and also longer in proportion to the thorax in comparison to obligately *Macaranga*-associated *Crematogaster* species, which may be an adaptation to the life-style in the latter group (Fiala & Maschwitz, 1990). In contrast to the *Macaranga*-associated *Crematogaster borneensis*-group species all three species are dimorphic and possess a pronounced metanotal groove.

Concluding remarks

More species may be present in other regions within the distribution range of this ant-plant symbiosis that were not extensively sampled by us (such as Sumatra), which is due to the fact that we (as well as other research groups) conducted most of our ecological studies in the regions treated here. Quek et al. (2007) have sampled over the entire distributional range of the association, and have found 19 distinct lineages of *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group) based on mitochondrial DNA. Lineages between Peninsula Malaysia and Sumatra overlapped greatly (with only one endemic haplotype in Sumatra), and our limited material from Sumatra suggest that species between these two land masses may also overlap in morphology and colonize the same host plants (see also Fiala et al., 1999). *Crematogaster roslihashimi*, and *C. maryatii* do not occur on Sumatra. The number of lineages found in Borneo was considerably greater, with ten lineages found exclusively there (Quek et al., 2007). The number of lineages based on mitochondrial DNA may overestimate the number of species present in a given area though, as we have found that within-species sequence divergence can be very high (e.g. up to 14% within *C. maryatii*, formerly *C. msp. 7* among samples collected only 50 km apart (Feldhaar et al., 2010)). Similarly high intraspecific divergence of mitochondrial DNA lineages has also been described within *Crematogaster kelleri* Forel, 1891 (Blaimer & Fisher, 2013). In contrast, the morphologically distinct species *C. decamera* and *C. roslihashimi* show only very little genetic differentiation on Peninsula Malaysia (Feldhaar et al., 2003a; Feldhaar et al., 2010). In spite of large intraspecific variation of mitochondrial DNA, nuclear markers have underscored our species concept based on morphology. Microsatellite markers of five of the seven species analysed (Feldhaar et al., 2004; Feldhaar et al., 2010; Türke et al., 2010, unpubl. results) show species-specific patterns that are congruent

with the species described here. Based on nuclear DNA only these would thus be considered the same lineage. In contrast to Ueda et al. (2015) we found no complete congruence of mtDNA and microsatellite markers. They excluded geographical variability by using samples collected from a single site. Nonetheless they also found admixture and thus evidence for hybridization in 3% of their samples. In conclusion, our data suggests that the number of species described here may be close to the number of species found even with geographically more extensive sampling. For the time being, the present classification will in any case allow to apply species names in future studies instead of morphospecies numbers varying among different authors that cannot be assigned without reference material.

In general, queens as well as workers of all species are quite variable in morphometric measurements. We have found consistent geographic variability among species, e.g. with queens of *C. decamera* collected from Peninsula Malaysia having generally smaller heads than those collected from Borneo. Nonetheless absolute measurements of queens will generally allow species identification. As workers vary considerably in size in dependence of colony size only relative measurements allow specification (e.g. SI or PI). The total body length of workers increases by up to one third in workers from small to those from large and older colonies. Likewise, workers of all species described above tend to be darker in colour with increasing colony size.

In former publications we had included *Crematogaster* morphospecies 5 (Fiala et al., 1999) based on its seeming endemism, as it was found in Sarawak (Lambir Hills) only with a strong host plant preference. In addition, those queens grouped into *C. msp. 5* possessed slightly darker longitudinal stripes on the upper surface of the thorax. However, when later comparing a larger number of queens of all species of the *captiosa*-group, comparatively lightly coloured individuals often also bore these stripes. Here, we have neither described it as a new species nor could we attribute it to a formerly described species. Individuals formerly subsumed under this morphospecies could not be grouped into a species distinctly different from other species described here. Likewise, individuals of this morphospecies did not form a distinct clade in a molecular phylogeny (Feldhaar et al., 2003b; Feldhaar et al., 2010). Based on their morphological characters the few individuals (queens) ever assigned to *C. msp. 5* show a combination of characters that would group them with either *C. borneensis*, *C. linsenmairi* or *C. captiosa*, but usually with one character contradicting the others and hampering a distinct placement into either species. However, as we have found individuals of different species of the *captiosa*-group (*C. claudiae* and *C. captiosa*) to hybridize locally (Feldhaar et al., 2008; Feldhaar et al., 2010) individual queens with phenotypes intermediate between two species of the *captiosa*-group may be the result of such hybridization events. We found a hybridization level of 2.5% (Feldhaar et al. 2008), which is nearly congruent with that published by Ueda et al. (2015). Hybridization events may tend to be more common in areas with relatively small population sizes of potentially hybridizing species such as small

islands or isolated patches containing few *Macaranga* hosts only.

Species identification of *Macaranga*-associated *Crematogaster* (*Crematogaster borneensis*-group) is easier and more conclusive based on queens as they possess more distinct characters than workers (i.e. length of compound eyes and the ocelli; see Table 1 for overview of distinct characters). Female sexuals can often be collected easily and should be collected together with workers. Queens tend to be in the lower part of the stem in small host plants recently colonized. Once *Macaranga* hosts grow larger the queen remains in the lower part of the lignified tree trunks and then becomes almost inaccessible (Feldhaar et al., 2003b). Nonetheless, virgin queens can often be collected together with workers by cutting off a larger branch of the host. After the reproductive stage has been reached by the colony, female as well as male sexuals are often present and can often be found in the proximal part of the branches close to tree trunks. In this way sexuals can be collected without destroying the whole colony. *Crematogaster* (*Crematogaster borneensis*-group) associated with *Macaranga* have never been observed away from their hosts, with the exception of queens and males during mating flights. Colonies never extend over more than one host tree. Identity of the host-plant can help to confirm species identification; a myrmecologist with limited knowledge of *Macaranga* species should at least pay attention to whether the host plant's stem is covered by a glaucous wax-cover or not as most *Macaranga*-associated *Decacrema* species will either colonize waxy or non-waxy hosts.

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Supplementary material

Fig S1.1A-D to S1.8A-B: Overview of queens of all species of the *Macaranga*-associated *Crematogaster* (*borneensis*-group) ants and workers of all species except for *C. roslihashimi*. Pictures were taken with a Leica M165C stereomicroscope and a mounted Leica DFC290 digital camera.

Supplementary Figures S1.1A-D; S1.2A-D.

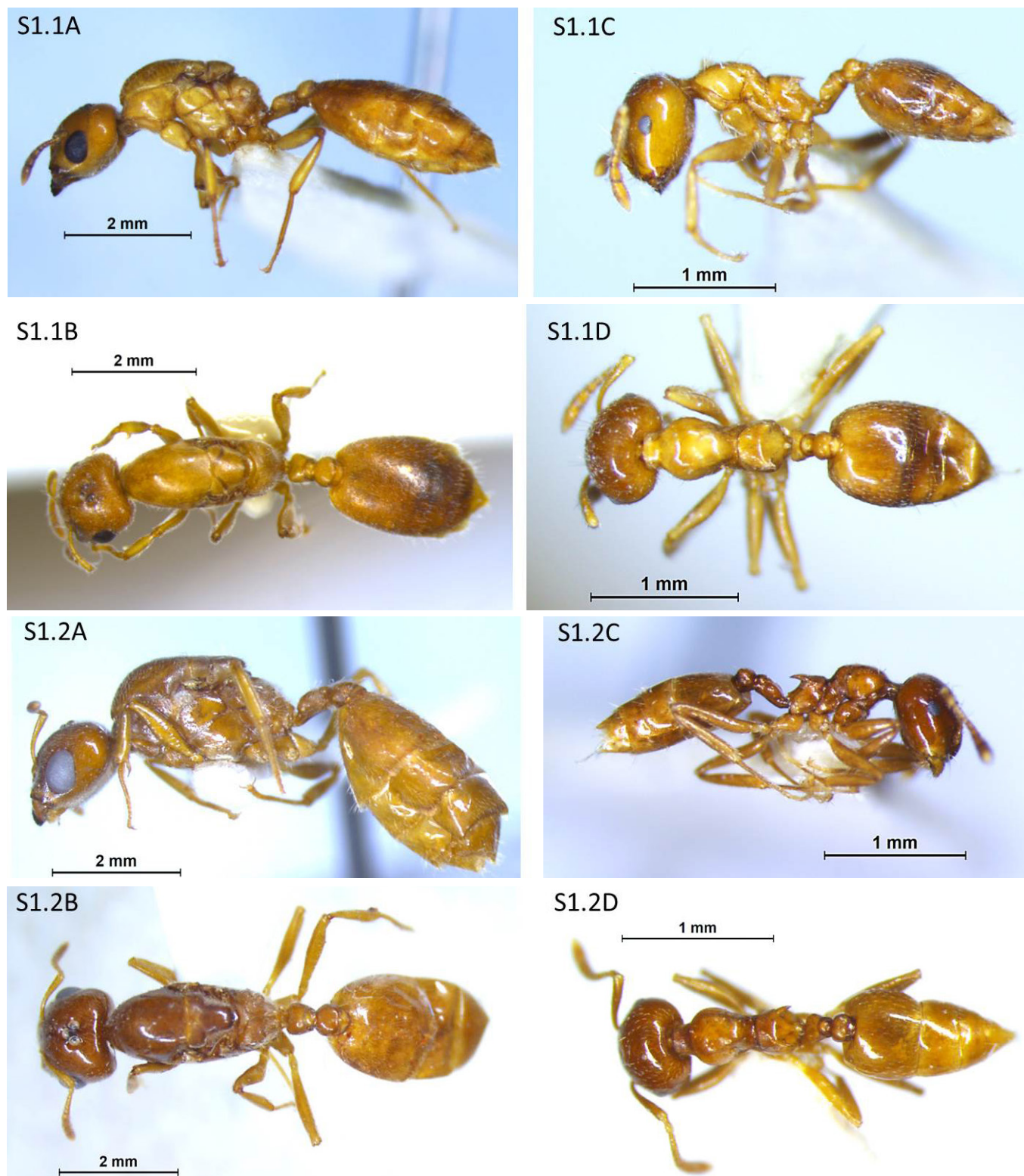


Fig S1.1A-D: *C. borneensis*, leg. H. Feldhaar, 18.10.2001, Poring Hot Springs (Sabah) from *Macaranga indistincta*; S1.1A: lateral view queen, S1.1B dorsal view queen, S1.1C lateral view worker, S1.1D dorsal view worker.

Fig S1.2A-D: *C. linsenmairi*, leg. H. Feldhaar, 10.9.2002, Poring Hot Spring (Sabah) from *Macaranga pearsonii*; S1.2A: lateral view queen, S1.2B dorsal view queen, S1.2C lateral view worker, S1.2D dorsal view worker.

Supplementary Figures S1.3A-D; S1.4A-D.

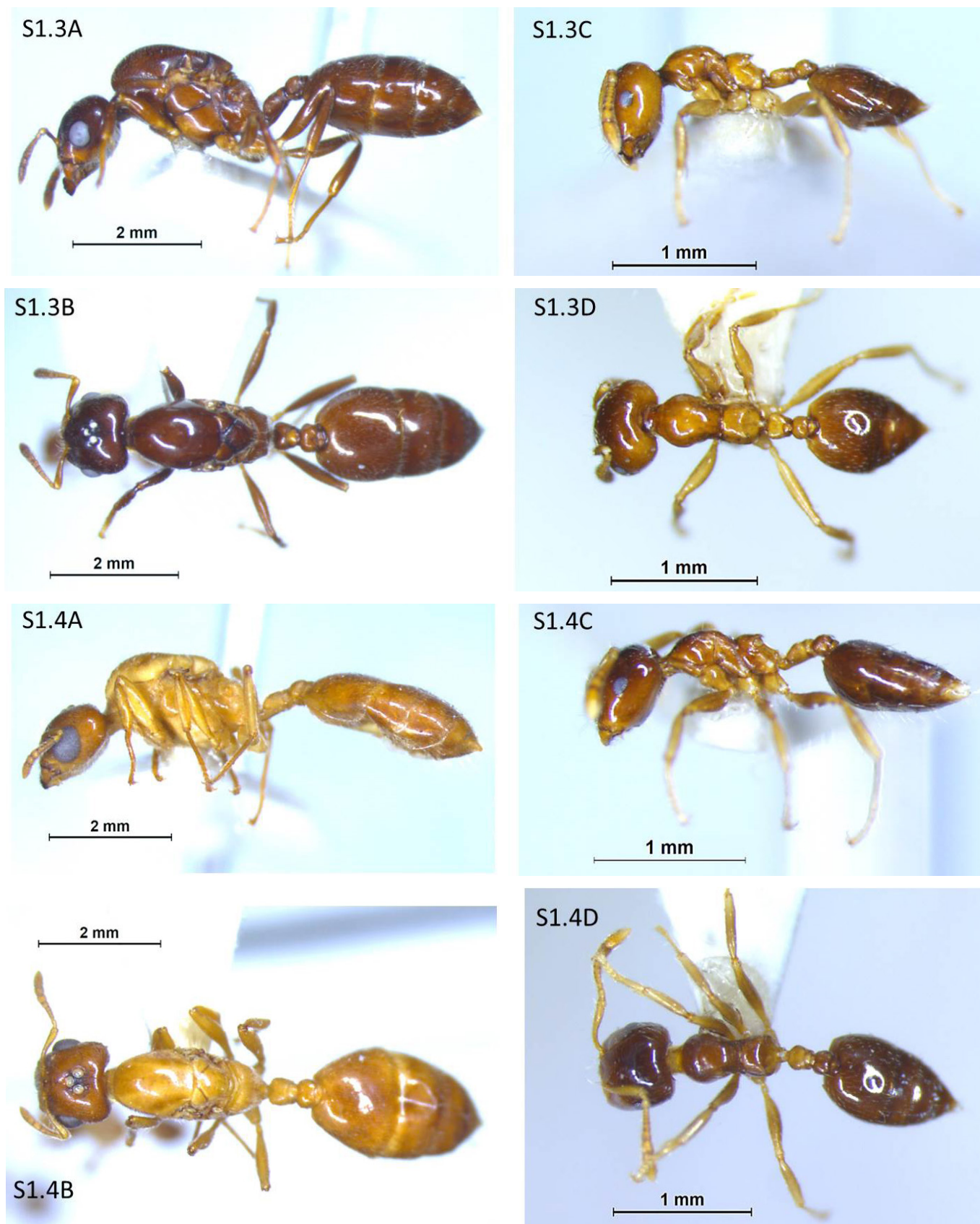


Fig S1.3A-D: *C. hullettii*, leg. H. Feldhaar, 9.2.2000, Genting Highlands (Pen. Malaysia) from *Macaranga hullettii*; S1.3A: lateral view queen, S1.3B dorsal view queen, S1.3C lateral view worker, S1.3D dorsal view worker.
 Fig S1.4A-D: *C. captiosa*, leg. A. Meenken, 7.9.2002, Poring Hot Springs (Sabah) from *Macaranga indistincta*; S1.4A: lateral view queen, S1.4B dorsal view queen, S1.4C lateral view worker, S1.4D dorsal view worker.

Supplementary Figures S1.5A-D; S1.6A-D.

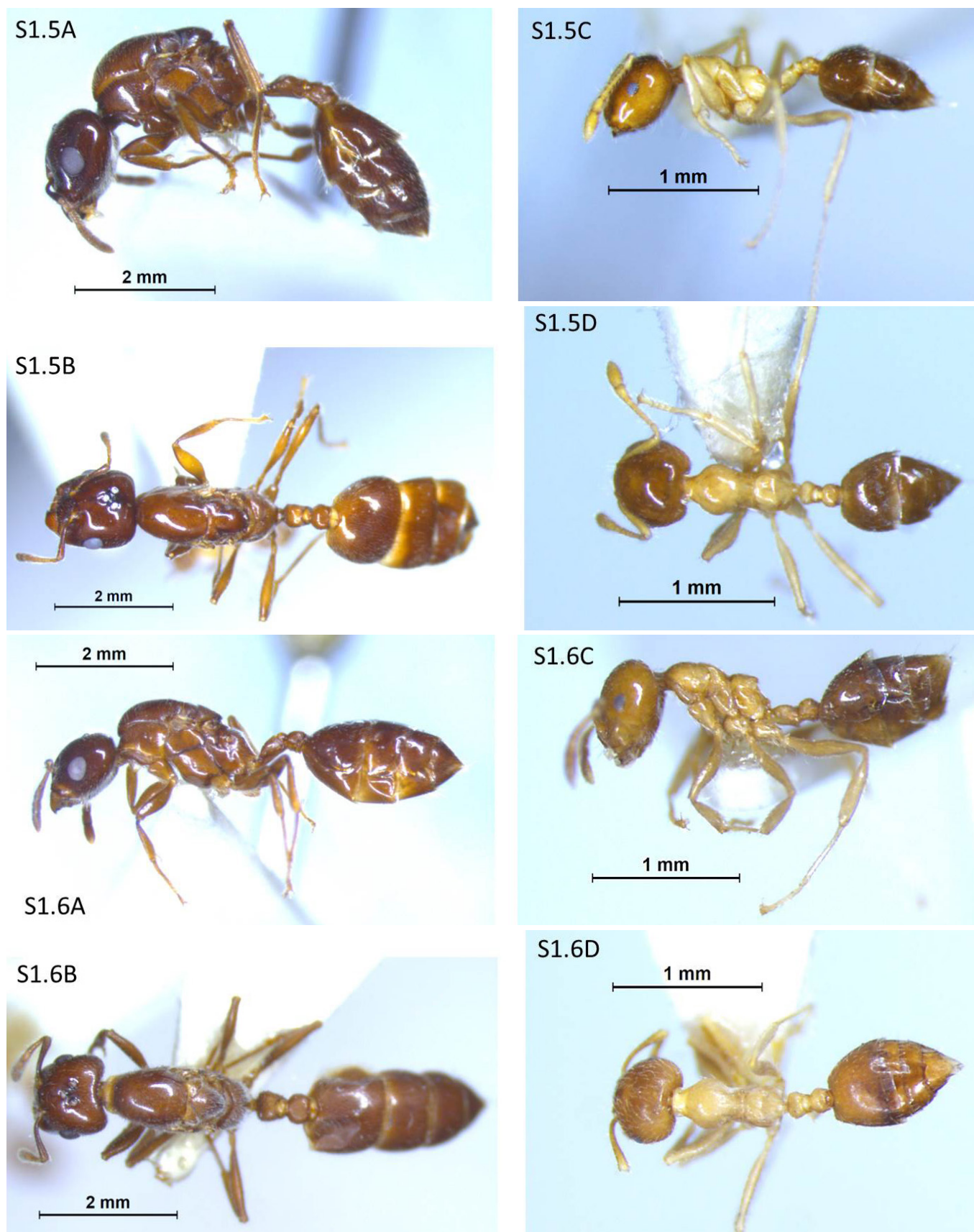


Fig S1.5A-D: *C. decamera*, leg. B. Fiala, 2.9.2007, near Lambir (Sarawak) from *Macaranga hypoleuca*; S1.5A: lateral view queen, S1.5B dorsal view queen, S1.5C lateral view worker, S1.5D dorsal view worker.

Fig S1.6A-D: *C. maryatii*, leg. H. Feldhaar, 3.10.2002, Kampung Madai (Sabah) from *Macaranga motleyana*; S1.6A: lateral view queen, S1.6B dorsal view queen, S1.6C lateral view worker, S1.6D dorsal view worker.

Supplementary Figures S1.7A-D; S1.8A-B.

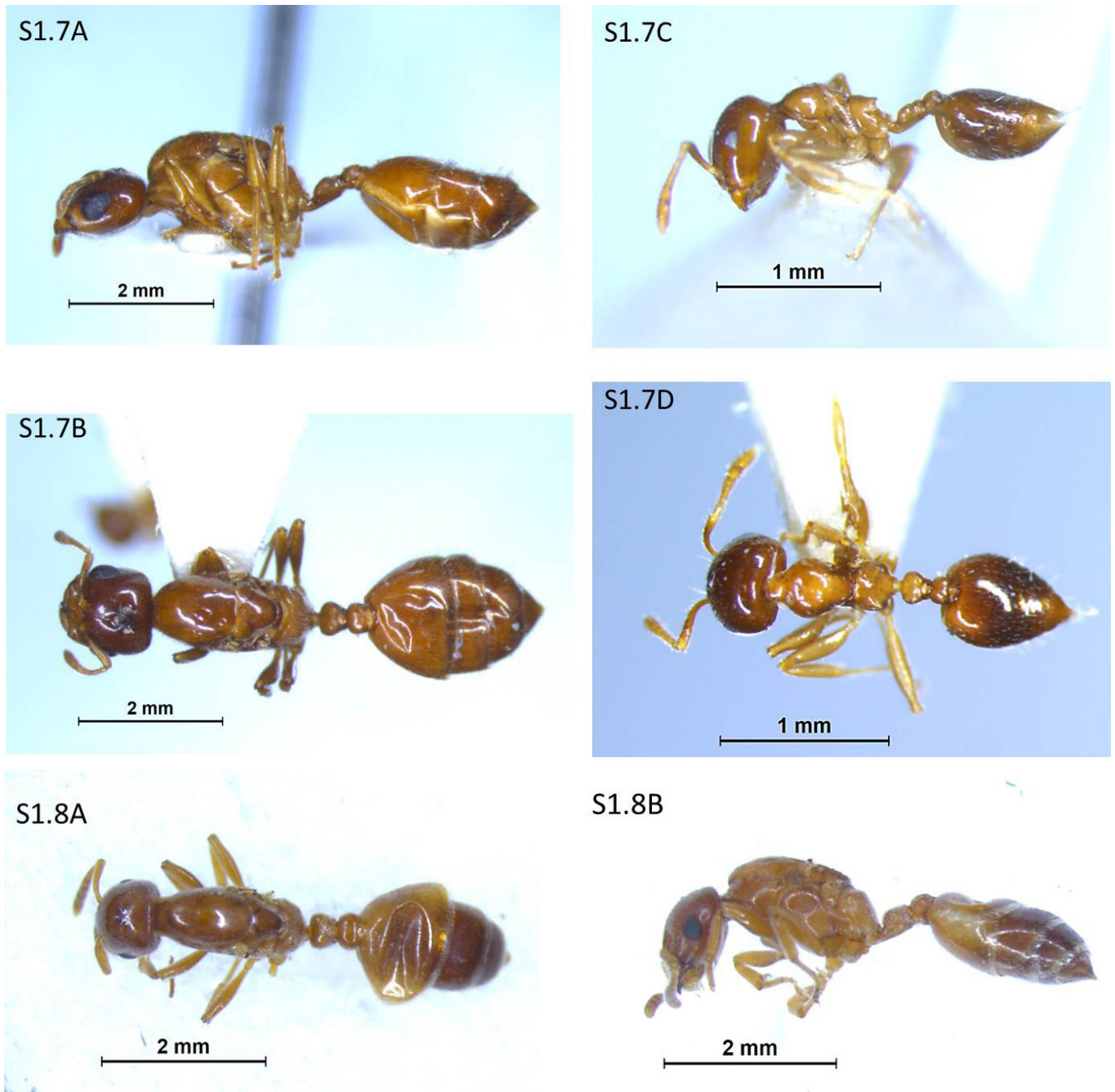


Fig S1.7A-D: *C. claudiae*, leg. H. Feldhaar, 6.10.2002, Bukit Tawau (Sabah) from *Macaranga indistincta*; S1.7A: lateral view queen, S1.7B dorsal view queen, S1.7C lateral view worker, S1.7D dorsal view worker.

Fig S1.8: *C. roslihashimi*, leg. U. Maschwitz, 1.12.1996, Kuantan (Peninsula Malaysia) from *Macaranga constricta*; S1.8A: dorsal view of queen, S1.8B: lateral view of queen.

Supplementary Figures S2.1A-B; 2A-D; 3A-B ; 4A-B.

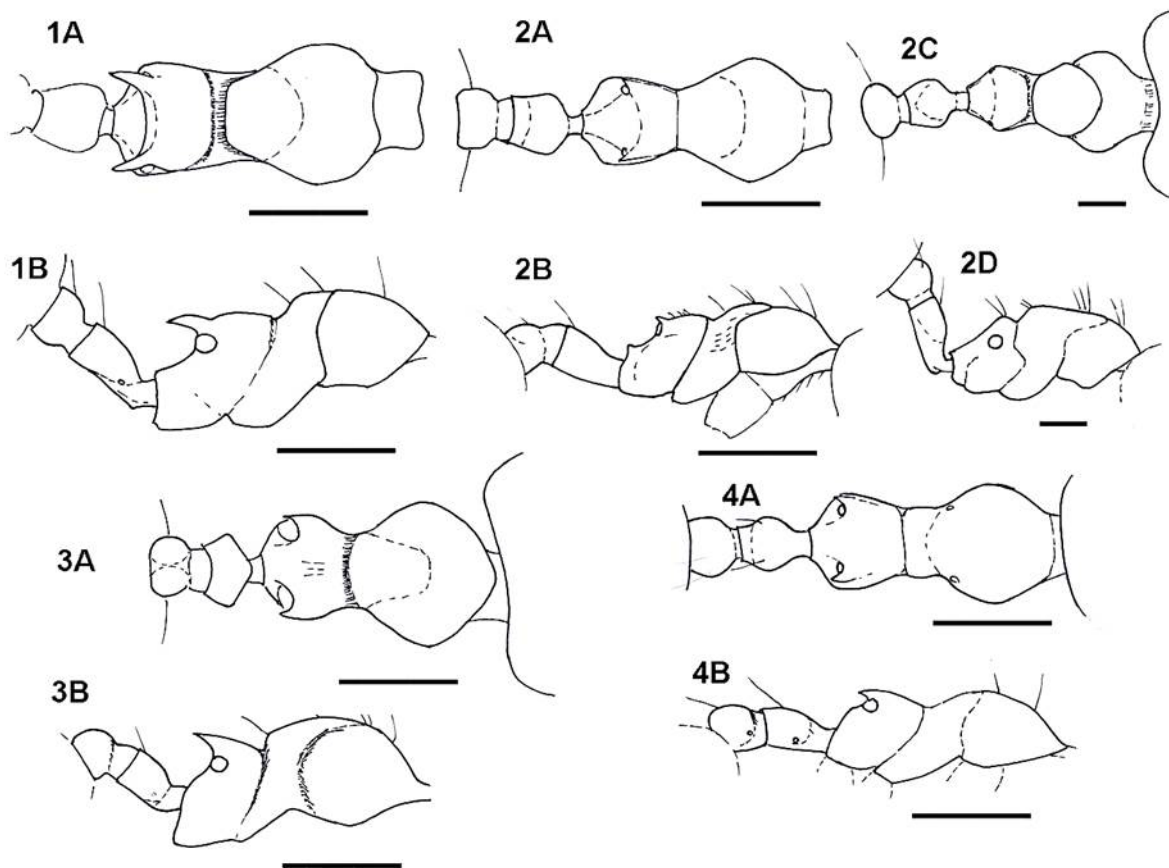


Fig S2: Dorsal and lateral view of SE Asian *Crematogaster* (*Decacrema*): S2.1A and S2.1B: *Crematogaster angulosa*; S2.2A and S2.2B: minor worker of *Crematogaster biformis*, S2.2C and S2.2D: major worker of *Crematogaster biformis*; **S2.3A and S2.3B:** *Crematogaster cephalotes* minor worker; both majors and minors carry propodeal spines; **S2.4A and S2.4B:** *Crematogaster borneensis* (*Macaranga*-associated). Scale bar corresponds to 0.375mm.

Table S.1: Overview of morphospecies numbers formerly used for *Macaranga*-associated *Crematogaster* (*borneensis*-group) ants in publications of Feldhaar, Federle, Fiala, Heil, Maschwitz and coworkers vs. synonymised or newly described species.

Morphospecies	Synonym with / newly described as	Main <i>Macaranga</i> host plants (Further details see text)
C. msp. 1	<i>C. borneensis</i>	waxy species sect. <i>Pachystemon</i> and <i>Pruinosae</i> (saplings of <i>M. griffithiana</i> , <i>M. pearsonii</i> <i>M. pruinosa</i> , <i>M. motleyana</i> , and mature trees of several other species)
C. msp. 2	<i>C. linsenmairi</i> sp. nov.	waxy species sect. <i>Pruinosae</i> (<i>M. aetheadenia</i> , <i>M. hosei</i> , <i>M. pearsonii</i> , <i>M. pruinosa</i>)
C. msp. 3	<i>C. hullettii</i> sp. nov.	non-waxy species sect. <i>Pachystemon</i> (<i>M. bancana</i> , <i>M. hullettii</i> , <i>M. kingii</i> , <i>M. trachyphylla</i> , <i>M. umbrosa</i>)
C. msp. 4	<i>C. captiosa</i>	non-waxy species sect. <i>Pachystemon</i> (e.g., <i>M. angulata</i> , <i>M. indistincta</i>), slightly waxy <i>M. glandibracteolata</i>
C. msp. 5	(<i>C. borneensis</i> , <i>C. captiosa</i>)	
C. msp. 6	<i>C. decamera</i>	waxy species sect. <i>Pachystemon</i> (<i>M. beccariana</i> , <i>M. havilandii</i> , <i>M. hypoleuca</i>)
C. msp. 7	<i>C. maryatii</i> sp. nov.	waxy species sect. <i>Pachystemon</i> (<i>M. havilandii</i> , <i>M. hypoleuca</i> , <i>M. motleyana</i>)
C. msp. 9	<i>C. roslhashimi</i> sp. nov.	<i>M. constricta</i> (rarely <i>M. hypoleuca</i>)
C. msp. 10	<i>C. claudiae</i> sp. nov.	non-waxy species sect. <i>Pachystemon</i> (e.g., <i>M. angulata</i> , <i>M. indistincta</i>), slightly waxy <i>M. glandibracteolata</i>

Supplemental text:**Morphometric measurements of the three other described *Crematogaster* (*Decacrema*) species from SE-Asia:*****Crematogaster angulosa* André***Crematogaster angulosa* (André, 1896)*Type material examined**Crematogaster angulosa* André. Holotype, 1 worker, Borneo (E. André) (MNHN).*Worker measurements (n=1)*

HL 0.81, HW 0.78, EL 0.17, SL 0.57, WL 0.97, MTW 0.46, LHT 0.66, DPW 0.22, DPPW 0.21, CI 0.96, SI 0.73, REL 0.21, PI 1.01, RLEG 0.68 LPS 0.17 (TL 3.0)

Description of worker

Colour uniformly medium brown. Head and gaster shiny and with smooth surface, propodeum slightly striated. All body parts bear appressed pubescent hairs. Long flexuous setae present on head, gaster and abdomen. Head subquadratic but slightly elongated, being longer than wide and only slightly convex on sides. Anterior clypeal margin slightly convex and with a row of long erect hairs projecting anteriorly. Antennae relatively long in comparison to head width (SI 0.73) and covered in short pubescent hair. Terminal three funicular segments form a distinct club. Compound eyes elliptically shaped and not protruding over margin of head in full face view.

Metanotal groove distinctly visible and more pronounced than in the *Macaranga*-associated *Decacrema* species. Propodeal spines long, acute and thin (see Fig. S2.1A and S2.1B). In dorsal view petiole and postpetiole round in shape, with petiole being slightly more elongate than postpetiole. Petiole slightly wider than the postpetiole. Femur distinctly thicker than other parts of legs.

In dorsal view petiole and postpetiole round in shape. In lateral view the anterior face of the petiolar node flattened and sloping downwards anteriorly and petiole longer than postpetiole. Dorsal surface of the postpetiolar node in profile rounded, lateral nodes visible. Anteroventral tooth of petiole present.

Crematogaster biformis* AndréC. biformis* (André, 1892)*Material examined**C. biformis* André. 1 worker, Borneo Forel (MHNG)*Worker measurements (minor worker) (n=1)*

HL 0.85, HW 0.85, EL 0.15, SL 0.55, WL 0.9, MTW --, LHT 0.55, DPW 0.23, DPPW 0.22, CI 1.0, SI 0.64, REL 0.18, PI 1.03, RLEG 0.61, LPS 0.13 (TL 3.0)

Description of worker

Workers of *Crematogaster biformis* are dimorphic, with minor and major workers. Colour of workers uniformly dark brown. All body parts bear long erect hairs, including the legs. Head subquadratic, as wide as long. Short propodeal spines are present in minor worker but absent in major worker (Fig. S2.2A and S2.2B, lateral view of alitrunk). The metanotal groove is distinctly visible and more pronounced than in the *Macaranga*-associated *Decacrema* species. Terminal three funicular segments form a distinct club. In dorsal view petiole round to trapezoid and postpetiole round in shape. In lateral view the anterior face of the petiolar node flattened and sloping downwards anteriorly. Petiole longer than postpetiole. Dorsal surface of the postpetiolar node in profile rounded. Anteroventral tooth of petiole present but rounded.

Crematogaster cephalotes* SmithCrematogaster cephalotes* (Smith, 1857)*Type material examined**Crematogaster cephalotes* Smith. Syntypes, 2 workers, Borneo (Smith), (OXUM).*Worker measurements: major worker (n=1)*

HL 0.8, HW 0.74, EL 0.15, SL 0.49, WL 0.75, MTW 0.44, LHT 0.42, DPW 0.23, DPPW 0.2, CI 0.92, SI 0.65, REL 0.19, PI 1.17, RLEG 0.56, LPS 0.09 (TL 2.8)

Worker measurements: minor worker (n=1)

HL 0.54, HW 0.52, EL 0.11, SL 0.37, WL 0.58, MTW 0.3, LHT 0.32, DPW 0.16, DPPW 0.14, CI 0.97, SI 0.70, REL 0.21, PI 1.16, RLEG 0.56, LPS 0.1 (TL 2.1)

Description of worker

Workers of *Crematogaster cephalotes* are distinctly dimorphic (Fig S2.3A and S.3B). Head and alitrunk medium brown in colour, gaster darker brown. Head of minor and major worker shiny and nearly devoid of pubescence. Only few short erect setae present on clypeus. Propodeum as well as mesonotum slightly striated. Minor workers show a pronounced two-segmented antennal club, whereas in the major worker the first three antennal segments form a distinct club. Both, minors and majors have acute propodeal spines. Petiole trapezoid in dorsal view, postpetiole a node comprised of two lateral bulbs. Promesonotum and mesonotum form a convex dome in profile. Posterodorsal surface of mesonotum sloping downwards steeply towards propodeum. Metanotal groove distinctly visible and more pronounced than in the *Macaranga*-associated *Decacrema* species.