Revision of the oriental ant genus *Cladomyrma*,
with an outline of the higher classification
of the Formicinae (Hymenoptera: Formicidae)

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Abstract. The Oriental ant genus *Cladomyrma* is revised and possible phylogenetic relationships are discussed. *Cladomyrma hewitti* and *hobbyi* are newly synonymized with *andreii*. *Cladomyrma cryptata*, *maschwitzi*, *mossyna* and *petalae* are described as new species. A lectotype for *Cladomyrma hewitti* is designated. A synopsis of the classification of Formicinae, based on new morphological characters, is provided. New morphological characters at the generic level are described and the relationships of *Cladomyrma* within Formicinae are discussed.

Introduction

This study was initiated by a discussion of the phylogenetic relationships of the old world genera *Aphomomyrmex*, *Cladomyrma* and *Petalomyrmex* and the new world genus *Myrmelachista*; all, except some in *Myrmelachista*, obligatory inhabitants of internodes of rainforest trees, especially legumes (McKey, 1991). Their life style, living in branches and hollow internodes of climbers and trees, which are actively opened by the queen, is a possible synapomorphy for these genera (U. Maschwitz and D. McKey, pers. comm.). All the queens of these ant genera show a similar flattened head and alitrunk, which has been interpreted as an adaptation to their life in plant cavities (Wheeler, 1910; Snelling, 1979; McKey, 1991), and therefore the question has been raised as to whether they form a monophyletic taxon (Maschwitz et al., 1991; D. McKey, pers. comm.).

The old world genera of this assemblage of arboreal ant genera (i.e. *Aphomomyrmex*, *Cladomyrma* and *Petalomyrmex*) are all rarely collected and thus are poorly represented in our collections. Furthermore, the descriptions of the three *Cladomyrma* species are based on queens, which are mainly caught by light traps. This makes the association of recently collected workers with the described queens difficult. Samples collected during recent biological studies of *Cladomyrma* in Malaysia (Maschwitz et al., 1991), could not be identified to species level, and it became apparent that there were several undescribed species.

This paper has three purposes: to discuss the phylogenetic placement of *Cladomyrma* within the Formicinae; to assess possible relationships of *Cladomyrma* with *Aphomomyrmex*, *Myrmelachista* and *Petalomyrmex*; and to provide a revision of *Cladomyrma* species needed by workers currently studying their biology.

The Formicinae includes forty-eight recent genera, with approximately 3000 described species mostly in tropical regions. Members of this subfamily are diagnosed by the acidopore at the apex of the terminal gastral sternite, by the reduction of the sting apparatus to two lateral spiracular plates, a median connection and an anal arc, and a replacement of the sting with an acid-spraying system, and by a highly modified proventriculus (Emery, 1925; Eisner, 1957). Beside the proventricular structure, no external morphological characters are known to diagnose the males of Formicinae. Nevertheless,
the Formicinae are considered a monophyletic taxon, with the above-mentioned characters as autapomorphies. Keys to the subfamilies and the genera, a synopsis of the genera and an overview of formicine behaviour and ecology is provided by Hölldobler & Wilson (1990); the distribution of the genera is summarized by Brown (1973).

Cladomyrma was described by Wheeler (1920) as a myrmelachistine genus with eight- to ten-segmented antennae in the queen and worker caste, ten to eleven in the male sex, and the proventriculus with only short sepals. Wheeler also included in the same tribe Aphomomyrmex, Brachymyrmex and Myrmelachista. Emery (1925) redefined Myrmelachistini to include only the two genera Myrmelachista and Stigmatomachus, both with the female castes with less than twelve antennal segments and a distinct antennal club formed by the three to four terminal segments. He placed Aphomomyrmex, Brachymyrmex, Cladomyrma, Dimorphomyrmex and Geosmyrmex in Dimorphomyrmicini based on the eight- to nine-segmented antennae, the large eyes and the short frontal carinae.

Based on a combination of larval characters Wheeler & Wheeler (1976, 1985) included Aphomomyrmex, Brachymyrmex, Cladomyrma and Petalomyrmex in Brachymyrmecini and Myrmelachista in Myrmelachistini. This arrangement in two different tribes excluded Aphomomyrmex + Cladomyrma + Myrmelachista + Petalomyrmex as a monophyletic group and, furthermore, did not resolve the relationships of these arboreal genera. This is not reflected in Hölldobler & Wilson’s (1990) classification, where they included Aphomomyrmex, Brachymyrmex, Cladomyrma, Myrmelachista, Petalomyrmex and Pseudaphomomyrmex in the tribe Myrmelachistini and therefore did not exclude a possible monophyletic origin for those genera.

Snelling (1979) confirmed, after the examination of one queen syntype of Cladomyrma hewitti and the comparison of it with Petalomyrmex phylax and Aphomomyrmex after, that Cladomyrma and Aphomomyrmex represent distinct ant genera. Snelling did not comment on possible relationships.

Measurements and indices

Morphological terminology in the text follows Hölldobler & Wilson (1990).

Alitrunk length (AL). The diagonal length of the alitrunk in profile from the point at which the pronotum meets the cervical shield to the posterior base of the metapleuron.

Cephalic index (CI). HW×100/HL.

Eye index (EI). EL×100/HW.

Eye length (EL). The maximum diameter of the eye.

Head length (HL). The length of the head proper, excluding the mandibles, measured from the mid-point of the anterior clypeal margin to the mid-point of the occipital margin, in full-face view.

Head width (HW). The maximum width of the head in full-face view, measured below the eyes.

Palp formula (PF). Number of maxillary palp segments followed by number of labial palp segments; e.g. PF 6, 4.

Scape index (SI). SL×100/HW.

Scape length (SL). The maximum straight line length of the antennal scape excluding the basal constriction or neck to the condylar bulb.

All measurements are given as minimum, maximum and in parentheses the median, the unit is mm; e.g. AL 1.23–1.45 (1.40).

Abbreviations of museums

CDA: Collection of D.Agosti, Uster, Switzerland. FRIMK: Forest Research Institute of Malaysia, Kepong, Malaysia. MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A. MHNG: Muséum d’Histoire Naturelle, Geneva, Switzerland. MNSG: Museo Civico di Storia Naturale, Genoa, Italy. BMNH: The Natural History Museum, London, U.K. RNHL: Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

The phylogenetic relationships of Cladomyrma

I am currently involved in a study on the phylogeny of the Formicinae (Agosti, in prep.), detailed results of which will be provided in the future. However, preliminary results indicate that Cladomyrma is not closely related to Aphomomyrmex, Myrmelachista and Petalomyrmex, and even belongs to an entirely different lineage (genus-group) within the Formicinae.
The following characters are of potential significance for the phylogeny of this subfamily, and were used in defining the genus-groups.

**Hind coxae.** In ventral view, the petiolar insertion either is not extended anterior to an imaginary line between the two anteriormost points of the hind coxal cavity (Fig. 1B) or reaches anterior to the imaginary line (Figs 2B, 3B; Agosti & Bolton, 1991: Figs 3, 4). In parallel, the hind coxae are closely set in the first (Fig. 1A) or widely separated (Fig. 3A). This is obscured when the anterior part of the petiolar cavity is covered with a non-sclerotized membrane (Fig. 2). When the hind coxae are widely separated, the mesocoxae meet medially, forming a U-shaped concavity (Fig. 3A) to accommodate the petiole when the latter is downflexed.

**Ventral side of the petiole.** In profile the ventral face of the petiole is v-shaped or u-shaped, corresponding to the respective position of the hind coxae.

Functionally the position of the hind coxae and the shape of the ventral side of the petiole seem to be two differently evolved methods for keeping the petiole in a defined position, e.g. during defensive behaviour of *Formica* species, where the ant is spraying poison gland compounds by pulling the gaster under the ventral side of the alitrunk in the direction of the enemy.

**Helcium.** The helcium or collar-like pretergite and pre sternite of the third abdominal segment (Bolton, 1990) is situated either in the tergite, or between tergite and sternite, or in the sternite of the first gastral segment, and is either simple or bipartite. In the case where the helcium is situated in the tergite, the ventral part of the helcium is separated from the adjacent sternite by a distinctive transverse groove, which is easily seen as a brighter strip across the anteriormost part of the segment (Fig. 4).

The position of the helcium is, in all genera except *Oecophylla*, ventral on the anterior face of the first gastral segment. In the *Formica* genus-group the helcium is never concealed by the segment as is the case in most of the genera of the *Lasius* and the *Pseudolasius* genus-group.

**First gastral segment.** The ventral position of the helcium coincides with three main structural types of the first gastral segment. The *Lasius*-type (Fig. 5) has the helcium surrounded by the sternite, but the anteriormost part of the tergite is extended ventrally, so that the lateral sides of the helcium are effectively part of the pretergite and only the ventral side part of the pre sternite. The gastral tergites conceal the sternites laterally. The *Pseudolasius*-type (Fig. 6) has the helcium entirely in the sternite and the first gastral tergite and sternite are anteriorly fused. The gastral tergites and sternites meet laterally. The *Formica* (Fig. 4) and *Oecophylla*-type (Fig. 7) have the helcium entirely within the first gastral tergite, which is much more extended than the sternite, which is restricted to the ventral face. The helcium of the *Oecophylla*-type (Fig. 7) is bipartite, with the pre sternite forming the ventral face. The *Formica*-type (Fig. 4) has the helcium separated by a suture from the sternite.

The combination of those characters diagnose the following four genus-groups within the Formicinae:

**Oecophylla genus-group**

**DIAGNOSIS.** Hind coxae closely set (as in Fig. 1); in profile petiole ventrally v-shaped; helcium bipartite; helcium set medially with the sternite and the tergite of about the same size or ventrally with an enlarged tergite; tergite and sternite not fused anteriorly (Fig. 7).

*Anoplolepis pro parte* (*Anoplolepis custodiens* species-group and *longipes* species-group), *Gigantiops, Myrnoteras, Oecophylla*.

**Formica genus-group**

**DIAGNOSIS.** Hind coxae closely set (Fig. 1); in profile petiole ventrally v-shaped; helcium simple, the sternite separated from the helcium by a suture; helcium set ventrally with an enlarged tergite; tergite and sternite not fused anteriorly (Fig. 4).

*Alloformica, Bajcaridris, Calomyrmex, Camponotus, Cataglyphis, Dendromyrmex, Echinopla, Forelphilus, Formica, Gesomyrmex, Lasiothanes, Melophorus, Myrmecorhynchus, Notoncus, Notostigma, Opisthopsis, Phasmosmyrmex, Polyergus, Polyrhachis, Pseudonotoncus, Proformica, Rossomyrmex, Teratomyrmex.*

**Lasius genus-group**

**DIAGNOSIS.** Hind coxae widely separated (Figs 2, 3); in profile petiole ventrally u-shaped; helcium bipartite; helcium set ventrally with a
tergite which is extended anteriorly to the ventral side of the helcium; tergite and sternite not fused anteriorly (Fig. 5).

*Acanthomyops, Acropyga s.lat., Cladomyrma, Myrmecocystus, Lasius, Prenolepis, Prolasius.*

*Pseudolasius* genus-group

**DIAGNOSIS.** Hind coxae widely separated (Figs 2, 3); in profile petiole ventrally u-shaped; helcium simple; helcium antero-ventral, often concealed by the anteriorly fused sternite and tergite, which meet laterally (Fig. 6).

*Acantholepis, Anoplolepis triemenii species-group, Aphomomyrmex, Brachymyrmex, Bregmatomyrma, Euprenolepis, Malacomyrma, Myrmelachista, Paratrechina, Petalomyrmex, Plagiolepis, Pseudolasius.*

*Incertae sedis*

(No material analysed).

*Overbeckia, Santschiella, Stigmacros, Pseudostigmacros.*

A comparison of the above-described characters with those within the Dolichoderinae, the supposed sister group of the Formicinae, indicates that the *Oecophylla* type of the first gastral segment and the petiolar articulation which does not reach in front of a line spanned between the two anteriormost points of the hind coxal cavities are the plesiomorphic states. The occurrence of the first gastral structures of the *Pseudolasius* and the *Lasius* type might be...
Figs 4–7. The four structural types of the first gastral segment of formicine ants, in ventral view. 4, Formica-type (worker of *Cataglyphis nodus*). 5, Lasius-type (worker of *Cladomyrma maschwitzi*). 6, Pseudolasius-type (worker of *Aphomomyrmex afer*). 7, Oecophylla-type (worker of *Oecophylla longinoda*).

Independently derived as they are present in highly derived dolichoderine genera, such as *Frogatella* and *Turneria*, and *Bothriomyrmex* respectively (S. O. Shattuck, pers. comm.).

This classification contradicts the old system (e.g. Emery, 1925), which has mainly been based on the structure of the proventriculus, from an asepalous state in the Melophorini to a long sepalous state in Camponotini or Formicina (i.e. Euformicinae). The last two tribes are characterized by two different types of proventriculus (Eisner, 1957) inferring that those two structures are not homologous and that possibly there have been further transformations from an asepalous to a sepalous proventriculus. This supports the proposed arrangement, with the Melophorini split between the *Formica*- and the *Lasius*-group.
The use of larval characters supports Emery’s system, with minor changes (Wheeler & Wheeler, 1976, 1985), but a complete assessment of larval characters for the Formicinae needs to be done to understand the main points of discordance.

The classification of Hölldobler & Wilson (1990) would support the suggested monophyly of those arboreal ants; however, they did not provide a diagnosis for their classification.

The genus groups presented in this paper contradict previous classifications. A complete cladistic analysis of the Formicinae will be provided later. However, the proposed placement of Cladomyrma in the Lasius genus-group and Aphomomyrmex, Myrmelachista and Petalomymrnex in the Pseudolasius genus-group, inferred by the use of the above-mentioned characters, make the monophyly of Aphomomyrmex, Cladomyrma, Myrmelachista and Petalomymrnx highly unlikely.

Within the Lasius genus-group Acropyga could be considered as the possible sister group of Cladomyrma. The similar alitrunk structure and head shape of the workers of species such as Acropyga acutiventris could also be convergences, as a similarly structured alitrunk is also present in some species groups of Camponotus (e.g. subgenus Tanaemymrnx).

**CLADOMYRMA Wheeler**

Cladomyrma Wheeler, 1920: 53. Type-species Aphomomyrmex hewitti Wheeler, 1910: 132 (C. andrei (Emery)), by original designation.

**DIAGNOSIS**

**Worker.** Arboreal formicine ants with the following diagnostic characters.

1 Dimorphic worker caste (see comments); AL of major workers 0.8–1.7 mm, AL of minor workers 0.6–1.0 mm; robust ants.
2 Foramen magnum set close to the centre of the ventral surface of the head.
3 Mandible with 7 to 9 teeth in minor workers, 4 teeth in major workers. In major workers with an angulate anterior margin (Fig. 8).
4 Palp formula 6, 4; the segments short, each segment not longer than two times the width.
5 In major workers clypeus truncated and distinctly shorter than the projecting mandibular articulation, not reaching between frontal carinae (Figs 8, 10).
6 Frontal carinae obsolete, closely set, not forming a distinct ridge nor directed towards the anterior part of the eye (Figs 9, 10).
7 Torulus not covered by the frontal carinae, not closely set to the posterior margin of the clypeus (Figs 9, 10).
8 Antennae with 8 segments.
9 Eyes with less than 100 ommatidia.
10 Ocelli absent.
11 In lateral view, dorsum of alitrunk straight, not separated by a ventrally set metanotum (Fig. 12).
12 Metapleural gland a simple open orifice, opened caudad (Figs 19–23).
13 Propodeal spiracle round and set posterodorsally (Fig. 12).
14 Hind coxae widely set, the articulation of the petiole in the metasternum reaching anteriorly to a line spanned between the two anteriormost points of the metasternal coxal cavities (Fig. 2B).
15 First gastral segment of Lasius-type (Fig. 5).
16 Scattered, long erect hairs all over the body, not on the pleurae of the alitrunk.
17 Major worker with sparse pubescence on the occiput (hairs shorter than their inter space); alitrunk and gaster covered by dense pubescence (interspace much shorter than the length of the hairs); minor worker with a uniform, dense pubescence.
18 Proventriculus with sepal short, half the length of the calyx.

**Queen.** As major worker, but with the following additional diagnostic characters.

1 Larger than major worker (AL 1.8–2.5 mm).
2 Ocelli present.
3 Eyes larger, with more than 100 ommatidia.
4 Complete set of flight sclerites (Figs 13, 14).
5 Petiole dorsally flat, in dorsal view wider than long.

**Male.** Formicine ant with the following diagnostic characters.

1 Of intermediate size between major workers and queens.
2 Mandible pointed, with a small cleft anteriorly (Figs 15, 16).
3 Antennae filiform, the terminal six funicular segments at least twice as long as wide, scape shorter than the three proximal funicular segments.

4 Antennae 9-segmented.

5 Subgenital plate with a cranial process (Figs 23–25), reaching beyond the genitalia.

6 Genitalia large, in dorsal view the stipites forming an enclosure (Fig. 26).

7 Stipes and squamula fused, no sulcus visible; in lateral view, stipes large and apically truncated, in dorsal view, basally with a mediadorsal appendage (Fig. 26).

8 Sagitta not serrated.

**Figs 8–11.** 8, Mandible of the major worker of *Cladomyrma maschwitzii*; arrow indicating angle in the outer margin of the mandible. Figs 9–11. Frontal view of the head of *C. maschwitzii*: 9, minor worker (HL = 0.65 mm); 10, major worker (HL = 0.9 mm); 11, queen (HL = 1.3 mm).
Comment. The workers of *Cladomyrma* seem to be strictly dimorphic; nevertheless, in a few cases minor workers have been found having the same head length as the major workers.

Characters given in the phylogenetic section (above) place *Cladomyrma* in the *Lasius* genus-group. The combination of eight antennal segments, the club-shaped funiculus including the terminal six segments, the eyes set laterally to the frontal carinae in the worker and female castes (Figs 9–11), the filiform long antennae with nine segments, the scape shorter than the basal three funicular segments and the presence of a distal process of the subgenital plate, reaching ventrally of the genitalia in situ in the male sex (Figs 23–25) differentiate *Cladomyrma* from all the other Formicinae genera.

**Distribution.** *Cladomyrma* is a Malaysian ant genus and has, so far, only been recorded from Borneo and the Malaysian peninsula. The only record from Sumatra (Roepke, 1930) is probably a misidentification of an *Acropyga* sp., as within the Formicinae only the queens of *Acropyga* are known to carry mealybugs in their mandibles during the mating flight (Bünzli, 1935; Buschinger et al., 1987; Agosti, unpubl.), and eight antennal segments are also present in some undescribed *Acropyga* spp. (Agosti, unpubl.). In RNHL some material labeled 'Roepke' from Sumatra is present but none could be identified either as *Acropyga* or *Cladomyrma* species.

**Biology.** Species of *Cladomyrma* are purely arboreal. The nests are excavated in the inter-nodes of trees and the different species have been found nesting in a single species of either woody climber, *C. cryptata* in *Milletia nieuwenhuisii* (Papilionaceae), or tree species: *maschwitzi* in *Crypteronia griffithii* (Crypteroniaceae) and *mossyna* and *petalae* in *Saraca thaipingensis* (Caesalpiniaceae) (Maschwitz et al., 1991). The nests are actively excavated by the ants themselves (Maschwitz et al., 1989).

Winged sexuals have been found in January, February, April and August to November, but might be produced through the year as during the other months nobody went out to collect *Cladomyrma* (Maschwitz, pers. comm.). Queens fly at night and are attracted to light but have also been observed in daytime, searching for a nesting place. Maschwitz et al. (1991) described the nesting place searching behaviour of the queens as sphecid wasp-like.

Little is known about the behaviour. The workers generally seem to be shy (Wheeler, 1910; Bolton, pers. comm.; Maschwitz et al., in prep.), but can be very aggressive after disturbance and even cause small irritated spots on the human skin (Maschwitz et al., 1989).
Figs 15–16. Outline drawing of the male head in full frontal view. 15, Cladomyrma maschwitzi. 16A and 16B, Variation of head shape of C. petalaef.

Synopsis of the Cladomyrma species

andrei (Emery)

hewitti Wheeler syn. n.
hobbyi Donisthorpe syn. n.
cryptata sp. n.
maschwitzi sp. n.
mossyna sp. n.
petalaef sp. n.

Key to the species

Major workers

1 Metapleural gland a narrow orifice (Fig. 20); body colour brown to dark brown ................ 2
   - Metapleural gland a wide open orifice (Fig. 19); body colour uniform yellow or brown ........ 3
2 AL >1.20 mm; CI >91; Malaysian peninsula .................................................. petalaef
   - AL <1.20 mm; CI <91; Malaysian peninsula ................................................ mossyna
3 Body colour uniform yellow; AL <1.10 mm; Malaysian peninsula ......................... maschwitzi
   - Body colour dark brown; AL >1.10 mm; Borneo .............................................. 4
4 CI >85 .............................................. cryptata
   - CI <86 .............................................. andrei

Minor workers

1 Metapleural gland a narrow orifice (Fig. 20); body colour brown to dark brown ............ 3
Figs 19–22. Metapleural gland orifice, indicated by an arrow. 19, major worker of *Cladomyrma maschwitzi*. 20, major worker of *C.petalae*. 21, queen of *C.maschwitzi*. 22, queen of *C.mossyna*.

- Metapleural gland a wide open orifice (Fig. 19); body colour uniform yellow or brown ....... 2
  2 AL <0.85 mm; CI >84 ................. *mossyna*
  - AL >0.85 mm; CI <84 ................. *petalae*

- Body colour uniform yellow: AL <0.72 mm ............................................. *maschwitzi*
  - Body colour brown ........................................ 4
  4 Body bicoloured with a dark gaster and brighter alitrunk and head; CI <88 ............... *andrei*
  - Body colour uniform dark brown to reddish brown; CI >88 ............................... *cryptata*

Queens

1 Upper portion of katepisternum smooth and without erect hairs or pubescence (Fig. 17) .... 2
  - Katepisternum completely punctate and with some erect hairs and pubescence (Fig. 18) ..... 3
  2 Alitrunk depressed (Fig. 14), front coxae not reaching below the level of the mesopleural sulcus ............................................. *mossyna*
  - Alitrunk as in Fig. 13, front coxae reaching well below the level of the mesopleural sulcus ............................................. *petalae*
  3 AL <2.10 mm; whole body yellowish brown with the antennae and tibiae yellowish ............................................. *maschwitzi*
  - AL >2.10 mm; whole body dark brown ....... 4
  4 CI <81; posterior part of the clypeus smooth; katepisternum shining ....................... *andrei*
- CI >84; posterior part of the clypeus striate; katepisternum mat and coarsely sculptured (Fig. 18) cryptata

Males
(The males of andrei and mossyna are unknown.)

1 Petiole in lateral view dorsally flat, petiolar spiracle set anterodorsally; subgenital plate caudally broad, truncated (Fig. 25); metapleural gland orifice smaller than the propodeal spiracle; AL >1.70 mm ................. petalae

- Petiole in lateral view dorsally domed, petiolar spiracle set at midlength at the base of the peduncle; subgenital plate caudally narrowed (Figs 23, 24); metapleural gland orifice large, round, wider than the propodeal spiracle ...... 2

2 AL <1.25 mm; head with eyes smaller than half the head length, ocelli small (Fig. 15); mandibles acute; subgenital plate caudally emarginate, distally with two rounded ends (Fig. 24) .................................. maschwitzi

- AL >1.50 mm; head with eyes covering most of the lateral parts of the head, ocelli large (Fig. 16); mandibles blunt; subgenital plate caudally emarginate, distally with two acute ends (Fig. 23) .................................. cryptata

Cladomyrma andrei (Emery)

Dimorphomyrmex andrei Emery, 1894: 73. Syntypes queens, EAST MALAYSIA (Poulolaut, Doherty). [Later combinations: Aphomomyrmex andrei (Emery); Wheeler, 1910: 132; Cladomyrma andrei (Emery); Wheeler, 1922: 697.]

Aphomomyrmex hewitti Wheeler, 1920: 132. Lectotype major worker (here designated), BORNEO (EAST MALAYSIA) (Bidi, Hewitt), here designated. [Later combination: Cladomyrma hewitti (Wheeler); Wheeler, 1920: 53.] Syn.n.

Cladomyrma hobbyi Donisthorpe, 1937: 620. Holotype queen, EAST MALAYSIA (Sarawak, Mt Dulit, 4500 ft, moss forest, 14.x.1932, Hobby). BMNH [examined]. Syn.n.

DIAGNOSIS

Major worker (Lectotype of hewitti). AL 1.24, HL 1.28, HW 1.09, EL 0.25, SL 0.56, CI 85, EI 23, SI 51.

1. Metapleural gland orifice large, engaging the ventrad part of the metapleuron along entire length of the posteriorly directed section of the metapleuron to the articulation of the petiole (as in Fig. 19).

2. Body bicoloured, brown with a darker gaster, shining.

3. CI 85.

Minor worker. AL 0.80–0.94 (0.88), HL 0.71–0.80 (0.74), HW 0.60–0.64 (0.64), EL 0.14–0.16 (0.16), SL 0.38–0.40 (0.40), CI 82–88 (86.5), EI 22–26 (22.9), SI 60–64 (62.5).

1. Metapleural gland orifice large, engaging the ventrad part of the metapleuron along entire length of the posteriorly directed section of the metapleuron to the articulation of the petiole (as in Fig. 19).

2. Body bicoloured, brown with a darker gaster.

3. AL 0.80–0.95 mm.

Queen. AL 2.08–2.22 (2.20), HL 1.30–1.40 (1.36), HW 1.02–1.10 (1.06), EL 0.47–0.50 (0.50), SL 0.61–0.65 (0.64), CI 76–79 (78.5), EI 45–47 (46.7), SI 58–62 (60.4); n=8.

1. Body brown with the antennae and mouthpart yellowish, clypeus and genae variable brown to red yellowish.

2. Frons smooth, distance between punctures equal to the length of the pubescence hairs.

3. Clypeus medially without longitudinal carinae, only with some lateral, longitudinal striae; medioposterior part smooth and shining.

4. CI <82.

5. Upper part of katepisternum with some pubescence.

6. Metapleural gland orifice a simple almondshaped opening with a dorsoventral diameter the same length as the distance from the ventral side to the margin above the hind coxae; few scattered hairs below the orifice pointing anteriad.

7. Front coxae reaching beyond the anepisternum (as in Fig. 13).

Male. Unknown.

Comment. The type of Dimorphomyrmex andrei was not available for study. Nevertheless, the drawing following the original descriptions is accurate enough to see the elongate head, typical for this species.

The queen and major worker of andrei have a longer head and the clypeus is posteromedially
shining and smoother than in cryptata.

C. andreii, cryptata and maschwitzi all have a wide open metapleural gland orifice in the worker caste, by which they can easily be separated from the other two species.

From the type series of hewitti, only one minor and two major workers are available. The designated lectotype is a major worker and, based on the long head, hewitti is synonymized with andreii. The minor worker of the type series is a Myrmelachista species, and it is doubtful whether it was collected together with the major workers in the internode of a shrub in South-East Asia, as Myrmelachista is restricted to the Neotropics.

Distribution. C. andreii is restricted to Borneo. The known distribution is from the lowland forest up to 1500 m in moss forest.

Biology. All the queen samples have been collected either at light, by fogging, or from an unnamed shrub (Wheeler, 1910), and the workers have either been collected with the queen in the above-mentioned shrub, or by using a beating tray (D. H. Burckhardt, pers. comm.), in secondary forest.

Material examined. Lectotype (hewitti), 1 major worker, BORNEO, Bidi, viii.1907, Hewitt (MCZ). Paralectotype (hewitti), 1 major worker, same series as lectotype (MCZ).

Non type material. 6 queens, EAST MALAYSIA, Sarawak, 4th Division, Gn. Mulu NP., light trap, ii.1978 (Holloway) (BMNH); 1 queen, EAST MALAYSIA, Sarawak, foot of Mt Dulit, Junction of rivers Tinjar and Lejok, B.M.1933–254, light trap, 30.vii, 1932 (Hobby & Moore) old secondary forest (BMNH); 8 workers, EAST MALAYSIA, Sabah, Poring Hot Springs, 9.v.1987 (Löbl & Burckhardt) (BMNH, MHNG); 1 queen, BRUNEI, Bukit Sulang nr Lamunin, B.M.1982-388. T15/1, fogging, 20.viii–10.ix.1982 (Stork) (BMNH).

Cladomyrma cryptata sp.n.
(Figs 2, 18, 23)

DIAGNOSIS

Major worker. AL 1.18–1.76 (1.48), HL 1.14–1.46 (1.32), HW 1.04–1.36 (1.18), EL 0.22–0.30 (0.26), SL 0.52–0.64 (0.62), CI 86–98 (91.2), EI 19–25 (21.1), SI 47–56 (50.0).

1. Metapleural gland orifice wide open, engaging the ventral part of the propodeum from lateral to the insertion of the petiole; dorsal of the orifice a distinct carina.

2. CI >80.

3. Dorsal part of katepisternum with some pubescence.

4. Metapleural gland with a simple almond shaped opening with a dorsoventral diameter of the same length as the distance from the ventral side to the margin above the hind coxae; the orifice covered by long hairs (as in Fig. 21).

5. Subgenital plate caudally subparallel.

Minor worker. AL 0.88–1.00 (1.00), HL 0.78–0.86 (0.82), HW 0.70–0.80 (0.76), EL 0.16–0.20 (0.18), SL 0.42–0.46 (0.46), CI 89–93 (90.7), EI 20–27 (24.3), SI 56–62 (60.0).

1. As major workers but with the differences listed under the generic diagnosis for minor workers.

2. CI >88.

3. Dorsal part of katepisternum with some pubescence.

4. Metapleural gland orifice wide open, engaging the ventral part of the propodeum from lateral to the insertion of the petiole; dorsal of the orifice a distinct carina.

5. Subgenital plate caudally subparallel.
emarginate with the two ends acute (Fig. 23).

*Holotype.* Queen. AL 2.50, HL 1.52, HW 1.26, EL 0.55, SL 0.78, CI 82.9, EI 43.7, SI 61.9.

*Alate queen.* Anterior part of the head and antennae yellowish, gaster shining, yellowish brown, otherwise body dark brown. Pubescence on the dorsal part of the first two gastral ter-
gites thicker, fading on the subsequent tergites, appressed as on the dorsum of the alitrunk. Erect hairs on the propodeum and the dorsal sides of the petiole and first gastral tergite of equal length.

Paratypes. 4 queens, AL 2.40–2.54 (2.50), HL 1.52–1.55 (1.54), HW 1.24–1.28 (1.27), EL 0.56–0.57 (0.57), SL 0.78–0.80 (0.80), CI 80–84 (82.6), EI 43–46 (45.2), SI 62–63 (62.9); 7 major workers AL 1.34–1.74 (1.48), HL 1.22–1.46 (1.36), HW 1.10–1.36 (1.20), EL 0.22–0.30 (0.26), SL 0.58–0.66 (0.62), CI 86–93 (90.1), EI 19–25 (21.7), SI 47–56 (52.0); 5 minor workers AL 0.94–1.00 (1.00), HL 0.82–0.86 (0.82), HW 0.74–0.80 (0.76), EL 0.18–0.20 (0.19), SL 0.44–0.46 (0.46), CI 90–93 (92.7), EI 23–27 (25.0), SI 57–62 (60.5). 3 males AL 1.62–1.78 (1.68).

Comment. Cicryptata differs from andreii by the shorter head in the female caste and the longer alitrunk in the worker caste. The metapleural gland is wide open, as in andreii but not as in the other species with brown workers, petalae and mossyna.

One queen from Balikpapan has a higher, domed petiole as cryptata.

Distribution. This species is restricted to Borneo and has only been recorded from Sabah, Poring Hot Springs and Sarawak, Gunung Mulu in lowland rainforest.

Biology. Cicryptata has only been collected on the woody climber Milletia nieuwenhuisii (Papilionaceae) or without reference in lowland rainforest.

Cicryptata lives inside the hollow stems of M. nieuwenhuisii with pseudococcids. After disturbance, the workers leave the nest via numerous nest entrances, bite and release formic acid and other irritating substances. The attack can last for more than one hour (Maschwitz et al., 1989).

Material examined. Holotype: 1 queen, EAST MALAYSIA, Sabah, Poring Hot Springs, #815, 22.1.1989, ex Milletia nieuwenhuisii (BMNH).

Paratypes. 4 queens, 3 males, 15 workers, EAST MALAYSIA, Sabah, Poring Hot Springs, 500 m, no. 20b, 11.5.1987 (Löbl & Burckhardt) (BMNH, MHNG); 5 queens, 3 males, 15 workers, EAST MALAYSIA, Sabah, Poring Hot Springs, no. 815, 22.1.1989, ex Milletia nieuwenhuisii (Maschwitz); 1 queen, EAST MALAYSIA, Sarawak, 4th Division, G. Mulu NP, Royal Geographical Society Expedition Long Pala, lowland rainforest, malaise trap, 18.x.1977 (Bolton) (BMNH); 4 workers, EAST MALAYSIA, Sarawak, 4th Division, G. Mulu NP, Royal Geographical Society Expedition Long Pala, lowland rainforest, malaise trap, x.1977 (Bolton) (BMNH).

Cladomyrma maschwitzi sp.n.

(Figs 5, 8–12, 15, 19, 21, 24)

DIAGNOSIS

Major worker. AL 0.80–1.00 (0.90), HL 0.81–0.96 (0.92), HW 0.68–0.82 (0.78), EL 0.15–0.20 (0.18), SL 0.38–0.48 (0.42), CI 83–87 (84.1), EI 22–25 (23.2), SI 53–59 (56.1).

1. Metapleural gland orifice large, set in the caudolateral angle of the metapleuron, not extended to the insertion of the petiole, dorsoventral diameter larger than the maximal diameter of the propodeal spiracle (Fig. 19).

2. Body colour uniform yellow.

3. Median part of clypeus coarsely sculptured (Fig. 8).

4. AL <1.10 mm.

Minor worker. AL 0.68–0.71 (0.69), HL 0.62–0.65 (0.63), HW 0.52–0.56 (0.54), EL 0.12–0.14 (0.12), SL 0.32–0.34 (0.34), CI 81–87 (85.9), EI 21–25 (23.1), SI 57–63 (61.8).

1. As major workers, but with the differences listed under the generic diagnosis.

2. AL <0.75 mm.

Queen. AL 1.82–2.04 (2.02), HL 1.22–1.30 (1.30), HW 0.98–1.02 (1.00), EL 0.44–0.48 (0.46), SL 0.62–0.65 (0.65), CI 75–80 (78.5), EI 22–24 (23.0), SI 63–66 (64.0).

1. Body uniform yellowish brown, the ocellar area and the posttergites somewhat darkened.

2. Clypeus with longitudinal, diverging striae originating around a central, coarsely sculptured field; few very distinct hair pits.

3. Frons with dense punctuation, the individual points set a point’s diameter apart; the semierect pubescence hair
longer than the distance between the two closest points.

4. Dorsal part of katepisternum with pubescence.

5. Metapleural gland orifice reniform; set apart from the ventral margin of the propodeum by the dorsoventral diameter of the orifice; covered by some long curved hairs (Fig. 21).

6. Front coxae reaching beyond the anepisternum (as in Fig. 13).

7. AL <2.10 mm.

**Male.** AL 1.10–1.20 mm.

1. Mandible apically truncated.

2. Face in full frontal view with eyes of half the head length and ocelli as in Fig. 15.

3. Petiole with a rounded peduncle; in lateral view, the petiolar spiracle in the centre.

4. Metapleural gland orifice wide open, engaging ventrad the caudolateral part of the propodeum, but not reaching to the insertion of the petiole; dorsolateral diameter larger than the diameter of the propodeal spiracle.

5. Subgenital plate caudally narrow, sub parallel, emarginated with the two ends rounded (Fig. 24).

6. AL <1.25 mm.

**Holotype.** Queen. AL 1.82, HL 1.62, HW 0.92, EL 0.44, SL 0.62, CI 80.3, EI 44.9, SI 63.3. The holotype queen is slightly physogastric.

**Paratypes.** 3 female; 10 minor workers, 2 majors (measurements see above).

**Comment.** *C. maschwitzi* is the only species with yellow workers. The queen differs from all the other species by its uniform light brown colour and the coarse anterior median part of the clypeus from which all the striae radiate like sunrays.

The samples show only a minor variation between them.

**Distribution.** *C. maschwitzi* has been recorded from the Malaysian peninsula.

**Biology.** *C. maschwitzi* has been collected in the hostplant *Crypteronia griffithii* (Crypteroniaceae) and showed, in comparison to the other species, no aggressive behaviour (Maschwitz et al., 1991).

**Material examined. Holotype.** 1 queen, WEST MALAYSIA, Ulu Gombak, 1990, no. 3, ex Crypteronia griffithii (Moog) (BMNH).

**Paratypes.** 10 minor workers, 1 major worker, same nest as holotype (FRMK, BMNH, MHNG, CDA); 3 workers, WEST MALAYSIA, Ulu Gombak, no. 707, 22.ii.1988, ex *C. griffithii* (Maschwitz) (BMNH); 1 queen, 2 workers, WEST MALAYSIA, Temple's Park, no. 859, 1.11.1988, ex *C. griffithii* (Maschwitz) (MCZ, CDA); 1 queen, WEST MALAYSIA, Temple's Park, no. 862, 1.11.1988, ex *C. griffithii* (Maschwitz) (BMNH); 1 queen, 2 workers, WEST MALAYSIA, Ulu Gombak, 1980, ex *C. griffithii* (Moog) (MHNG); 3 workers, WEST MALAYSIA, Maxwell Hills, no. 947, 21.1.1988, ex *C. griffithii* (Maschwitz) (BMNH). 12 workers, WEST MALAYSIA, Gombak, no. 871, 30.x.1988 (Maschwitz) (BMNH); 3 workers, WEST MALAYSIA, Pasoh (80 km South of Kuala Lumpur), 2.iv.1990, in secondary forest (Rosciszewski) (BMNH), 1 queen, 2 workers, WEST MALAYSIA, Ulu Gombak, 1990, ex *C. griffithii* (Moog) (CDA); 2 males, WEST MALAYSIA, Pasoh (80 km South of Kuala Lumpur), 2.iv.1990, in secondary forest (Rosciszewski).

### Cladomyrma mossyna sp.n.

(Figs 14, 17, 22)

**DIAGNOSIS**

*Cladomyrma* ant with the following diagnostic characters.

**Major worker.** AL 0.86–1.10 (0.96), HL 0.86–1.10 (1.00), HW 0.78–0.94 (0.82), EL 0.16–0.21 (0.18), SL 0.38–0.49 (0.44), CI 84–90 (88.0), EI 19–21 (19.5), SI 48–53 (50.5).

1. As major workers, but with the differences listed under the generic diagnosis.

2. Body uniform brown.

3. AL <0.9 mm.

4. CI 84–91.

**Minor worker.** AL 0.60–0.88 (0.76), HL 0.63–0.82 (0.76), HW 0.53–0.74 (0.63), EL 0.12–0.18 (0.15), SL 0.31–0.24 (0.36), CI 84–91 (88.2), EI 22–26 (24.2), SI 48–65 (57.6).

1. Metapleural gland orifice narrowed, dorsoventral diameter the same as the propodeal spiracle, far away from the ventral margin of the metapleuron (as in Fig. 20).

2. Body uniform brown.

3. The whole clypeus longitudinally striated.

4. AL <1.10 mm.

5. CI 84–90.
**Queen.** AL 2.30–2.56 (2.50), HL 1.42–1.56 (1.52), HW 1.15–1.26 (1.26), EL 0.46–0.53 (0.52), SL 0.68–0.70 (0.69), CI 81–83 (81.3), EI 40–43 (42.1), SI 55–59 (55.7).  
1. Body bicoloured yellow brownish black to uniform brownish black.  
2. Clypeus longitudinally with subparallel striae.  
3. Frons shining, with widely set punctation  
4. Dorsal part of katepisternum smooth (Fig. 17).  
5. Metapleural gland orifice narrow; part below the orifice and dorsal of the hind coxae extended (Fig. 22).  
6. Alitrunk depressed (Fig. 14).  
7. Front coxae short, not reaching beyond the anepisternum (Fig. 14).  

**Male.** The male of *mossyna* is unknown.

**Holotype.** Queen. AL 2.30; HL 1.42, HW 1.15, EL 0.46, SL 0.68, CI 81.0, EI 40.0, SI 59.1.  
Queen without wings, shining; head, legs, scutellum and petiole yellowish brown; dorsal half of pronotum and propodeum somewhat darkened; anterior half of the first and anterior margin of the second gastral tergite yellow, the remaining parts dark brown; the three apical segments of the funiculus darker than the previous.  
Anterior part of the head truncated, finely longitudinally striate on genae and clypeus.  
The whole body pilose.  

**Paratypes.** 5 major workers AL 0.90–1.02 (0.96); HL 0.94–1.00 (0.98), HW 0.81–0.88 (0.84), EL 0.16–0.18 (0.18), SL 0.40–0.44 (0.42), CI 84–88 (87.2), EI 19–21 (19.8), SI 49–52 (50.0); 5 minor workers AL 0.66–0.80 (0.68); HL 0.64–0.74 (0.66), HW 0.55–0.66 (0.60), EL 0.14–0.16 (0.15), SL 0.32–0.16 (0.16), CI 84–90 (87.5), EI 23–26 (25.0), SI 49–64 (57.1).  

**Comment.** *C.mossyna* differs from the Bornean species by the narrow metapleural gland orifice (Figs 14, 22) and from *maschwitzi* by the brown coloured workers and either bicoloured or dark brown queens and by the larger size and by the shape of the subgenital plate.  
*C.mossyna* and *petalae* are separated by the depressed alitrunk of the *mossyna* queens and the smaller alitrunk length of the *mossyna* workers.  
The queens of both species have a variable alitrunk length and body colour, which varies from a distinct bicoloured pattern to uniform dark brown. The variation within nest series is distinctly smaller than within different colonies.  
This is the rare species of Maschwitz et al. (1991).  

**Distribution.** *C.mossyna* has only been recorded from the Malaysian peninsula.  

**Biology.** *C.mossyna* has only been recorded nesting in *Saraca thaipingensis* (Caesalpiniaeae).  
**Material examined.** Holotype. Queen, WEST MALAYSIA, Ulu Gombak, no. 873, 1.11.1988, ex *Saraca thaipingensis* (Maschwitz) (BMNH).  
**Paratypes.** 5 minor workers and 5 major workers from the same nest as holotype (CDA, FRIMK, MCZ, MHNG, BMNH).  
**Non type material.** 6 workers, WEST MALAYSIA, Gombak 29.ix.1973 (Bolton) (BMNH); 6 workers, WEST MALAYSIA, Ulu Gombak, no. 872, 1.11.1988 (Maschwitz) (BMNH); 1 queen, WEST MALAYSIA, Ulu Gombak, no. 888, 2.1.1989, ex *S.thaipingensis* (Maschwitz) (BMNH); 1 queen, WEST MALAYSIA, Ulu Gombak, no. 891, 12.11.1988, ex *S.thaipingensis* (Maschwitz) (MHNG); 1 queen, WEST MALAYSIA, Ulu Gombak, no. 1131, 2.1.1989, ex *S.thaipingensis* (Maschwitz) (MCZ); 15 workers, WEST MALAYSIA, Ulu Gombak, 1990, ex *S.thaipingensis* (Moog) (MHNG, BMNH, CDA).  

**Cladomyrma petalae sp.n.**
(Figs 16A, 16B, 13, 20, 25, 26)

**DIAGNOSIS**

**Major worker.** AL 1.20–1.42 (1.28); HL 1.12–1.24 (1.16), HW 1.02–1.16 (1.08), EL 0.20–0.23 (0.22), SL 0.50–0.60 (0.54), CI 89–95 (93.3), EI 18–21 (20.3), SI 47–52 (49.6).  
1. Metapleural gland narrowed, dorsoventral diameter smaller than the distance between the ventral margin of the metapleuron and the ventral margin of the gland’s orifice (Fig. 20).  
2. Body bicoloured brown, with a darker gaster. If head and alitrunk dark brown, then gaster black.  
3. AL >1.20 mm.  
4. CI 91–95.  

**Minor worker.** AL 0.86–0.98 (0.92); HL 0.76–0.86 (0.80), HW 0.68–0.82 (0.74), EL 0.16–0.18 (0.17), SL 0.39–0.44 (0.42), CI 87–95 (90.4), EI 19–24 (23.0), SI 53–60 (59.5).
1. As major workers, but with the differences listed under the generic diagnosis.
2. Body bicoloured brown, with a darker gaster.
3. AL >0.80 mm.

**Queen.** AL 2.26–2.56 (2.42), HL 1.46–1.53 (1.50), HW 1.20–1.27 (1.24), EL 0.46–0.54 (0.52), SL 0.66–0.72 (0.70), CI 82–84 (82.6), EI 38–43 (41.3), SI 53–58 (55.6).
1. Body bicoloured yellow brownish black to uniform brownish black.
2. Clypeus with longitudinal, subparallel striae.
3. Frons smooth, with widely set punctation.
4. Dorsal part of katepisternum smooth (as in Fig. 17).
5. Metapleural gland orifice narrow; part below the orifice and dorsal of the hind coxae extended (Fig. 20).
6. Front coxae reaching beyond the anepisternum (Fig. 13).

**Male.** AL 1.72–1.80 (1.74)
1. Mandible apically pointed.
2. Face in full frontal view with eyes of half the head length and ocelli as in Fig. 16; head shape polymorphic (Figs 16A, 16B).
3. Petiole dorsally truncated, flat; in lateral view, the petiolar spiracle craniodorsal.
4. Metapleural gland orifice small; diameter smaller than the diameter of the propodeal spiracle.
5. Subgenital plate caudal, broad, subparallel, emarginated with the two ends rounded (Fig. 25).
6. AL <1.80 mm.

**Holotype.** Queen, AL 2.56, HL 1.51, HW 1.24, EL 0.52, SL 0.72, CI 82.1, EI 41.9, SI 58.1.

**Paratypes.** 2 females, AL 2.56; HL 1.50–1.53, HW 1.26–1.27, EL 0.52–0.54, SL 0.70–0.71, CI 83–84, EI 41–43, SI 55–56; 5 major workers AL 1.24–1.36 (1.28), HL 1.14–1.21 (1.18), HW 1.08–1.13 (1.08), EL 0.22–0.23 (0.23), SL 0.52–0.56 (0.54), CI 91–95 (93.3), EI 19–21 (20.4), SI 48–50 (49.6); minor workers AL 0.86–0.98 (0.94), HL 0.77–0.86 (0.82), HW 0.68–0.83 (0.74), EL 0.16–0.18 (0.17), SL 0.39–0.44 (0.43), CI 87–95 (90.2), EI 19–24 (23.0), SI 52–60 (56.8).9 males AL 1.72–1.80 (1.74).

**Comment.** For comments see mossyna.

**Distribution.** *C. petalae* has only been recorded from the Malaysian peninsula.

**Biology.** The only hostplant record from *C. petalae* is the tree *Saraca thaipingensis* (Caesalpiniaceae). In places where *mossyna* and *petalae* co-occur, *petalae* is more often collected (Maschwitz et al., 1991).

**Material examined.** Holotype. Queen, WEST MALAYSIA, Ulu Gombak, 12.1.1990, ex *Saraca thaipingensis* (Moog) (BMNH).

**Paratypes.** 2 queens, 6 males, 24 workers, same nest as holotype (BMNH, CDA, FRIMK, MCZ, MHNG).

**Non type material.** 1 queen MALAYSIA, Ulu Gombak, 1.11.1988, no. 882, ex *S. thaipingensis* (Maschwitz) (BMNH); 1 queen, 1 male, 3 workers, WEST MALAYSIA, Ulu Gombak, 1.11.1988, no. 1067, ex *S. thaipingensis* (Maschwitz) (BMNH, CDA); 1 queen MALAYSIA, Ulu Gombak, 1.11.1988, no. 886, ex *S. thaipingensis* (Maschwitz) (BMNH); 1 queen MALAYSIA, Ulu Gombak, 1.11.1988, no. 586, ex *S. thaipingensis* (Maschwitz) (BMNH); 16 workers, WEST MALAYSIA, Ulu Gombak, 1990, ex *S. thaipingensis* (Moog) (MHNG, CDA).

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