A taxonomic revision of the Asian endemic subgenus Physocrema of the genus Crematogaster (Hymenoptera: Formicidae)

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Abstract

The subgenus Physocrema of the genus Crematogaster is revised. Twelve species are recognized in the subgenus, of which two are new to science: C. (Physocrema) tanakai sp. nov. and C. (P.) yamanei sp. nov. An identification key based on the worker caste is provided. Taxonomic relationships between C. (P.) difformis and similar species are clarified. Crematogaster (P.) vacca Forel 1911 is raised to species level. The following new synonymies are proposed: C. (P.) inflata F. Smith 1857 = C. (P.) moorei Donisthorpe 1941 syn. nov.; C. (P.) mucronata Emery 1900 = C. (P.) fulmeki Forel 1922 syn. nov.; C. (P.) vacca Forel 1911 = C. (P.) stethogompha Wheeler 1919 syn. nov. = C. (P.) stethogompha detritinodis Wheeler 1919 syn. nov. Crematogaster (P.) onusta Stitz 1925 is referred to the subgenus Physocrema. C. tumidula Emery 1900 is transferred to the subgenus Oxygyne from Physocrema.

Key words: taxonomy, ant

Introduction

The genus Crematogaster Lund 1831 (Myrmicinae: Crematogastrini) is one of the most common groups of ants and occurs worldwide but is most abundant in the tropics (Hölldobler & Wilson, 1990). The genus contains more than 900 available species-level names (Bolton et al., 2006) and is a hyperdiverse genus similar to Camponotus and Pheidole. A survey of ants carried out in a lowland rainforest in northwestern Borneo found that Crematogaster comprised 14.2 % of all species found (Eguchi & Yamane, 2003). In a lowland rainforest at Poring, Sabah, it comprised 6.7 % of all species (Brühl et al. 1998). Apart from a few faunistic investigations (e. g. Longino [2003] for Costa Rica, Wu & Wang [1995] for China and Buren [1968] for North America), no comprehensive taxonomic studies have been carried out since the early twentieth century. Much taxonomic work remains to be done on Crematogaster ants, both in terms of species diagnosis and phylogenetic evaluation. The resolution of such taxonomic subjects requires careful analysis of character variation using colony samples from wide-ranging geographic areas.

A subgeneric classification of the genus was established by Santschi (1918), Emery (1922) and Wheeler (1922). Currently, the genus is conventionally divided into 16 subgenera (Bolton et al., 2006), but the traditional subgenera include taxonomically problematic ones. Diagnostic characters for the subgenera are sometimes obscure because of intra- or interspecific variation. Some subgenera are out of date and incorrect because diagnostic features are not discussed, but other subgenera are useful for taxonomic studies. Taxonomic work at the subgeneric and species group-levels would be useful (Ward, 2007), especially as the genus contains such a large number of species.

As a first attempt to deal with the higher classification of the genus, this study focused on the subgenus Physocrema Forel, 1912. It was established as a subgenus of Crematogaster (Forel, 1912) with Crematogaster inflata F. Smith 1857 subsequently designated as the type species by Wheeler (1913). The subgenus presently consists of 10 species and 4 subspecies (Bolton, 1995, 2006). The subgenus has been characterized by the...
swollen propodeum (Forel, 1912) and seems to be monophyletic. The subgenus is an Asian endemic group and widely distributed in Southeast Asia. Keys to species were given in Bingham (1903) and Donisthorpe (1941), but these keys have no utility now because of undescribed species. This paper provides a new revision of the subgenus Physocrema, based on worker material.

Materials and methods

Sources of material

Specimens were examined and/or deposited in the collections listed below. Codes for public institutions mainly follow those in Brandão (2000).

BMNH  The Natural History Museum, London, U. K.
FRC   Forest Research Centre, Kuching, Sarawak, Malaysia
IEGG  Istituto di Entomologia “Guido Grandi”, Bologna, Italy.
KUM   Kyushu University, Fukuoka, Japan.
MCCO  Museo Civico di Storia Naturale “Giacomo Doria,”, Genoa, Italy.
MCZC  Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.
MHNG  Musee d’Histoire Naturelle, Geneva, Switzerland.
MZB   Museum Zoologicum Bogoriense (Cibinong), Bogor, Java, Indonesia.
NHMB  Naturhistorisches Museum, Basel, Switzerland.
OXUM  Hope Entomological Collections of Oxford University Museum, Oxford, U. K.
UASK  Institute of Zoology, Ukrainian National Academy of Sciences, Kiev, Ukraine.
ZMHB  Museen fur Naturkunde der Humboldt-Universitat Berlin, Berlin, Germany.

Observation

Most observations were made using a Nikon SZX12 stereomicroscope. The scanning electron micrographs (SEM) were prepared with a JSM-5600LV scanning electron microscope. Images were processed using Helicon Focus 4.47.1 Pro.

Measurements and indices

Measurements were made under a Nikon SMZ-U microscope using micrometers. All measurements are expressed in millimeters, to the second decimal place. Small, medium and large workers were measured for each species to encompass polymorphism.

Head Width (HW): Maximum width of head in full-face view, excluding the eyes.
Head Length (HL): Perpendicular distance from vertex margin to line tangent to the anterior-most projections of clypeus in full-face view.
Cephalic Index (CI): HW/HL x 100.
Scape Length (SL): Length of the first antennal segment, excluding the neck and basal condyle.
Scape Index (SI): SL/HW x 100.
Eye Length (EL): Maximum length of the compound eye.
Picranal Width (PW): Maximum width of the pronotum in dorsal view.
Weber’s Length of the mesosoma (WL): Diagonal length, measured in lateral view from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the propodeal lobe.
Propodeal Spine Length (PSL): measured from tip of propodeal spine to closest point on outer rim of propodeal spiracle.
Petiole Length (PtL): Viewed in lateral profile and measured in same plane as anterodorsal face, distance from inflection point marking juncture of posterolateral lobes and cylindrical posterior portion of segment to anterior inflection point where petiole curves up to condyle or, if inflection point not visible, where petiole is obscured by posteroventral lobes of propodeum (Longino, 2003).
Petiole Width (PtW): Maximum width of petiole in dorsal view.

Petiole Height (PtH): Viewed in lateral profile, perpendicular distance from ventral margin to highest point of posterolateral tubercles; if ventral margin is concave upward, measured from line tangent to uppermost portion of curve and oriented as close as possible to long axis of petiole (Longino, 2003).

Postpetiole Length (PpL): Viewing at an angle that maximizes length, perpendicular distance from line tangent to anterior inflection point (narrowest point when postpetiole is hourglass-shaped where it joins the helcium, point immediately anterior to node when helcium is sharply differentiated from node as a distinct cylindrical stem) to line tangent to posterior-most lobes if bilobed, to posterior-most point if globular (Longino, 2003).

Postpetiole Width (PpW): Maximum width of postpetiole in dorsal view, excluding the helcium.

Petiole Height Index (PtHI): PtH/PtL x 100.

Petiole Width Index (PtWI): PtW/PtL x 100.

Postpetiole Width Index (PpWI): PpW/PpL x 100.

Waist Index (WI): PpW/PtW x 100.

The subgenus Physocrema Forel

Physocrema Forel, 1912: 220 [as subgenus of Crematogaster]. Type-species: Crematogaster inflata, by subsequent designation of Wheeler 1913: 82.


Diagnosis of worker. Head subquadrate, slightly broader than long, with weakly concave posterior margin, angular posterior corners and subparallel sides. Occipital carinae developed. Mandible striate, with four teeth in small workers and five in larger workers, apical and subapical teeth large. Anterior margin of clypeus convex with slightly impressed median portion (Figs 1, 2); anterolateral margins of clypeus protruded anteriorly, resulting in an appearance of the anterolateral and anteromedian margins being at about the same level (Figs 1, 2); posterior margin of clypeus rounded between frontal lobes. Frontal carinae almost parallel. Antennae 11 segmented; antennal club 4-jointed. Compound eyes large but not distinctly projecting beyond lateral margins of head in full face view.

Pronotum and mesonotum usually without defined suture, rarely promesonotal suture present in large workers. Mesothoracic spiracle reduced to form small pit dorsoventrally. Variable extent of posterior mesosoma enlarged and swollen (Figs 3, 4). Metapleural gland opening circular; propodeal spiracle facing posterolaterally (Figs 3, 4).

Petiole flattened without node nor subpetiolar process; spiracle situated anteriorly midway between dorsal and ventral margins of petiole in lateral view, directed laterally; in dorsal view, elliptical with convex sides, longer than broad (Fig. 5). Postpetiole without distinctly longitudinal median sulcus, weakly bilobed behind in large workers (Fig. 5); spiracle situated distinctly anteriorly on the lateral surface.

Comments. Workers of the subgenus Physocrema can be distinguished from those of all other subgenera of Crematogaster by the features of (1) anteromedian margin of clypeus convex with slightly impressed median portion; (2) anterolateral margins of clypeus produced anteriorly; (3) 4-jointed antennal club (but, 3-jointed in mucronata); (4) propodeum swollen; (5) metapleural gland orifice circular; (6) petiole elliptical; (7) petiole without node-like process posteriorly. The subgenus is unique among Asian Crematogaster ants in having features (4), (5), (6) and (7). The workers of the subgenus Physocrema share features (1), (2), (3) and (7) with the subgenus Paracrema. In Asian Crematogaster specimens examined, the workers of the subgenera Crematogaster, Decacrema, Mesocrema, Oxygyne, Paracrema, Physocrema and Xiphocrema share features (2) and (7).
**Distribution.** Southeast Asia: Vietnam (southern parts), Laos, Cambodia, Thailand, Myanmar (southeastern parts), Malaysia (Peninsula and Borneo), Singapore, Indonesia (Sumatra, Mentawai, Java, Bali, Lombok, Kalimantan, Sulawesi, Timor), Philippines (Fig. 21).

**FIGURES 1−2.** Clypeus in dorsal view: 1—*C. (P.) inflata*; 2—*C. (P.) aurita*. White arrow indicates anterolateral margin of clypeus.

**FIGURES 3−4.** Mesosoma in lateral view: 3—*C. (P.) ampullaris*; 4—*C. (P.) physothorax*.

**FIGURE 5.** Petiole and postpetiole in dorsal view: *C. (P.) physothorax*.

**Synonymic list of the subgenus Physocrema Forel**

*ampullaris* F. Smith, 1861.

*aurita* Karavajew, 1935.
Key to species based on the worker caste (except for *C. bakeri*, which is incertae sedis.)

1 Propodeal spines developed and with pointed apices .......................................................... 2
   - Propodeal spines undeveloped and forming obtuse lobes .............................................. 4
2 Antennal club 3-jointed. Pronotum raised steeply toward mesonotum in lateral view ......... mucronata
   - Antennal club 4-jointed. Pronotum raised moderately toward mesonotum in lateral view .......................................................... 3
3 In lateral view, pronotum and mesonotum forming a single convexity, propodeum distinctly raised relative to promesonotum, metanotal groove deep .......................................................... vacca
   - In lateral view, pronotum and mesonotum forming a single convexity, propodeum slightly raised relative to promesonotum, metanotal groove less deep .......................................................... yamanei sp. nov.
4 Dorsal median portion of head swollen .................................................................................tanakai sp. nov.
   - Dorsal median portion of head not swollen .................................................................... 5
5 Propodeal spiracle situated near the metapleural gland orifice, the distance between them about the same as the propodeal spiracle diameter (Fig. 4) ................................................................. 6
   - Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter (Fig. 3) ................................................................. 9
6 Clypeus smooth and shining without longitudinal rugulae (Fig. 1) ....................................... inflata
   - Clypeus striated with rugulae (Fig. 2) ............................................................................. 7
7 Dorsal face of head strongly striated with abundant longitudinal rugulae. Scape not reaching posterior corner of head in large workers. Workers with pronounced size polymorphism ...................................................... aurita
   - Dorsal face of head not strongly striated with longitudinal rugulae. Scape reaching posterior corner of head. Workers monomorphic in size .................................................................................. 8
8 The posterior portion of pronotum with transverse rugulae in dorsal view (Fig. 6) ............... physothorax
   - The posterior portion of pronotum without distinct rugulae in dorsal view (Fig. 7) ............... onusta
9 Dorsal setae on posterior portion of fourth abdominal tergite directed medially (Fig. 8) ........ difformis
   - Dorsal setae on fourth abdominal tergite directed posteriorly (Fig. 9) ................................. 10
10 In lateral view, dorsal profile of promesonotum convex, propodeum distinctly raised relative to promesonotum, metanotal groove very deep .................................................................................. sewardi
   - In lateral view, dorsal profile of promesonotum convex, propodeum slightly raised relative to promesonotum, metanotal groove not so deep in dorsal median portion ......................................................ampullaris

Species accounts

*Crematogaster (Physocrema) ampullaris* F. Smith
(Figs 3, 10, 22)

Measurements and indices. HW 1.12–1.34; HL 1.04–1.28; CI 100–108; SL 0.95–1.02; SI 76–84; EL 0.22–0.24; PW 0.66–0.82; WL 1.26–1.48; PSL 0; PtL 0.34–0.48; PtW 0.28–0.34; PtH 0.19–0.24; PpL 0.24–0.28; PpW 0.29–0.36; PtHI 50–56; PtWI 70–74; PtWI 71–84; PpWI 117–129; WI 93–106 (Three workers measured).

Description of worker. Workers with pronounced size polymorphism.

In lateral view, pronotum and mesonotum forming a single convexity, propodeum slightly raised relative to mesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Metanotal groove convex posteriorly in dorsal view, deep and situated posterior to the posterior ridge of pronotum in lateral view; thorax strongly constricted in middle in dorsal view. In dorsal view, some longitudinal rugulae connecting between mesonotum and propodeum; the boundary distinct except for median portion. Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter. Propodeal spines absent.

Clypeus sculptured with longitudinal rugulae.

Standing pilosity sparse on dorsal face of head, abundant on mesonotum. Dorsal face of head with decumbent setae. Clypeus with short setae. Dorsal setae on fourth abdominal tergite appressed and directed posteriorly.

Body color reddish brown to black.

Distribution. This species is known from Indonesia (Sulawesi, Timor) and Philippines (Fig. 22).

Remarks. We have not been able to examine the types of ampullaris. According to Mr. Barry Bolton (pers comm Jan 2008), a search in the collection of BMNH and OXUM revealed that types of C. (P.) ampullaris were no longer present. But the original description and Donisthorpe’s key (1941) closely match the specimens examined.

This species is very similar to sewardi, but can be distinguished by the dorsal outline of the mesosoma and the depth of the metanotal groove.


Crematogaster (Physocrema) aurita Karavajew
(Figs 2, 11, 23)


Measurements and indices. HW 0.95–1.84; HL 0.89–1.8; CI 102–110; SL 0.91–1.4; SI 76–96; EL 0.22–0.34; PW 0.5–1.04; WL 1.07–2.13; PSL 0; PtL 0.31–0.62; PtW 0.23–0.48; PtH 0.16–0.32; PpL
0.18–0.42; PpW 0.26–0.49; PtHI 50–52; PtWI 74–80; PpWI 117–146; WI 100–112 (Three workers measured).

**Description of worker.** Workers with pronounced size polymorphism.
Scape of large workers not reaching posterior corner of head.

In lateral view, pronotum and mesonotum forming a single convexity; mesonotum differentiated from pronotum in large workers; propodeum slightly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Metanotal groove almost straight in dorsal view, not so deep and situated slightly posterior to the posterior ridge of pronotum in lateral view; thorax not strongly constricted in middle in dorsal view. In dorsal view, no longitudinal rugulae connecting between mesonotum and propodeum; the boundary distinct. Propodeal spiracle situated near the metapleural gland orifice, the distance between them about the same as the propodeal spiracle diameter. Propodeal spines absent.

Clypeus sculptured with longitudinal rugulae. Dorsal face of head covered with abundant longitudinal rugulae. Propodeal and metapleural area more or less smooth and shining in small workers, but distinctly rugulose and punctate in large workers.

Standing pilosity abundant, some pairs on dorsal face of head and abundant on dorsal portion of mesonotum. Dorsal face of head with appressed setae. Clypeus with short and long setae. Fourth abdominal tergite with suberect and appressed setae.

Body bicolored with head, promesonotum, petiole, postpetiole, gaster and legs dark-brown and with metanotal and propodeal area red-brown.

**Distribution.** This species is known from Indochinese Peninsula; Vietnam (southern parts), Laos, Cambodia, and Thailand (except for southern parts) (Fig. 23).

**Remarks.** This species is similar to *inflata* in the coloration, but can be distinguished by the rugulae on the clypeus and the sculptured body.


*Crematogaster* (*Physocrema*) *bakeri* Menozzi

*Crematogaster* (*Physocrema*) *bakeri* Menozzi, 1925: 447, fig. 6, worker from PHILIPPINES: Mindanao, Davao (6947) (probably in IEGG). [not seen]

**Remarks.** We have not been able to examine type-material of *C. (P.) bakeri*. From the original description and figure, this species is close to *C. (P.) inflata*, *C. (P.) onusta* and *C. (P.) physothorax*. But it is impossible to isolate *C. (P.) bakeri* from those species on the basis of the original description. It lacks the detailed description of the clypeus and promesonotum for separating the similar species. The taxonomic status of this species will remain uncertain until type-material can be examined.
**Crematogaster (Physocrema) difformis** F. Smith
(Figs 8, 12, 24)


*Crematogaster edentata* Mayr, 1867: 104. Holotype queen from INDONESIA: Java [not seen; location of type not known]. [junior synonym of *difformis* by Emery, 1901: 574].

**Measurements and indices.** HW 0.88–1.5; HL 0.84–1.34; CI 105–112; SL 0.74–1.06; SI 71–85; EL 0.15–0.28; PW 0.46–0.8; WL 1.01–1.74; PSL 0; PtL 0.26–0.48; PtW 0.19–0.4; PtH 0.15–0.26; PpL 0.16–0.28; PpW 0.2–0.4; PtHI 54–65; PtWI 74–95; PpWI 121–143; WI 90–107 (Three workers measured).

**Description of worker.** Workers with pronounced size polymorphism.

Scape just or not reaching posterior corner of head in large workers. Anterior-most portions of clypeus distinctly protruded anteriorly in large workers.

In lateral view, pronotum and mesonotum forming a single convexity; propodeum slightly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Promesonotal suture sometimes visible in large workers. Metanotal groove convex posteriorly in dorsal view, deep and situated posteriorly to the posterior ridge of pronotum in lateral view; thorax strongly constricted in middle in dorsal
view. In dorsal view, some longitudinal rugulae connecting between mesonotum and propodeum; the boundary distinct. Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter. Propodeal spines absent.

Clypeus sculptured with longitudinal rugulae.

Standing pilosity sparse on dorsal face of head, abundant on promesonotum. Dorsal face of head with decumbent setae. Clypeus with short setae. Fourth abdominal tergite with appressed setae. Dorsal setae on fourth abdominal tergite appressed and directed medially in the posterior portion.

Body color black.

**Distribution.** This species is known from Malay Peninsula and Borneo (Fig. 24).

**Remarks.** We have not been able to examine type-material of *C. edentata* Mayr. Although Emery synonymised it with *C. (P.) difformis*, it is impossible to clarify the synonymy from the original description and figure.

This species is similar to *C. (P.) ampullaris* and *C. (P.) sewardi*, but can be distinguished by the medially directed setae on the posterior portion of the fourth abdominal tergite.

**Specimens examined.** MALAYSIA: 1 worker, 1 male, 1 queen, Tower Region, Lambir N. P., Miri, Sawarak, 17. viii. 1995 (T. Yumoto); 7 workers, Tower Region, Lambir N. P., Miri, Sarawak (Sk. Yamane); 1 worker, 1 male, 1 queen, Lambir N. P., Miri, Sarawak, Borneo, 28. ix. 2005 (from epiphyte *Coronarium* sp.) (H. Tanaka); 2 workers, Gn. Mulu NP., 4th Division, Sarawak, ii. 1978 (light trap) (G. Holloway); 10 workers, 2 males, 1 queen, Lambir N. P. Miri, Sarawak, Borneo, 28. ix. 2005 (from *Platycerium* sp.) (H. Tanaka); 5 workers, 1 male, 1 queen, Lambir N. P., Miri, Sarawak, Borneo, 18. ix. 2005 (from *Platycerium* sp.) (H. Tanaka); 6 workers, Lambir N. P., Miri, Sarawak, Borneo, 18. ix. 2005 (from *Lecanopteris* sp.) (H. Tanaka); BRUNEI: 1 worker, Mixed Dipt. For., *Dryobalanops beccarii*, Site 7. 50m alt., Fog 11, Andalau, viii. 1991 (N. Mawdsley).

*Crematogaster (Physocrema) inflata* F. Smith (Figs 1, 13, 25)

*Crematogaster inflatus* F. Smith 1857: 76. LECTOTYPE worker from SINGAPORE (left OXUM worker of TYPE HYM: 1016 3-4 / 5) (by present designation) and four paralectotype workers: one paralectotype worker from SINGAPORE (OXUM) and three paralectotype workers from MALAYSIA: Sarawak, Borneo (BMNH) [examined]. Combination in *C. (Physocrema)* by Forel, 1912: 220. Description of queen by Santschi, 1928: 128.

*Crematogaster (Physocrema) moorei* Donisthorpe, 1941: 225. Holotype worker from PHILIPPINES: Bagnio, Luzon, (A. Moore) (BMNH) [examined]. *Syn. nov.*

et al.

**Measurements and indices.** HW 0.86–1.08; HL 0.85–1.05; CI 101–103; SL 0.85–0.96; SI 89–98; EL 0.20–0.22; PW 0.61–0.66; WL 1.18–1.34; PSL 0; PtP 0.32–0.38; PtW 0.23–0.27; PtH 0.16–0.19; PpL 0.18–0.20; PpW 0.24–0.30; PtHI 46–50; PtWI 67–71; PpWI 139–147; WI 106–110 (Three workers measured).

**Description of worker.** Workers polymorphic in size.

Scape exceeding posterior corner of head even for large workers.

In lateral view, pronotum convex; mesonotum and propodeum forming a single convexity. Anterior margin of pronotal collar distinctly concave in dorsal view. Metanotal groove slightly convex in dorsal median portion, not so deep and situated almost in the same line with the posterior ridge of pronotum in lateral view; thorax not strongly constricted in middle in dorsal view. In dorsal view, no longitudinal rugulae connecting between mesonotum and propodeum; the boundary distinct except for median portion. Propodeal spiracle situated near the metapleural gland orifice, the distance between them about the same as the propodeal spiracle diameter. Propodeal spines absent.

Clypeus smooth and shining without longitudinal rugulae. Integument smooth and shining.
Standing pilosity sparse, some pairs on dorsal face of head and dorsal portion of mesonotum. Dorsal face of head with appressed setae. Clypeus with abundant short and long setae. Fourth abdominal tergite with abundant appressed setae.

Body bicolored with head, promesonotum, petiole, postpetiole, gaster and legs red-brown and with metanotal and propodeal area yellow.

Distribution. This species is a wide-ranging species found from southern Thailand and Malaysia (Peninsula and Borneo) to the Philippines (Fig. 25).

Remarks. The bicolored pattern of yellow and red-brown is distinctive and unique to this species. This coloration is possibly a model in Batesian mimicry with other arthropods (Maruyama et al. 2003; Ito et al., 2004).


Crematogaster (Physocrema) mucronata Emery stat. rev.
(Figs 14, 26)

*Crematogaster deformis* var. *mucronata* Emery, 1900: 690. Holotype worker from INDONESIA: Pangherang-Pisang, Sumatra (*E. Modigliani*) (MCSN) [examined]. Combination in *C. (Physocrema)* and raised to species by Emery, 1922: 140; Donisthorpe, 1941: 226.

*Crematogaster (Physocrema) fulmeki* Forel, 1922: 95. LECTOTYPE worker (MHNG worker) (by present designation) and two paralectotype workers from INDONESIA: Sumatra (*L. Fulmeki*) (MCSN, MHNG) [examined]. See also Santschi, 1928: 127. *Syn. nov.*

Measurements and indices. HW 0.96–1.00; HL 0.92–0.97; CI 103–104; SL 0.68–0.69; SI 68–72; EL 0.16–0.19; PW 0.57–0.65; WL 1.03–1.09; PSL 0.10–0.12; PtL 0.28–0.32; PmL 0.22–0.24; PtH 0.16–0.19; PpL 0.19–0.20; PpW 0.26–0.28; PtHI 53–62; PtWI 70–76; PpWI 127–140; WI 117–119 (Three workers measured).

Description of worker. Workers monomorphic in size.

Scape not reaching posterior corner of head.

In lateral view, pronotum rises steeply; pronotum and mesonotum forming a single convexity; propodeum distinctly raised relative to promesonotum. Anterior margin of pronotal collar not concave in dorsal view. Metanotal groove convex posteriorly in dorsal view, deep; thorax strongly constricted in middle in dorsal view. In dorsal view, no longitudinal rugulae connecting between mesonotum and propodeum; the boundary distinct. Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter. Propodeal spines present.

In dorsal view, petiole subquadrate with subparallel sides, longer than broad. Postpetiole weakly bilobed but longitudinal median sulcus distinctly undeveloped, posterior corners acute.

Clypeus smooth and shining without distinct rugulae. Integument smooth.

Standing pilosity sparse, some pairs on dorsal face of head and many on dorsal portion of pronotum. Dorsal face of head with decumbent setae. Clypeus with long and short setae. Mesosoma with abundant setae. Fourth abdominal tergite with abundant appressed long setae.

Body color rufous to brown.
FIGURES 10–17. Physocrema species in lateral view. Scale bars are all 0.5mm. 10—C. (P.) ampullaris, [Sampulage (1000m), nr Mangktana, S. Sulawesi]; 11—C. (P.) aurita, [Maeklong Watershed Research Station, Kanchanaburi Prov.]; 12—C. (P.) difformis, [Lambar N. P., Miri, Sarawak, Borneo]; 13—C. (P.) inflata, [Ulu Gombak, Malay Peninsula]; 14—C. (P.) mucronata, [Satar’s House, Ulu Gadut, nr Padang, Sumatra]; 15—C. (P.) onusta, [Barito Ulu 150m alt., Kalimantan]; 16—C. (P.) physothorax, [Universiti Kebangsaan Malaysia Forest, Malay Peninsula]; 17—C. (P.) sewardi, [7miles, Cameron Highland, Malay Peninsula].
FIGURES 18–20. *Physocrema* species in lateral view. Scale bars are all 0.5mm. 18—*C. (P.) tanakai*, holotype [Lambir N. P., Miri, Sarawak, Borneo]; 19—*C. (P.) vacca*, [Old Tower R., Lambir N. P., Miri, Sarawak, Borneo]; 20—*C. (P.) yamanei*, holotype [Parapat (900m alt), Danau Toba, N. Sumatra].

**Distribution.** This species is known from Sumatra (Fig. 26).

**Remarks.** This species is uniquely characterized by the combination of (1) 3-jointed antennal club; (2) steeply raised pronotum; (3) developed propodeal spines; (4) moderately swollen propodeum; and (5) processes of the posterior corners of the petiole in dorsal view. In the future, this species may be referred to another subgenus by these unique characters.


*Crematogaster (Physocrema) onusta* Stitz
(Figs 7, 15, 27)

*Crematogaster (Physocrema) onusta* Stitz, 1925: 118. LECTOTYPE worker (ZMHB worker, GBIF-D/FoCol 1439) (by present designation) and seven paralectotype workers from PHILIPPINES: Palawan (*G. Boettcher*) (MCZC, ZMHB) [examined]. Combination in *C. (Paracrema)* by Donisthorpe, 1941: 226.

**Measurements and indices.** HW 0.82–1.05; HL 0.76–0.95; CI 109–111; SL 0.66–0.85; SI 80–81; EL 0.18–0.22; PW 0.46–0.51; WL 1–1.22; PSL 0; PtL 0.28–0.34; PtW 0.22–0.26; PtH 0.14–0.16; PpL 0.16–0.19; PpW 0.2–0.24; PtHI 42–52; PtWI 67–86; PpWI 125–129; WI 94–100 (Three workers measured).

**Description of worker.** Workers monomorphic in size.

Scape reaching posterior corner of head.
In lateral view, pronotum and mesonotum forming a single convexity; propodeum slightly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Metanotal groove almost straight in dorsal view, not so deep and situated posterior to the posterior ridge of pronotum in lateral view; thorax not strongly constricted in middle in dorsal view. In dorsal view, several longitudinal rugulae connecting between mesonotum and propodeum; the boundary indistinct. Propodeal spiracle situated near the metapleural gland orifice, the distance between them about the same as the propodeal spiracle diameter. Propodeal spines absent.

Clypeus sculptured with longitudinal rugulae. Pronotum punctate, but without distinct rugulae. Standing pilosity sparse, a few pairs on dorsal face of head and dorsal portion of mesonotum. Dorsal face of head with decumbent setae. Clypeus with setae. Fourth abdominal tergite with decumbent setae.

Body color varies from red (specimens from Tioman Island) to brown (specimens from other localities).

**Distribution.** This species is known from Tioman Island and Borneo (Fig. 27).

**Remarks.** This species is very similar to *C. (P.) physothorax*, but can be distinguished by the rugulae on the pronotum. This species was transferred to *Paracrema* by Donisthorpe (1941), but is here replaced in *Physocrema*.


*Crematogaster (Physocrema) physothorax* Emery
(Figs 4, 5, 6, 16, 28)


**Measurements and indices.** HW 1.09–1.19; HL 0.97–1.13; CI 104–111; SL 0.89–1.01; SI 84–88; EL 0.20–0.23; PW 0.55–0.63; WL 1.12–1.39; PSL 0; PtL 0.32–0.38; PtW 0.23–0.28; PtH 0.16–0.19; PpL 0.19–0.24; PpW 0.24–0.26; PtHI 50–54; PtWI 71–83; PpWI 106–129; WI 90–106 (Three workers measured).

**Description of worker.** Workers monomorphic or weakly polymorphic in size.

Scape reaching posterior corner of head.

In lateral view, pronotum and mesonotum forming a single convexity; propodeum slightly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Metanotal groove almost straight in dorsal view, not so deep and situated posteriorly to the posterior ridge of pronotum in lateral view; thorax not strongly constricted in middle in dorsal view. In dorsal view, a few longitudinal rugulae connecting between mesonotum and propodeum; but the boundary distinct. Propodeal spiracle situated near the metapleural gland orifice, the distance between them about the same as the propodeal spiracle diameter. Propodeal spines absent.

Clypeus sculptured with longitudinal rugulae. Integument essentially smooth and shining. Rugulae present on the anterior portion of dorsal face of head. Transverse rugulae present on the posterior portion of pronotum.

Standing pilosity sparse, a few pairs on dorsal face of head and promesonotum. Dorsal face of head with appressed setae. Clypeus with decumbent setae. Fourth abdominal tergite with appressed setae.

Body color black.

**Distribution.** This species is known from Malay Peninsula; Myanmar (southeastern parts), Thailand (southern parts) and Malaysia (Peninsula) (Fig. 28).
Remarks. This species is very similar to C. (P.) onusta, but the dorsal portion of the pronotum is characteristic with transverse rugulae.


Crematogaster (Physocrema) sewardi Forel
(Figs 9, 17, 29)

Crematogaster deformis r. sewardi Forel, 1901: 64. LECTOTYPE worker (top specimen of two on one pin) (by present designation) and one paralectotype worker and queen from MALAYSIA: Borneo (H. Seward) (MHNG) [examined]. Combination in C. (Physocrema) by Emery, 1922: 140. Raised to species by Hosoishi & Ogata 2008: 7.

Measurements and indices. HW 0.85–1.32; HL 0.77–1.22; CI 105–111; SL 0.70–0.96; SI 72–83; EL 0.16–0.24; PW 0.51–0.74; WL 0.96–1.40; PSL 0; PtL 0.28–0.42; PtW 0.21–0.36; PtH 0.15–0.22; PpL 0.19–0.28; PpW 0.23–0.34; PtHl 52–57; PtWI 74–86; PpWI 113–129; WI 94–116 (Three workers measured).

Description of worker. Workers with pronounced size polymorphism.

Scape not reaching posterior corner of head in large workers.

In lateral view, dorsal profile of promesonotum convex; propodeum distinctly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Metanotal groove convex posteriorly in dorsal view in large workers, deep and situated posteriorly to the posterior ridge of pronotum in lateral view; thorax strongly constricted in middle in dorsal view. In dorsal view, some longitudinal rugulae connecting between mesonotum and propodeum; the boundary distinct. Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter. Propodeal spines absent.

Clypeus sculptured with longitudinal rugulae.

Standing pilosity sparse on dorsal face of head, abundant on promesonotum. Dorsal face of head with decumbent setae. Clypeus with short setae. Fourth abdominal tergite with appressed setae. Dorsal setae on fourth abdominal tergite directed posteriorly.

Body color black.

Distribution. Crematogaster (P.) sewardi is the most wide-ranging species of the subgenus Physocrema (Fig. 29). This species ranges from Thailand to Malaysia (Peninsula and Borneo) and to Indonesia (Kalimantan, Sumatra, Krakatau Island, Java, Bali and Lombok).

Remarks. This species is very similar to C. (P.) ampullaris, but can be distinguished by the dorsal outline of the mesosoma and the depth of the metanotal groove.

The MHNG syntypes were lighter colored than normal, but otherwise match the characters of the specimens examined.

Among the Physocrema species, C. (P.) ampullaris, C. (P.) difformis, and C. (P.) sewardi are very similar to each other. Crematogaster (P.) sewardi is widely distributed in South East Asia, but almost all have been referred to as C. (P.) difformis in the past. It is also likely that C. (P.) sewardi has been misidentified as C. (P.) difformis in the literature (Attygalle et al. 1989; Gay & Hensen, 1992; Ito et al. 2001; Jaitrong & Nabhitaabtha, 2005; Jones et al. 2005). Based on the key above, C. (P.) difformis can be easily distinguished from ampullaris and sewardi, but as revealed above, the latter two species are very similar to each other and have been frequently confused. Crematogaster (P.) difformis and C. (P.) sewardi are geographically sympartric in the Malay Peninsula and Borneo, whereas C. (P.) ampullaris and C. (P.) sewardi are allopatric. Crematogaster (P.) ampullaris is found in Sulawesi, Timor and Philippines, and C. (P.) sewardi in Indochina.
Malay Peninsula, Borneo, Sumatra, Krakatau Island, Java, Bali and Lombok. The slight morphological differences and allopatric distribution may imply that the two species are relatively new taxa.


*Crematogaster* (*Physocrema*) *tanakai* Hosoishi & Ogata sp. nov.

(Fig. 18, 30)


Paratypes. 1 male, same data as holotype (FRC).

**Measurements and indices.** HW 1.66; HL 1.52; CI 109; SL 0.98; SI 59; EL 0.26; PW 0.74; WL 1.42; PSL 0; PtL 0.4; PtW 0.34; PtH 0.24; PpL 0.24; PpW 0.34; PtHI 60; PtWI 85; PpWI 142; WI 100 (one worker measured).

**Description of worker.** Scape not reaching posterior corner of head. Dorsal median portion of the head swollen.

In lateral view, promesonotum convex; mesonotum differentiated from pronotum; propodeum slightly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Promesonotal suture visible. Metanotal groove convex posteriorly in dorsal view, deep and situated posteriorly to the posterior ridge of pronotum in lateral view; thorax strongly constricted in middle in dorsal view. In dorsal view, some longitudinal rugulae connecting between mesonotum and propodeum; the boundary distinct. Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter. Propodeal spines absent.

**Head** red, mesosoma and gaster brown.

**Distribution.** This species is known only from the type locality in Borneo (Fig. 30).

**Remarks.** This species is unique among the Asian *Crematogaster* ants in having a swollen dorsal median portion of the head.

This species was collected together with *C. (P) difformis* nesting within the epiphyte *Platycerium* sp., suggesting the possibility that it might be associated with *C. (P) difformis*.

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**Crematogaster (Physocrema) vacca Forel, stat. nov.** (Fig. 19, 31)

*Crematogaster deformis vacca* Forel, 1911: 384. LECTOTYPE worker (by present designation) from MALAYSIA: Berhentian Tingi, Nigri Sembilan, Malacca (R. Martin) (MHNG) [examined]. Combination in *C. (Physocrema)* by Emery, 1922: 140.

*Crematogaster (Physocrema) stethogompha* Wheeler, W. M., 1919: 75. LECTOTYPE worker (by present designation) and paralectotype workers from MALAYSIA: Kuching, Borneo, No. 8948 (*H. Smith*) (MCZC). [examined]. Syn. nov.


**Measurements and indices.** HW 1.09–1.62; HL 1.03–1.46; CI 106–111; SL 0.91–1.14; SI 70–83; EL 0.20–0.26; PW 0.64–0.84; WL 1.32–1.76; PSL 0.16–0.18; PtL 0.41–0.54; PtW 0.37–0.42; PtH 0.23–0.30; PpL 0.23–0.30; PpW 0.30–0.42; PtHI 56–57; PtWI 78–90; PpWI 129–140; WI 81–100 (Three workers measured).

**Description of worker.** Workers with pronounced size polymorphism.

Scape not reaching posterior corner of head in large workers.

In lateral view, pronotum and mesonotum forming a single convexity; propodeum distinctly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Metanotal groove convex posteriorly in dorsal view, deep and situated posteriorly to the posterior ridge of pronotum in lateral view; thorax not strongly constricted in middle in dorsal view. In dorsal view, many longitudinal rugulae connecting between mesonotum and propodeum; but the boundary distinct. Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter. Propodeal spines present.

Postpetiole slightly bilobed behind without longitudinal median sulcus.

Clypeus sculptured with longitudinal rugulae. Reticulate rugulae on dorsal face of head, pronotum, mesonotum and propodeum.

Standing pilosity sparse on dorsal face of head and mesosoma. Dorsal face of head with appressed setae. Fourth abdominal tergite with a few erect setae and abundant appressed setae.

Body color dark brown to black.

**Distribution.** This species is known from Malay Peninsula and Borneo (Fig. 31).

**Remarks.** The name on the labels of the type specimen,"*Crematogaster stethogompha laevinodis*" does not correspond to the name "*Crematogaster stethogompha detritinodis*" used in Wheeler’s description. He presumably changed the name between the time the labels were prepared and the manuscript submitted.

This species is easily distinguished from *difformis* and its subspecies by the well developed propodeal spines. We treated it as a distinct species.

**Specimens examined.** MALAYSIA: 3 workers, Pasoh Forest Research Center, Negeri Sembilan, xi. 1994 (fog sample, *M. Brendell*, *K. Jackson* and *S. Lewis*); 1 worker, Old Tower R., Lambir N.P., Miri,
Sarawak, 20. i. 1993 (Sk. Yamane); 1 worker, Old Tower R., Lambir N.P., Miri, Sarawak, 22. i. 1993 (Sk. Yamane).

Crematogaster (Physocrema) yamanei Hosoishi & Ogata, sp. nov.
(Fig. 20, 32)

HOLOTYPE worker from INDONESIA: Parapat (900m alt), Danau Toba, N. Sumatra, 19. viii. 2002 (SU02-SKY-66) (Sk Yamane) (MZB).

Paratypes. 12 workers, same data as holotype (BMNH, KUM, MCSN, MCZC, MHNG, NHMB).

Measurements and indices. HW 1.15–1.7; HL 1.03–1.45; CI 112–118; SL 0.93–1.1; SI 65–81; EL 0.2–0.28; PW 0.63–0.9; WL 1.26–1.78; PSL 0.15–0.18; PtL 0.41–0.55; PtW 0.36–0.5; PtH 0.23–0.28; PpL 0.22–0.33; PpW 0.31–0.48; PtHI 50–57; PtWI 90–96; PtWI 143–146; WI 85–95 (Three workers measured).

Description of worker. Workers with pronounced size polymorphism.

Scape reaching posterior corner of the head in large workers.

In lateral view, pronotum and mesonotum forming a single convexity; propodeum slightly raised relative to promesonotum. Anterior margin of pronotal collar slightly concave in dorsal view. Metanotal groove not convex posteriorly in dorsal view, not very deep and situated posterior to the posterior ridge of pronotum in lateral view; thorax not strongly constricted in middle in dorsal view. In dorsal view, many longitudinal rugulae connecting between mesonotum and propodeum; but the boundary distinct. Propodeal spiracle situated away from the metapleural gland orifice, the distance between them much greater than the propodeal spiracle diameter. Propodeal spines present.

Postpetiole slightly bilobed behind without longitudinal median sulcus.

Clypeus sculptured with longitudinal rugulae. Longitudinal rugulae on dorsal face of head, pronotum, mesonotum and propodeum.

Standing pilosity sparse on dorsal face of head and mesosoma. Dorsal face of head with appressed setae. Fourth abdominal tergite with some erect setae and abundant appressed setae.

Body color black.

Distribution. This species is known only from the type locality in Sumatra (Fig. 32).

Remarks. This species is very similar to C. (P.) vacca. It differs in the reticulate rugulae on the head and promesonotum, and the relative depth of the metanotal groove.

Species excluded from the subgenus Physocrema

Crematogaster (Oxygyne) tumidula Emery


Remarks. Examination of syntype workers in MCSN reveals that tumidula does not belong to the subgenus Physocrema. Characteristic features include: frontal carinae not developed; anterior clypeal margin not concave; metapleural gland orifice slit-shaped; petiole broader anteriorly. These features are characteristic of the subgenus Oxygyne and we consider C. tumidula to be referred to that subgenus.

Discussion

Polymorphism

Most Physocrema species show strong polymorphism in size and sculpture and it is especially pronounced in C. (P.) ampullaris, C. (P.) aurita, C. (P.) difformis, C. (P.) sewardi, C. (P.) yamanei and C. (P.) vacca, and weakly so in C. (P.) inflata, C. (P.) mucronata, C. (P.) onusta and C. (P.) physothorax. In the especially pronounced group, small workers are very different from large workers. For example, in C. (P.) aurita, the scape clearly exceeds the posterior corner of the head in small workers, but it does not in large workers. In
general, the mandible has 5 teeth on the masticatory margin, but in some species smaller specimens have only 4 teeth. The postpetiole lacks a longitudinal median sulcus, but it is weakly bilobed posteriorly in large workers of some species. To diagnose *Physocrema* species, large workers are more useful than smaller workers, particularly in closely similar species.

Relationship of *Physocrema* to neotropical *Crematogaster* ants

In the past, Forel (1912, 1913) included two Neotropical ants, *C. arcuata* Forel and *C. montezumia* Smith, in the subgenus *Physocrema*. Later these two species were transferred to the subgenus *Orthocrema* Santschi, 1918 (Emery, 1922) and presently they are placed in the subgenus *Neocrema* Santschi, 1918 (Santschi, 1922; Kempf, 1972; Bolton, 1995, 2006). These two ants have clearly swollen propodeum and circular-shaped metapleural gland orifices, but none of the other diagnostic features of *Physocrema* listed above. They have the following features: 3-jointed antennal club in *arcuata* and 2-jointed in *montezumia*; anterior margin of clypeus straight; anterolateral margins of clypeus not protruded anteriorly; the shape of the petiole subquadrate in dorsal view. These two species should not be placed in the subgenus *Physocrema*.

Biology

Workers in some *Physocrema* species release defensive secretions from their metapleural glands when they are disturbed (Bushinger & Maschwitz, 1984). Two arthropods were reported to be possible Batesian mimics of *C. (P.) inflata*, because of the defensive mechanism. A *Camponotus* ant nests and forages near the nest of *C. (P.) inflata* and has similar body coloring pattern and walking behavior (Ito et al. 2004). The other is a staphylinid beetle, *Drusilla inflatae*, collected near colonies of *C. (P.) inflata* (Maruyama et al. 2003). The color pattern of the beetle closely resembles that of *C. (P.) inflata*. The secretions contain a mixture of phenols in *C. (P.) difformis* and *C. (P.) inflata* (Attygalle et al. 1989; Jones et al. 2005). Jones et al. (2005) suggest that analyses of the secretions may be useful for taxonomic and phylogenetic studies.

Some species of the subgenus *Physocrema* are reported to be mutualistic ants in ant plants. Several *Lecanopteris* fern species are inhabited by these ants in Malay Peninsula, Borneo, Sumatra and Sulawesi (Gay & Hensen, 1992). The rubiaceous tree, *Neonauclea cyrtopoda*, was occupied by these ants in North Sumatra (Maschwitz & Fiala, 1995). The authors identified the black *Crematogaster* ants with an inflated propodeum as *C. (P.) difformis*, but those identifications are doubtful because of the similar species. The reported associations were probably opportunistic, and there is no indication that any species of *Physocrema* form obligate associations with ant plants. This study should facilitate future studies of mimicry and mutualism.

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