

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3283, 24 pp., 35 figures, 2 tables December 8, 1999

Revision of the Oriental Plant-ant Genus *Cladomyrma*

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ABSTRACT

The oriental plant-ant genus *Cladomyrma* Wheeler is revised, including now 11 species. Six species are described as new (*aurochaetae*, *crypteroniae*, *dianeae*, *maryatiae*, *yongi*, *nudidorsalis*), *moossyna* is synonymized with *petalae*, and *cryptata* with *andrei*; *hobbyi* and *hewitti* are revived from synonymy and resurrected as species. A key to queen caste is provided. The biology of the species is briefly discussed and the occurrence of *Cladomyrma* in Sumatra is noted for the first time.

INTRODUCTION

Since the last revision of this genus eight years ago (Agosti, 1991), more material has become available, mainly through meticulous studies of ant/plant associations by the two research groups of Ulrich Maschwitz (Moog and Maschwitz, 1994; Moog et al., 1998) and Diane Davidson (Davidson and McKey, 1993). Their objective is to understand the ecology and evolutionary biology of ant-plant interactions. However, studies on such

systems face the problem of complex patterns of species associations. Whereas the number of involved plant-ant species is comparatively easily assessed, the diversity of plant-ants is often subject to speculation. This is true for the *Cladomyrma*-plant associations as well. During the last few years, many more host plants of *Cladomyrma* were found. According to present knowledge, *Cladomyrma* inhabits live stems of at least 18 species of host plants in nine different genera, thus colonizing about 50% of all plant genera (except epiphytes) which are regularly associated with specialized stem-nesting ant partners in the Oriental region (Moog et al., in press). It is expected that in future studies still more host plant species will be

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discovered. The ant partners of the recently found host plants not only belong to known species but to hitherto undescribed species as well, thus illustrating the need for a renewed basic taxonomic treatment. The extended number of *Cladomyrma* specimens of more than 150 samples, including many queens, is rather rare for tropical formicine ants. As most of the genera of formicine ants are characterized by the absence of discrete characters and an extensive variation in characters such as shape or position and number of hairs, large series are needed to extract species-specific characters. Thus, what might be a distinctive character in a limited number of samples might be just two extremes of a variation when many more specimens become available. Changes in the status of species might thus occur, and is well illustrated in this study. We nevertheless consider species acceptance better than the use of informal names not accompanied by diagnoses.

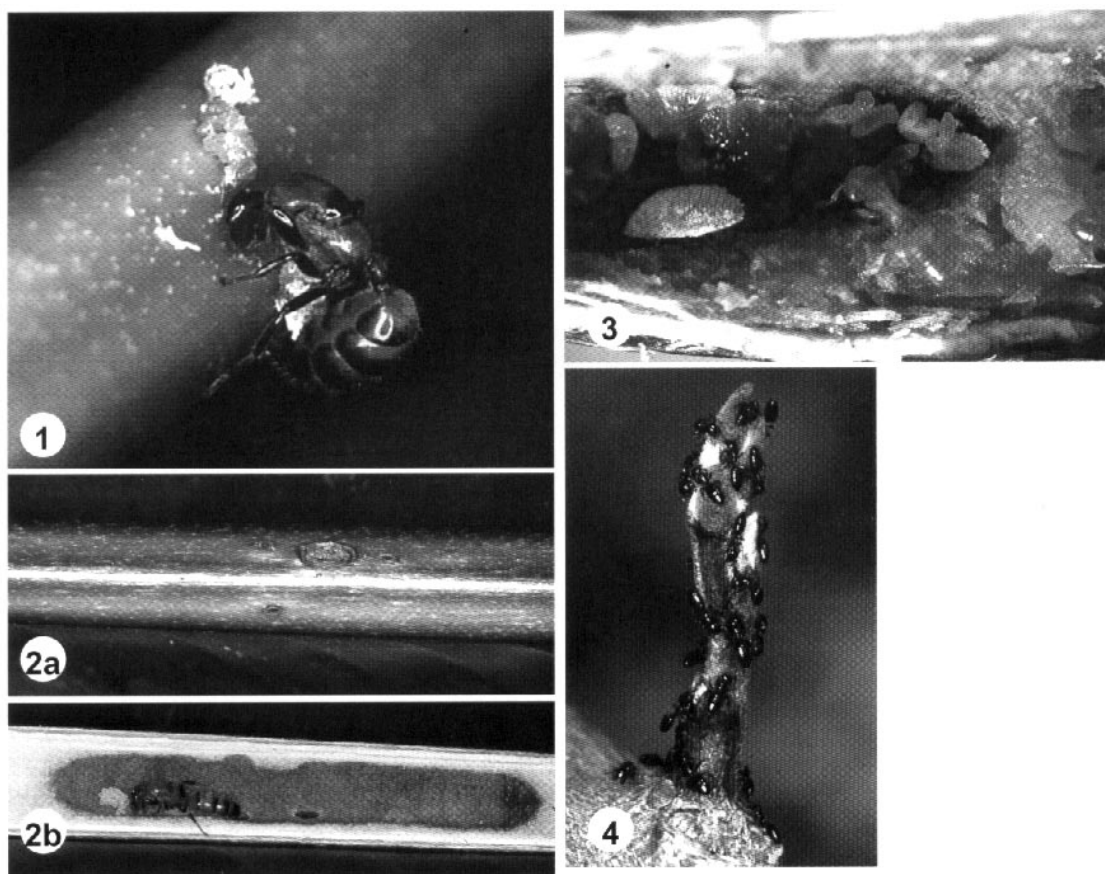
The best characters for separating species in *Cladomyrma* are in the male and the queen caste. Whereas few males are known, queens are unusually abundant in this material. Based on their variation, more species can be diagnosed than with workers alone. This, in turn, often makes it impossible to identify workers without their queen. This paper aims at reassessing the status of the previously described species, and describing the new species and their biology, and to present a key to the queen caste.

BIOLOGY OF *CLADOMYRMA*

A characteristic feature of all known species of *Cladomyrma* is the utilization of live pithy stems as nest sites: Colony-founding queens gnaw entrance holes in suitable soft young internodes and excavate a chamber in which they rear their first brood in isolation. The initial founding chamber is later expanded by the emerging workers (Maschwitz et al., 1991; Moog et al., 1998). Multiple colonizations of an individual plant sapling in different internodes are the rule, but eventually a single colony monopolizes the entire host plant. Sometimes foundress queens (e.g., those unsuccessful in penetrating comparatively old internodes) try to enter a nest chamber already occupied by another queen.

The result is either a chase-off or the death of at least one of the combatants (Moog et al., in prep.). Very rarely (< 0.5%), two queens are found to inhabit a single foundation chamber (e.g., in *C. dianeae* inhabiting *Neonauclea gigantea*), apparently without exhibiting aggressive behavior toward each other. With both increasing plant and colony size, other internodes will be colonized successively. Eventually the nest chambers run through stem, branches, and every twig (with the exception of *Neonauclea*, in which, even in adult trees, only swollen parts of the internodes (= ant domatia) are used as nest space. Size of mature colonies is variable, usually several thousand workers, but may reach 10,000 in a *Saraca* tree (8 m in height) and about 30,000 in *Neonauclea gigantea* (ca. 15 m).

In mature colonies the often physogastric queen is usually found in the lower part of the host plant, and the brood is dispersed throughout the colony space. There is probably a tendency toward a separation of male and queen alates. Whereas the alate queens concentrate in the proximate parts of the inhabited twigs, the males are often found closer to the apex. All *Cladomyrma* species tend coccoids inside the nest hollows and feed on honeydew excreted by their trophobionts (unpublished results). The majority of the coccoid partners are Pseudococcidae and the involved taxa belong to a large variety of species (D. Williams, personal commun.). The monogynous colonies of all species tested (*andrei*, *dianeae*, *maschwitzi*, *petalae*) protect young foliage of their host plants against herbivores and prune young plant tips of encroaching vegetation (*andrei*, *dianeae*, *maryatae*?, *maschwitzi*, *nudidorsalis*, *petalae*, *yongi*; Moog et al., 1994; Moog et al., 1998, unpublished results). It is assumed that these observations hold for all *Cladomyrma* species, but this requires further confirmation. In addition, *Cladomyrma* workers exhibit a conspicuous behavior on the plant surface, in which they appear to clean minute particles from young leaves (and sometimes stem)—regularly—probably initial colonies of epiphylls or fungus spores. As a rule, mature colonies of *Cladomyrma* display aggressive behavior if the nest (= plant) is violently disturbed, however, there seems to exist a



Figs. 1–4. Biology of *Cladomyrma*. **1.** Colony foundation by queen of *C. petalae* in *Saraca thaipingensis*. **2.** Internode of *Saraca thaipingensis* with nest of *C. petalae*; **2a.** Entrance hole made by the queen is closed with pith remains, the small, slit-shaped openings are gnawed by the queen from inside; **2b.** Dissected *Saraca* internode showing founding chamber, queen of *C. petalae*, and brood. Internode with nest of *C. petalae*; big opening entrance hole made by the queen, and small, slit-shaped opening gnawed by the queen from inside to allow mealybugs to enter. Crawlers of trophobiontic mealybugs readily use the slits to enter the founding chamber (JM, personal obs.). **3.** Mature nest of *C. maschwitz* with mealybugs. **4.** *C. petalae* workers on young bud of the woody climber *Spatholobus bracteolatus*.

species-dependent variation in the degree of aggression; e.g., *C. maschwitz* appears to be less aggressive in case of disturbance than other species. In some species the major workers will search for and bite into tender spots of any myrmecologist even two hours after he has broken up the nest. *Cladomyrma* workers (cf. *andrei*, *maschwitz*, and *petalae*) are not only able to bite but to spit as well. They ingest rainwater, which may intrude into their stem domatia and regurgitate it to the outside. It is not known if “water-bailing” is displayed by the other species as well; field and experimental data are lacking.

This unusual behavior, only once previously reported for ants, appears to be a trait connected to their obligate colonization of myrmecophytes (Moog et al., 1997).

DISTRIBUTION

Cladomyrma seems to be restricted in its distribution to the ever-wet part of the West Malaysian floristic region, comprising the Malay Peninsula, Borneo, and Sumatra (fig. 5). The western boundary lies across the Kra Isthmus, just north of the border between Malaysia and Thailand. The genus does not

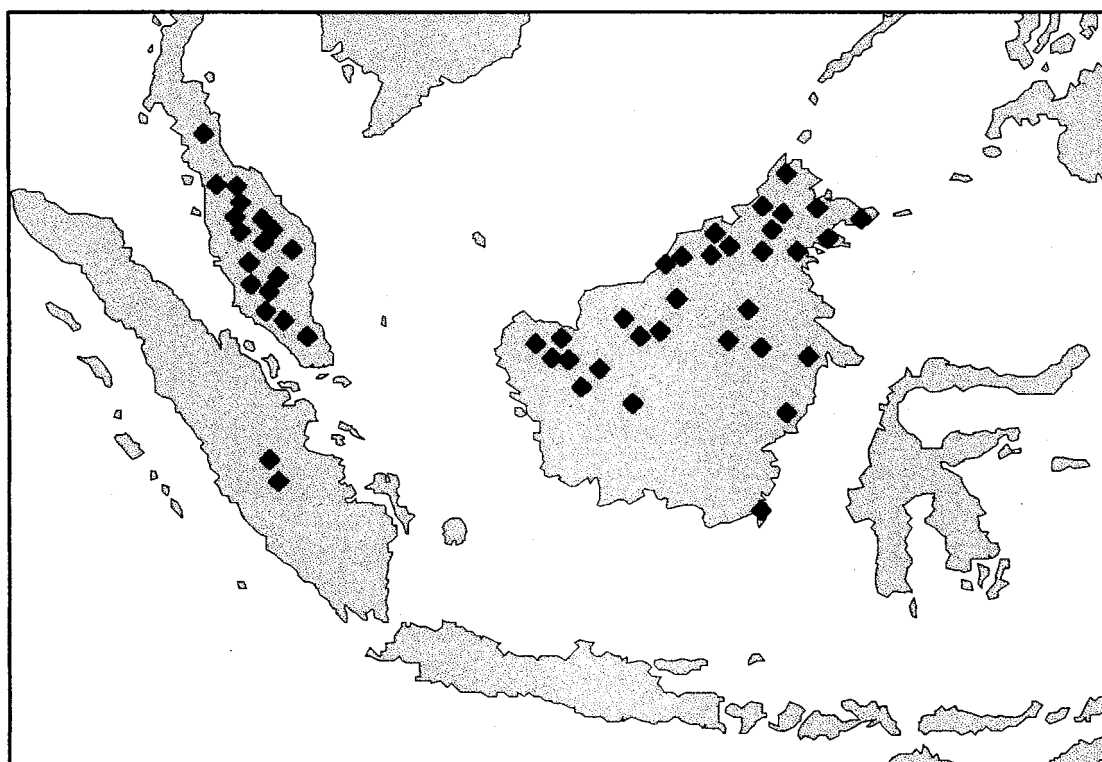


Fig. 5. Distribution map of *Cladomyrma* in Southeast Asia according to field and herbarium data.

extend northward beyond Borneo. Likewise, *Cladomyrma* is not known east of the Makassar Strait, in Sulawesi. Another clearly defined boundary appears to be the Sunda Strait; no records exist from Java with its drier climate. The majority of species are known to occur in Borneo and Peninsular Malaysia. A recent field trip first recorded two *Cladomyrma* species, *maschwitzii* and *crypteroniae*, in Sumatra. The previous record from Sumatra (Roepke, 1930) is a misidentification of an *Acropyga* species (Reyne, 1965). Field observations indicate that the uppermost altitudinal limit of *Cladomyrma* is about 1300–1350 m; thus its natural habitats comprise lowland, hill, and upper dipterocarp forests.

MATERIAL AND METHODS

Morphological terminology follows Bolton (1994). All measurements are given in millimeters. All the images are available in digital format on http://research.amnh.org/entomology/social_insects.

Anatomical Abbreviations

AL (alitrunk length)	The diagonal length of the alitrunk (= mesosoma) in profile from the anterior most point of the pronotum to the posteriormost point of the metapleuron
CI (cephalic index)	$HW \times 100/HL$
EI (eye index)	$EL \times 100/HW$
EL (eye length)	The maximum diameter of the eye
HL (head length)	The length of the head proper, excluding the mandibles, measured from the midpoint of the anterior clypeal margin to the midpoint of the occipital margin, in full-face view
HW (head width)	The maximum width of the head in full-face view, measured below the eyes
SI (scape index)	$SL \times 100/HW$
SL (scape length)	The maximum straight line of the antennal scape ex-

cluding the basal constriction or neck of the condylar bulb.

Institutional Abbreviations

AMNH	American Museum of Natural History, New York, USA.
CDA	Collection of D. Agosti.
FRIMK	Forest Research Institute of Malaysia, Kepong, Malaysia.
LACM	Los Angeles County Museum, Los Angeles, USA.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA.
MSNG	Museo Civico di Storia Naturale, Genoa, Italy.
NHM	The Natural History Museum, London, UK.

ACKNOWLEDGMENTS

We are grateful to Barry Bolton (NHM), Stefan Cover (MCZ), Valter Raineri (MCSN), and Roy Snelling (LACM) for loans of specimens. Diane Davidson, Brigitte Fiala, and Ulrich Maschwitz provided us with extensive new material. Barry Bolton, Diane Davidson, and Phil Ward generously reviewed the manuscript. This work has been supported by DFG (JM: Ma 373/ 17-4 and 17-5) and a contribution of the AMHH for the color plates. The names of *Cladomyrma dianeae*, *maryatiae*, and *yongi* refer to Profs. Diane Davidson, Mary Maryati, and Yong Hoi Sen who all contributed in significant ways to the understanding of biodiversity in Malaysia.

CLADOMYRMA WHEELER

Cladomyrma Wheeler, 1920: 53. Type species *Aphomomyrmex hewitti* Wheeler, 1910: 132, by original designation.

A single queen *Cladomyrma* from Borneo was first described as *Dimorphomyrmex andrei* (Emery, 1894: 73), later included in *Aphomomyrmex* by the same author after he had seen African *A. afer* (Emery, 1899: 494). Wheeler (1910: 132) listed both species and described a third, *A. hewitti*, based on two queens and eight workers collected in Borneo. In 1920, Wheeler (p. 53) placed the two Bornean members of *Aphomomyrmex* into a

new genus, *Cladomyrma*, with *A. hewitti* as genotype. Donisthorpe (1937: 620) described a third species, *C. hobbyi*, from three winged queens taken in Borneo. The first revision of the genus, based on new material from Malay Peninsula and Borneo, recognized five species (Agosti, 1991). The phylogenetic relationship of *Cladomyrma* within the Formicinae is unclear (review and new placement in Agosti, 1991, but see Chenuil and McKey, 1996).

Cladomyrma is easily recognized among formicine ants by (1) the presence of a minor worker and soldier caste (including some intermediates), (2) an angulate outer margin of the mandible in the soldier caste and the queen, (3) eight antennal segments in queens and workers, and (4) a well-developed acicopore. A full diagnosis and discussion of the genus is provided in Agosti (1991). The antennae of the males is 13-segmented, not 9-jointed as erroneously mentioned by Agosti (1991). A structural analysis of the proventriculus (gizzard) of *Cladomyrma* is given in Eisner (1957).

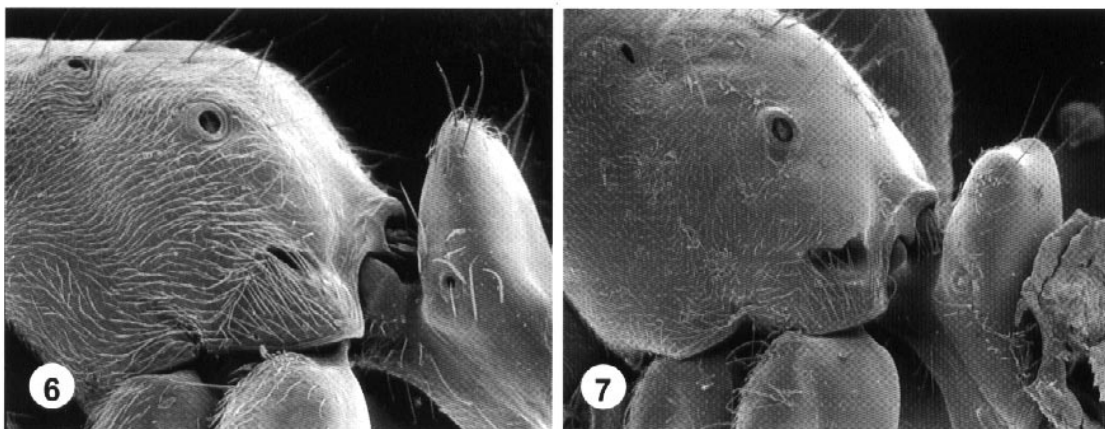
The lack of discrete characters makes it difficult to assess phylogenetic relationships within *Cladomyrma*. Two groups might be recognized by the shape of the queen petiole, which in one case is dorsally truncate and low, and in the other an erect node or scale. Whereas some species, such as *crypteroniae* and *maschwitzii* are very distinct, most other species require some expertise or reference collections for identification.

Size of minor workers is rather variable during a colony cycle, with the first workers (=nanitics) being much smaller than those after the presence of some thirty workers or more. Size is therefore a very ambiguous character for the identification of species.

SYNOPSIS OF SPECIES

depressed petiole group

- andrei* (Emery)
- cryptata* Agosti new syn.
- hobbyi* Donisthorpe rev. stat.
- maschwitzii* Agosti
- nudidorsalis* new species
- petalae* Agosti
- mossyna* Agosti new syn.
- yongi* new species



Figs. 6, 7. Metapleural gland orifice of workers. 6. *Cladomyrma petalae*; 7. *dianeae*.

raised petiole group

aurochaetae new species
crypteroniae new species
dianeae new species
maryatiae new species
hewitti (Wheeler) rev. stat.

KEY TO QUEEN CASTE

- 1 Dorsum of mesonotum without erect hairs (fig. 15) *nudidorsalis*
- Dorsum of mesonotum with erect hairs .. 2
- 2 Whole body yellow 3
- Body bicolored or light to dark brown; if light brown, gaster darker than alitrunk, or tergites bicolored 4
- 3 Wide alitrunk; petiole raised, in lateral view dorsally truncated (fig. 20) .. *crypteroniae*
- Narrow alitrunk; petiole in lateral view low and dorsally truncated (fig. 18) *andrei* (part)
- 4 Petiole in lateral view dorsally truncated, low, and dorsolaterally distinctly angulate .. 5
- Petiole in lateral view forming an upright scale or node, dorsolaterally rounded .. 9
- 5 Dorsal part of katepisternum shining and without pubescence (fig. 10) *petalae*
- Dorsal part of katepisternum punctuate and with pubescence (fig. 11) 6
- 6 Head and alitrunk bright yellowish brown with distinctly darker gaster; small (AL < 2.1 mm); larger metapleural gland orifice (fig. 16) *yongi*
- Head and alitrunk brown to dark brown or reddish; size variable 7
- 7 Whole body (light) brown (fig. 14) *maschwitzii*
- Whole body dark brown or bicolored, gen-

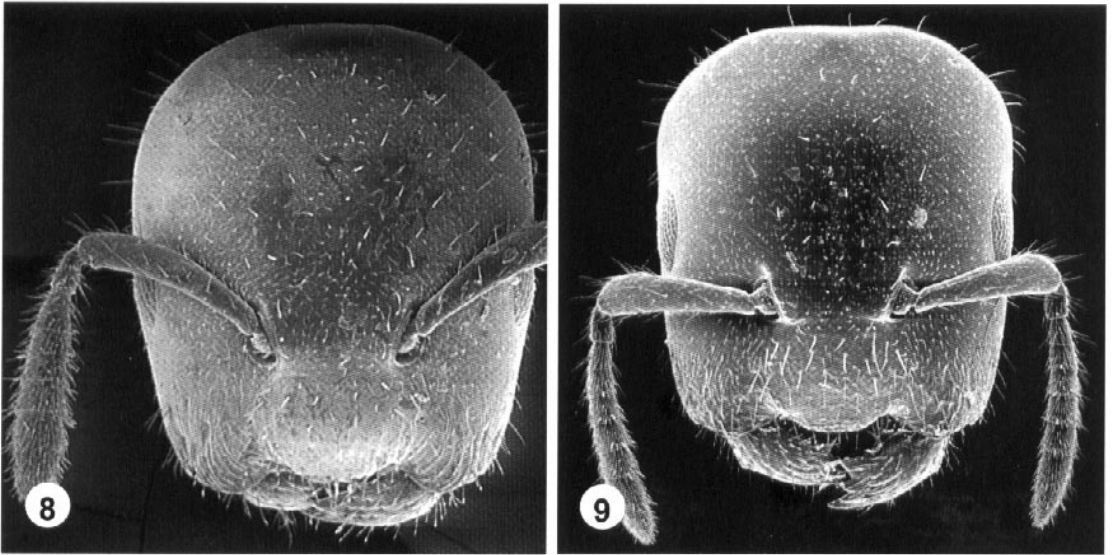
- erally with dorsum of alitrunk reddish brown 8
- 8 Dorsal part of katepisternum dull or at least covered with long pubescence; head short to somewhat elongate (fig. 24); larger ants (AL > 2.00 mm) *andrei* (part)
- Dorsal part of katepisternum punctulate, shining, and with a sparse pubescence with thin hairs; roundish, elongate head with genae distinctly brightest colored part of the head (fig. 25); generally smaller ants (AL < 2.20 mm) *hobbyi*
- 9 Erect hairs only on dorsal parts of gastral tergites 2 and 3 along posterior margin ... 10
- Erect hairs scattered all over second gastral tergite 11
- 10 None or very few short pubescent hairs on gastral tergite 2; long erect, curved hairs on gastral tergite 1; wide alitrunk, larger body (fig. 19) *aurochaetae*
- Regularly, but very widely spaced pubescence on gastral tergite 2; erect hairs on gastral tergite 1 not very long and not regularly curved; narrower alitrunk; smaller (fig. 23) *maryatiae*
- 11 Head longer, CI < 83, parallel sided in full frontal view (fig. 34); gastral tergites with long erect hair at most at posterior margin of tergites *hewitti*
- Head shorter, CI > 82 or at least sides slightly rounded in frontal view (fig. 33); gastral tergite covered with long erect hair *dianeae*

DEPRESSED PETIOLE GROUP

Cladomyrma andrei (Emery)

Figures 12, 24

Dimorphomyrmex andrei Emery, 1894: 73. (Later combinations: *Aphomomyrmex andrei* Emery,



Figs. 8, 9. Head in full frontal view of soldier. 8. *hobbyi*; 9. *maryatiaae*.

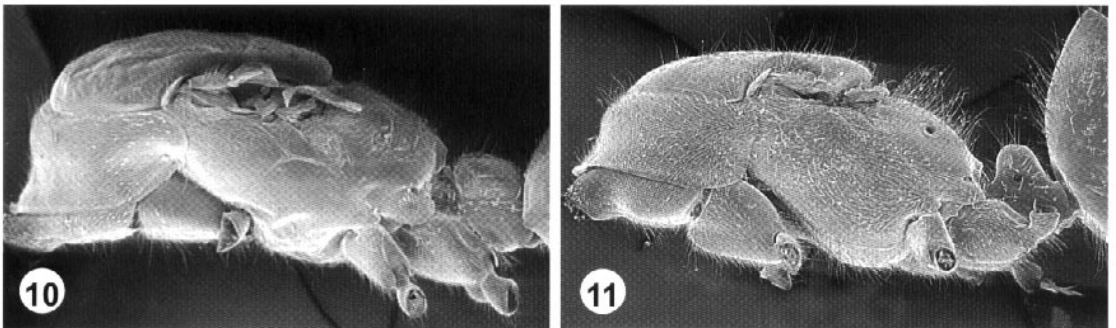
1899: 494; *Cladomyrma andrei*, Emery, 1925: 45). Syntype queen, BORNEO: Indonesia, South Kalimantan, Pulo Laut, Doherty; MCSN [examined].

Cladomyrma cryptata Agosti, 1991: 304. Holotype queen, BORNEO: East-Malaysia, Sabah, Poring Hot Springs, #815, Ulrich Maschwitz, ex *Calleya* (= *Millettia*) *nieuwenhuisii*; BMNH. New syn.

DIAGNOSIS: Major worker. AL 0.84–1.64, HL 0.86–1.42, HW 0.76–1.32, EL 0.16–0.30, SL 0.38–0.68, CI 89–98, EI 21–42, SI 44–53 (n = 8). Generally larger body size; pilosity and dorsum of alitrunk and gaster variable, generally short and not very dense; generally reddish dark brown to dark brown; clypeus angulate; gastral pubescence thin,

hair at least as long as distance between their insertions. **Minor worker.** AL 0.64–1.00, HL 0.59–1.04, HW 0.52–0.78, EL 0.13–0.22, SL 0.29–0.46, CI 83–95, EI 23–27, SI 55–66 (n = 8). Generally larger body size; pubescence on gaster dense, short, and appressed; metapleural gland orifice large.

Queen. AL 2.08–2.56, HL 1.30–1.46, HW 1.02–1.24, EL 0.47–0.54, SL 0.61–0.78, CI 76–86, EI 40–47, SI 58–66 (n = 17). Large body size (AL > 2.0 mm); body color usually dark brown to black (rarely uniform yellowish); head distinctly bicolored with genae and clypeus lighter than remainder of the head capsule; metapleural gland orifice large but covered with a bunch of hairs inserted ven-



Figs. 10, 11. Alitrunk and petiole of queens in lateral view. 10. *petalae*; 11. *maryatiaae*.

tral to the opening; petiole low and dorsally truncate; gaster with many long, erect hairs scattered all over the tergites and generally appressed, widely set pubescence. PARATYPE: Queen AL 2.28, HL 1.36, HW 1.14, SL 0.68, EL 0.53, CI 84, EI 46, SI 60.

COMMENTS: The species belongs to the larger Bornean species of *Cladomyrma*. At the same time, it is the most variable in size, in head shape from a very short to a medium long head, an almost black body color to brown (rarely uniform yellowish [one collection]), and long to short gastral hairs. The synonymy with *cryptata* indicates that the status of this species is similar to that of *petalae* (see below). Though there might be several species included, it is at the very moment impossible to separate them.

The typical *cryptata* and *andrei* differ somewhat in the fine chagrinata sculpture on the head and the matte surface, which is very distinct in *cryptata* as opposed to the brilliant shining and completely smooth surface in *andrei*. The type series of *cryptata* includes one queen with a short head and one with an elongate head, which is similar to the type of *andrei*.

Another variation includes workers from Poring Hot Springs (J. Moog, 95-018 and 95-017) which have a slightly elongated head, and very conspicuous long, heterogeneous hairs (some longer than others) on the dorsum of the alitrunk. In contrast, the workers of the typical *andrei* have subhomogeneous shorter setae. This variation is also the only population of *andrei* living in *Drypetes longifolia* (Euphorbiaceae). One collection (J. Moog, 93-061) shows a uniform yellowish-colored queen that closely resembles *andrei* (*cryptata* form) in most characters except body color. We observed a very slight difference in the density of the pubescence on the anterior and lateral parts of the mesonotum but since this character exhibits some variation in *andrei*, it was not used to erect a new species. Considerable variation in

body color of queens may be a rather common phenomenon in *Cladomyrma* (see under *petalae*).

BIOLOGY AND DISTRIBUTION: The species has been found colonizing the endemic woody climbers *Callerya* (formerly *Millettia*) *nieuwenhuisii* (Maschwitz et al., 1989), *Spatholobus oblongifolius* (both Papilionaceae) and the tree genus *Neonauclea* (Rubiaceae). In general, liana saplings usually possess a primary stem diameter too thin to allow ant inhabitation. However, saplings of these host lianas (*Callerya*, *Spatholobus*) provide some stem internodes with distinctly enlarged diameter (ant domatia) to permit colonization by foundress queens (Moog et al., in press). In Poring Hot Springs, Sabah, samples of this species have been obtained on a canopy walkway from a huge *Callerya*, about 40m above ground. Its supposed that *andrei* is distributed over all of Borneo since the type specimen was collected in South Kalimantan (Poulo Laut). Most records are, however, from Sabah and Sarawak, but Kalimantan is poorly sampled.

MATERIAL EXAMINED: TYPE: INDONESIA, South Kalimantan, Poulo Laut, Doherty, MCSN, queen. OTHER SPECIMENS: E-MALAYSIA, Sabah, Ranau, Poring Hot Springs, 11/14/1992, Brigitte Fiala, 0052, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sabah, Ranau, Poring Hot Springs, 1/22/1989, Ulrich Maschwitz, 0815, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sabah, Ranau, Poring Hot Springs, 1/28/1993, Joachim Moog, 93-061, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*, alt.: ca. 600 m, colony size: 11 workers; Sabah, Ranau, Poring Hot Springs, 1/26/1995, Joachim Moog, 95-017, ex: *Drypetes longifolia*, young colony: ca. 200 workers in total, alt.: ca. 800 m; Sabah, Ranau, Poring Hot Springs, 1/26/1995, 95-018, Joachim Moog, ex: *Drypetes longifolia*, mature colony, alt.: ca. 800 m; Sabah, Ranau Poring Hot Springs, 5/2/1987, Burckhardt and Löbl; Sarawak, Lambir NP, Miri, 2/25/1992, Ulrich Ma-

→

Figs. 12–23. Lateral view of queens of *Cladomyrma*. 12–18. Depressed petiole group: 12. *andrei*; 13. *hobbyi*; 14. *maschwitzii*; 15. *nudidorsalis*; 16. *yongi*; 17. *petalae*, dark form; 18. *petalae*, yellow form. 19–23. Raised petiole group: 19. *aurochaetae*; 20. *crypteroniae*; 21. *dianeae*; 22. *hewitti*; 23. *maryatia*.



schwartz, 92-222, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 2/25/1992, Ulrich Maschwitz, 92-224, 92-224a and 92-224c, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sarawak, Lambir NP, Miri, 2/25/1992, U. Maschwitz, 92-227, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sarawak, Lambir NP, Miri, 2/17/1995, Joachim Moog, 95-060, ex: *Spatholobus oblongifolius*, mature colony. INDONESIA, Kalimantan, 11/14/1992, Brigitte Fiala, 0126, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Kalimantan, Balikpapan, 11/16/1992, Brigitte Fiala, 0182, ex: *Spatholobus oblongifolius*.

Cladomyrma hobbyi Donisthorpe, rev. stat.

Figures 8, 13, 25

Cladomyrma hobbyi Donisthorpe, 1937: 620. Holotype queen, BORNEO: East Malaysia, Sarawak, Mt Dulit, 4500 ft, moss forest, 10/14/1932, B. M. Hobby; NHM [examined; synonym of *C. andrei*, Agosti, 1991: 303]. Rev. stat.

DIAGNOSIS: **Major worker.** AL 0.80–1.08, HL 0.94–1.02, HW 0.64–0.90, EL 0.14–0.18, SL 0.32–0.46, CI 82–89, EI 18–23, SI 50–53 ($n = 8$). Frons without longitudinal, brighter-colored spot; clypeus truncate (= angulate in lateral view); short, square head; small body size; gastral pubescence relatively widely set, but hair longer than the distance between their insertions. **Minor worker.** AL 0.57–0.82, HL 0.59–0.70, HW 0.48–0.64, EL 0.10–0.14, SL 0.28–0.36, CI 83–91, EI 21–29, SI 53–61 ($n = 8$). Small body size; body yellowish brown, with genae slightly more yellowish; metapleural gland orifice large; gastral pubescence relatively widely set, but hair longer than the distance between their insertions. **Queen.** AL 1.84–2.16, HL 1.18–1.28, HW 0.93–1.00, EL 0.40, SL 0.54–0.62, CI 75–80, EI 43–47, SI 57–63 ($n = 8$). Head elongate, clypeus smoothly rounded in lateral view; dorsal part of katepisternum with widely set, extremely thin and thus hardly visible pubescence, shining; low petiole, posteriorly gently declining; dense pubescence on gastral tergites; erect hairs scattered all over tergites; dorsum of alitrunk brownish red colored, distinct from head and gaster. **Male.** Petiole a high node; subgenital plate long, slender, parallel-sided, and apically truncated; stipites apically wide,

extended, and almost hemispherical; small body size. PARATYPE. Queen: AL 2.16, HL 1.28, HW 0.99, SL 0.62, EL 0.46, CI 77, EI 46, SI 63.

COMMENTS: All the series available have extremely small workers. The gently rounded dorsoposterior corner of the petiole of the queens is typical for this species, especially separating it from queens of *andrei*, which, in addition, have a rather bright colored and elongate head.

BIOLOGY AND DISTRIBUTION: This species has been collected from the woody climber *Spatholobus oblongifolius* (Papilionaceae) and the understory tree *Drypetes longifolia* (Euphorbiaceae) in Lambir NP, Miri, Sarawak. The type specimens have been obtained by light traps on Mt. Dulit at an altitude of ca. 4500 ft (= 1350 m). We assume that the host plant source was a *Spatholobus*. Whereas *Drypetes* does not occur above 900 m (personal obs.) the liana, according to herbaria notes, extends at least up to 1000 m and, furthermore, is known from that locality. The Malayan counterpart, *Spatholobus bracteolatus*, has been found by us at an elevation of 1300 m, by far exceeding the altitudinal range mentioned on herbarium labels. Therefore, it may be possible that the type specimens originate from *S. oblongifolius*.

MATERIAL EXAMINED: SYNTYPE (labeled "Cotype"): E-MALAYSIA, Sarawak, foot of Mt. Dulit, junction of Tinjar and Lejok rivers, 9/1/1932, B. M. Hobby and A. W. Moore, BNHM 1933-524, queen, ex: light trap, MCZ. OTHER SPECIMENS: E-MALAYSIA, Sarawak, Lambir NP, Miri, 2/25/1992, Ulrich Maschwitz, 92-218, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 2/25/1992, Ulrich Maschwitz, 92-221 b, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 2/27/1992, Ulrich Maschwitz, 92-233, ex: *Drypetes longifolia*; Sarawak, Lambir NP, Miri, 2/17/1995, Joachim Moog, 95-061, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 2/17/1995, Joachim Moog, 95-064, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 2/18/1995, Joachim Moog, 95-065, ex: *Spatholobus oblongifolius*, young colony: 150 workers in total; Sarawak, Lambir NP, Miri, 2/22/1995, Joachim Moog, 95-078, ex: *Drypetes longifolia*, col-

only size small (worker = nanitics), despite presence of males!! Whole plant dissected; not an artifact; Sarawak, G. Mulu NP, 2/1978, JH; G. Mulu, light trap; Sarawak, Mt. Dulit, F. Mjoeberg, MCZ; Sarawak, Lambir NP, Miri, 2/27/1992, Ulrich Maschwitz, 92-235, ex: *Drypetes longifolia*.

Cladomyrma maschwitzi Agosti

Figures 14, 26

Cladomyrma maschwitzi Agosti, 1991: 306. Holotype queen, WEST MALAYSIA, Selangor, Ulu Gombak, 1990, #3, ex *Crypteronia griffithii*, Joachim Moog, BNHM.

DIAGNOSIS: Major worker. AL 0.84–1.00, HL 0.81–0.98, HW 0.68–0.82, EL 0.15–0.20, SL 0.38–0.48, CI 83–85, EI 22–25, SI 53–59 (n = 8). Median part of clypeus coarsely sculptured; large, open metapleural gland orifice; whole body light yellow colored; few hairs on dorsum of mesonotum. **Minor worker.** AL 0.68–0.71, HL 0.62–0.65, HW 0.52–0.56, EL 0.12–0.14, SL 0.32–0.34, CI 84–87, EI 22–25, SI 57–63 (n = 8). Large, open metapleural gland orifice; whole body light yellow colored. **Queen.** AL 1.82–2.38, HL 1.22–1.41, HW 0.98–1.06, EL 0.44–0.48, SL 0.62–0.68, CI 74–80, EI 44–49, SI 63–66 (n = 6). Dense, subdecumbent pubescence on scape, occiput, and alitrunk; an- and katepisternum with few erect hairs, especially in the dorsal regions; large metapleural gland orifice; petiole low, dorsally truncated but slightly dorsally convex. **HOLOTYPE:** AL 1.82, HL 1.62, HW 0.92, SL 0.62, EL 0.44, CI 80.3, EI 55, SI 63.

COMMENTS: This species is easily recognized by its small, light yellow workers, the large metapleural gland orifice, and the uniform brown-colored queen with, at most, appendages and frontal part yellowish. The Sumatran specimens differ somewhat in the body coloration of the queens, which is of a dark brown color and they are larger (AL = 2.24–2.38), however, the workers are of the same yellowish appearance as the non-Sumatran specimens.

BIOLOGY AND DISTRIBUTION: This species is known only from *Crypteronia griffithii* (Crypteroniaceae) but may inhabit another *Crypteronia* species as well (see under *crypteroniae*). A detailed account of the protec-

tive function of *maschwitzi* to its host and colonization rates of different aged host trees are given in Moog et al. (1998). The ants patrol young foliage and deter or kill herbivores they encounter. In addition they clean the surface of young leaves from insect eggs.

Preliminary data suggest a competitive relationship of *maschwitzi* with *crypteroniae*, the sympatric second ant partner of *Crypteronia* in Borneo and Sumatra (unpubl. results). It appears that young *Crypteronia* saplings are occupied primarily by *maschwitzi*, due to the smaller twig diameter, giving the smaller *maschwitzi* queens priority of access to the host plant resource. However, a large percentage of older saplings has been subsequently colonized by *crypteroniae*. It will be interesting to study this phenomenon in detail, i.e. if the observed pattern is the consequence of direct or indirect (e.g. better performance of initial colonies) interactions between the two species. An alternative hypothesis—that the host plant is locally so abundant that founding queens do not compete for it—can be excluded both by a colonization rate of almost 100% and by the regular occurrence of multiple founding on individual host plants.

C. maschwitzi is the most widespread *Cladomyrma* species, occurring in Borneo, Peninsular Malaysia and in Sumatra (a distribution map is provided in Moog et al. (l.c.)). Mitochondrial DNA sequences of *maschwitzi* (and “*cryptata*” = *andrei*) are available through a molecular phylogenetic study of members of the tribe Myrmelachistini (inclusive *Cladomyrma*) by Chenuil and McKey (1996).

MATERIAL EXAMINED: W-MALAYSIA, Perak, Maxwell Hills (=Bukit Larut), 1/21/1988, Ulrich Maschwitz, 0947, ex: *Crypteronia griffithii*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0002, ex: *Crypteronia griffithii*; E-MALAYSIA, Sarawak, Lambir NP, Miri, 2/28/1992, Brigitte Fiala, 92-247, ex *Crypteronia griffithii*; SUMATRA, Jambi Province, Muarabungo, Muar Buat, 3/18/1998, Joachim Moog, 98-044, ex: *Crypteronia griffithii*, alt.: ca. 180m; Jambi Province, Muarabungo, Muar Buat, 3/18/1998, Joachim Moog, 98-046, ex: *Crypteronia griffithii*, alt.: ca. 180 m.



Cladomyrma nudidorsalis, new species

Figures 15, 27

DIAGNOSIS: Major worker. AL 0.90–1.14, HL 0.94–1.14, HW 0.81–0.94, EL 0.18–0.22, SL 0.44–0.54, CI 86–92, EI 19–22, SI 49–54 (n = 4). Small body size; clypeus angulate with longitudinal striae; metapleural gland orifice small; body color brown with mandibles and other appendages slightly lighter colored; gastral pubescence long and dense. **Minor worker.** AL 0.76–0.88, HL 0.67–0.76, HW 0.52–0.67, EL 0.13–0.16, SL 0.36–0.40, CI 78–90, EI 23–25, SI 54–69 (n = 7). Small body size; metapleural gland orifice small; body color brown to light yellowish brown; gastral pubescence long and dense. **Queen.** AL 2.20–2.40, HL 1.38–1.58, HW 1.18–1.26, EL 0.46–0.49, SL 0.62–0.68, CI 80–86, EI 39, SI 53–54 (n = 2). Clypeus gently rounded in profile, otherwise slightly longitudinally striate laterally; head uniformly yellowish brown; dorsum of alitrunk without any erect hairs; metapleural gland orifice small, with a bunch of large setae in front of it; petiole low, dorsally truncated; gastral tergites 2 to 4 with erect hairs only on the posterior margin; erect hairs on gastral tergite 1 only; in the anterior face and along the posterior margin; body color bright yellowish brown with posterior parts of tergites black. **HOLOTYPE:** Queen AL 2.40, HL 1.56, HW 1.24, EL 0.50, SL 0.70, CI 86, EI 39, SI 53.

COMMENTS: This species is easily recognized in the queen by the lack of erect hairs on the dorsum of the alitrunk and the very short hairs on the gastral tergites, unique characters within the genus. However, other queen characters are very similar to those of *petalae* (e.g., size, body color, petiole, pubescence), and the distinction from *petalae* is mainly based on the difference of the distribution of setae, a rather variable character in *petalae*. Another trait may prove to be of importance: the workers of *nudidorsalis* tend to be of a lighter body color than *petalae*, but a larger sample size is needed to assess possible variation.

BIOLOGY AND DISTRIBUTION: This is a species known from two records, one from Fraser's Hill in West Malaysia, collected in *Drypetes longifolia*, and the other from Belum, near the Thai border, collected in *Ryparosa fasciculata*. So far the species seems to be much less common than the syntopic *petalae*.

MATERIAL EXAMINED: HOLOTYPE: W-MALAYSIA, Perak, Gerik, Lake Temenggor, Belum, 3/1/1994, Joachim Moog, 94-086, ex: *Ryparosa fasciculata*, alt.: ca 650 m, colony size small, AMNH. PARATYPES: W-MALAYSIA, Pahang, Fraser's Hill, 2/22/1994, Joachim Moog, 94-070, ex: *Drypetes longifolia*, alt.: ca. 850 m, colony size: 660 worker in total, AMNH, FRIM, NHM, and collections of the others.

Cladomyrma petalae Agosti

Figures 6, 10, 17, 18, 29, 30

Cladomyrma petalae Agosti, 1991: 308. Holotype queen, W-MALAYSIA, Selangor, Ulu Gombak, 1/12/1990, Joachim Moog, ex: *Saraca thaipingensis*, BMNH.

Cladomyrma mossyna Agosti, 1991: 307. Holotype queen, W-MALAYSIA, Selangor, Ulu Gombak, 11/1/1988, Ulrich Maschwitz, #873, ex: *Saraca thaipingensis*, NHM, new syn.

DIAGNOSIS: Major worker. AL 0.86–1.42, HL 0.86–1.24, HW 0.78–1.16, EL 0.16–0.23, SL 0.38–0.60, CI 84–95, EI 18–21, SI 47–53 (n = 18). Clypeus with longitudinal sculpture; gastral pubescence dense and regular; erect pilosity all over alitrunk, without a distinct increase on the propodeum; short, erect hairs on gaster, mainly along posterior margin of tergites, but with scattered hairs in between; erect hairs white. **Minor worker.** AL 0.60–0.98, HL 0.63–0.86, HW 0.53–0.82, EL 0.12–0.18, SL 0.31–0.44, CI 84–95, EI 19–26, SI 48–65 (n = 18). Clypeus without longitudinal sculpture, smooth; few long erect hairs on dorsal face of propodeum; very dense decumbent pubescence on gaster; body color dark brown, with propodeum and petiole slightly brighter; small body size. **Queen.** AL 2.26–2.56, HL 1.42–1.56, HW

←

Figs. 24–35. Head of queens in full frontal view. 24–30. Depressed petiole group: 24. *andrei*; 25. *hobbyi*; 26. *maschwitzii*; 27. *nudidorsalis*; 28. *yongi*; 29. *petalae*, dark form; 30. *petalae*, yellow form. 31–35. Raised petiole group: 31. *aurochaetae*; 32. *crypteroniae*; 33. *dianeae*; 34. *hewitti*; 35. *maryatiae*.

1.15–1.27, EL 0.46–0.54, SL 0.66–0.72, CI 81–84, EI 38–43, SI 53–59 (n = 18). Dorsal part of an- and katapisternum without erect hairs; very flat, dorsally truncate petiole; very few erect hairs on base of first gastral tergite; coloration variable, even within one nest, from uniform yellowish with darker posterior margins of gastral tergites to completely dark brown; in most cases at least genae lighter colored. HOLOTYPE: Queen AL 2.56, HL 1.51, HW 1.24, SL 0.72, EL 0.52, CI 82, EI 42, SI 58.

COMMENTS: This species is distinguished from all other species in the queen caste by the shining dorsal part of the katapisternum, the lateral part of the propodeum below the spiracle being devoid of any pubescence, the small, narrow metapleural gland orifice, and the low, dorsally truncated petiole. *C. mossyna* and *petalae* are now synonymized because more material is available, showing a widely overlapping variation in coloration and pilosity, including the pubescence. A new inspection of the main difference between the two species, with *mossyna* having a much flatter alitrunk (Agosti, 1991: figs 13, 14), showed that this very distinct character is actually based on an artifact, with the ventral side of the alitrunk gently squashed. The correlation between this character, the size of the workers, was rather coincidental and based on a low number of specimens.

BIOLOGY AND DISTRIBUTION: This species has been found in a set of six syntopic host plants; the understory trees *Saraca thaipingensis* (Caesalpiniaceae), *Drypetes longifolia* (Euphorbiaceae), and *Ryparosa fasciculata* (Flacourtiaceae); and the woody climbers *Strychnos vanprukii* (Loganiaceae), *Luvunga* sp. (Rutaceae), and *Spatholobus bracteolatus* (Papilionaceae) (Maschwitz et al., 1991, Moog and Maschwitz, 1994, Moog et al., in press). Despite this highly diverse host range, both field studies and extensive examination of herbarium specimens have shown that congeneric host plant species are not colonized by *petalae* (Moog et al., in prep.). Preliminary results of "host acceptance" experiments with colony-founding queens collected from *Saraca* and *Spatholobus* and placed on one of the other syntopic host plants indicate that foundress queens sometimes accept an alternative host species (unpublished

results). However, they do not accept any other plant species with suitable internodes (controls). The mechanisms underlying this surprising queen response to particular, taxonomically diverse host plants is not yet understood and needs further study.

Water bailing is employed by workers to empty flooded nest chambers (Moog et al., 1997). In *Saraca* (and other hosts), worker activity on the plant surface is concentrated on young developing foliage and the ants reduce herbivore damage to young leaves significantly (Moog and Maschwitz, 1994; unpubl. results). This species also precludes oviposition by female lycaenid butterflies. In addition, lycaenid larvae, even myrmecophilic ones, placed on leaf flushes and confronted with patrolling workers never survive (Seufert and Fiedler, 1996). *C. petalae* is restricted to the Malay Peninsula.

MATERIAL EXAMINED: W-MALAYSIA, Selangor, Ulu Gombak, 2/23/1993, Joachim Moog, 93-105, ex: *Strychnos vanprukii*; Perak, Cameron Highlands, Iskandar Waterfall, 3/12/1993, Joachim Moog, 93-113, ex: *Saraca thaipingensis*; Pahang, Fraser's Hill, 2/19/1993, Joachim Moog, 93-134, ex: *Spatholobus bracteolatus*, alt.: ca. 1300 m, mature colony; Pahang, Fraser's Hill, 3/19/1993, Joachim Moog, 93-142, ex: *Spatholobus bracteolatus*, alt.: ca. 1300 m, colony size: ca. 630 workers; Pahang, Fraser's Hill, 3/14/1993, Ulrich Maschwitz, 93-146, ex: *Ryparosa fasciculata*, alt.: 835 m; Pahang, Fraser's Hill, 3/24/1993, Joachim Moog, 93-148, ex: *Ryparosa fasciculata*, alt.: ca. 830 m, mature colony: ca. 2000 workers; Pahang, Fraser's Hill, 3/24/1993, Joachim Moog, 93-149, ex: *Spatholobus bracteolatus*; Pahang, Fraser's Hill, 3/14/1993, Ulrich Maschwitz, 93-157, ex: *Ryparosa fasciculata*; Pahang, Fraser's Hill, 2/21/1994, Joachim Moog, 94-068, ex: *Luvunga* sp., alt.: 800 m; Pahang, Fraser's Hill, 2/21/1994, Joachim Moog, 94-072, ex: *Luvunga* sp., mature colony; Perak, Gerik, Lake Temenggor, Belum, 3/1/1994, Joachim Moog, 94-084, ex: *Ryparosa fasciculata*, alt.: ca. 780 m, mature colony; Perak, Gerik, Lake Temenggor, Belum, 3/2/1994, Joachim Moog, 94-092, ex: *Ryparosa fasciculata*, mature colony; Perak, Gerik, Lake Temenggor, Belum, 3/3/1994, Joachim Moog, 94-095, ex: *Drypetes longifolia*; Perak, Ge-

rik, Lake Temenggor, Belum, 3/3/1994, Joachim Moog, 94-105, ex: *Drypetes longifolia*; Pahang, Fraser's Hill, 2/22/1994, Joachim Moog, 94-109, ex: *Drypetes longifolia*, colony size: 2200 workers; Selangor, Genting Highlands, 3/22/1994, Joachim Moog, 94-141, ex: *Drypetes longifolia*, mature colony; Perak, Bintang Mountains, Gunung Inas, 3/15/1993, Joachim Moog, 93-128, ex: *Saraca thaipingensis*; Perak, Kelantan, 3/16/1993, Joachim Moog, 93-129, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0004-2, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0004-4, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0004-5, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0006-1, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0006-4, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0006-5, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, Joachim Moog, 0007, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 2/25/1987, Ulrich Maschwitz, 0586, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 11/1/1988, Ulrich Maschwitz, 0873, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 11/12/1988, Ulrich Maschwitz, 0875, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 11/12/1988, Ulrich Maschwitz, 0888, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 10/20/1988, Ulrich Maschwitz, 1067, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1/2/1989, Ulrich Maschwitz, 1131, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1/31/1991, Joachim Moog, 91-035, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1/7/1993, Joachim Moog, 93-015, ex: *Strychnos vanprukii*, colony size: ca. 300 workers, but probably same colony as 93-018, rather than mature colony, *Strychnos* liana climbing on *Saraca*; Selangor, Ulu Gombak, 1/7/1993, Joachim Moog, 93-018, ex: *Saraca thaipingensis*, probably same colony as 93-015 (see above); Selangor, Ulu Gombak, 3/7/1993, Joachim Moog, 93-111, ex: *Strychnos vanprukii*, colony size: ca. 550 workers; Perak, Gerik, Lake Temenggor, Belum, 3/1/1994, Joachim Moog, 94-085, ex: *Ryparosa fasciculata*; Selangor, Ulu Gombak, 2/20/1994, Joachim Moog, 94-057, ex: *Luvunga* sp., alt.:

ca. 300 m, mature colony; Pahang, Fraser's Hill, 2/20/1994, Joachim Moog, 94-058, ex: *Ryparosa fasciculata*, mature colony; Pahang, Fraser's Hill, 2/21/1994, Joachim Moog, 94-059, ex: *Ryparosa fasciculata*, young colony; 340 workers in total; Pahang, Fraser's Hill, 2/21/1994, Joachim Moog, 94-061, ex: *Ryparosa fasciculata*, probably same colony as 94-062, despite different host. Only 20 cm apart, apparently twigs have been in contact; Pahang, Fraser's Hill, 2/21/1994, Joachim Moog, 94-062, ex: *Drypetes longifolia*, probably same colony as 94-061 (see above); Pahang, Fraser's Hill, 2/21/1994, Joachim Moog, 94-063, ex: *Luvunga* sp. young colony: 85 workers in total; Pahang, Fraser's Hill, 2/21/1994, Joachim Moog, 94-065, ex: *Luvunga* sp.; Terengganu, Sekayu Waterfalls, K. Berang, 3/6/1993, Ulrich Maschwitz, 93-135, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, date?, Joachim Moog, "tangle," ex: *Saraca thaipingensis*.

Cladomyrma yongi, new species

Figures 16, 28

DIAGNOSIS: Major worker. AL 0.88–0.92, HL 0.86–0.92, HW 0.69–0.78, EL 0.16–0.20, SL 0.38–0.42, CI 80–86, EI 22–27, SI 52–58 ($n = 8$). Small body size; clypeus angulate; metapleural gland orifice large; scattered hairs all over the body; hairs on propodeum not distinctly longer than those on the mesonotum; gastral pubescence short, appressed, and dense; body bicolored, with head and gaster distinctly darker than the yellowish brown alitrunk. **Minor worker.** AL 0.66–0.70, HL 0.62–0.66, HW 0.48–0.54, EL 0.14–0.16, SL 0.30–0.36, CI 77–84, EI 26–31, SI 60–67 ($n = 8$). Small body size; metapleural gland orifice large; scattered hairs all over the body; hairs on propodeum not distinctly longer than those on the mesonotum; gastral pubescence short, appressed, and dense; body bicolored with head and gaster distinctly darker than the yellowish brown alitrunk. **Queen.** AL 1.80–2.06, HL 1.20–1.26, HW 0.92–1.00, EL 0.40–0.42, SL 0.56–0.60, CI 75–81, EI 40–45, SI 60–64. Clypeus slightly angulate with the anterior face straight; head elongate in lateral view; genae same color as remainder of

head; dorsal part of katepisternum punctulate and with thin pubescence; metapleural gland orifice large and open; petiole in lateral view quadrangular, dorsally evenly rounded with the posterior face gently sloped; whole body covered with long, erect hairs; gaster with short, widely set subdecumbent pubescence; gaster surface with silky shine; head and alitrunk evenly yellowish brown, gaster with at least the posterior parts of the tergites darker; small body size. HOLOTYPE: Queen AL 1.86, HL 1.26, HW 0.94, EL 0.42, SL 0.60, CI 75, EI 45, SI 64.

COMMENTS: This species is characterized in the queen caste by its small size and the light yellowish brown, bicolored coloration. The small body size might be a valid character, as the type series is part of a mature colony with many alate queens and workers. This species shares its host with *hobbyi*, the latter being of close resemblance to *yongi*. However, *yongi* queen differs in its evenly yellowish brown color, head not bicolored with the genae lighter colored than the rest, and petiole in lateral view dorsally evenly rounded and not truncated.

BIOLOGY AND DISTRIBUTION: *Yongi* has only been collected in *Drypetes longifolia* in two localities in Sabah and Sarawak. In "pruning experiments" this species attacked soft young twigs of climbers experimentally placed on the host plant, often destroying the alien plant parts in contact with the host (unpubl. results).

MATERIAL EXAMINED: HOLOTYPE: E-MALAYSIA, Sarawak, Lambir NP, Miri, 2/26/1992, Brigitte Fiala, 92-240, ex: *Drypetes longifolia*; AMNH. PARATYPE: E-MALAYSIA, Sarawak, Lambir NP, Miri, 2/27/1992, Ulrich Maschwitz, 92-234, ex: *Drypetes longifolia*, young colony; Sarawak, Lambir NP, Miri, 2/27/1992, Ulrich Maschwitz, 92-236a, ex: *Drypetes longifolia*; AMNH, FRIM, LACM, MCZ, MCSN, MHNG, NHM, and the collections of Agosti and Maschwitz. E-MALAYSIA, Sabah, Ranau, Poring Hot Springs, 5/9/1987, D. Burckhardt; Sarawak, Lambir NP, Miri, 2/28/1992, Ulrich Maschwitz, 92-239, ex: *Drypetes longifolia*; Sarawak, Lambir NP, Miri, 2/26/1992, Brigitte Fiala, 92-241c, ex: *Drypetes longifolia*; Sarawak, Lambir NP, Miri, 2/26/1992, Brigitte Fiala, 92-244b, ex: *Drypetes longifolia*.

RAISED PETIOLE GROUP

Cladomyrma aurochaetae, new species

Figures 19, 31

DIAGNOSIS: **Major worker.** AL 1.04, HL 1.02, HW 0.92, EL 0.18, SL 0.48, CI 90, EI 20, SI 52 (n = 1). Small body size; body color light brown, and surface shining; clypeus in lateral view rounded, shining, and not longitudinally striate; gaster cuticle thin (when prepared out of ethanol, gaster collapsed); metapleural gland orifice small; gastral pubescence widely set, but hair longer than the space between their insertions. **Minor worker.** AL 0.60–0.68, HL 0.62–0.66, HW 0.56–0.62, EL 0.10–0.14, SL 0.30–0.36, CI 85–97, EI 18–24, SI 50–58 (n = 5). Small body size; body color light brown, and surface shining; gastral pubescence widely set, but hairs longer than the space between their insertion. **Queen.** AL 2.36–2.72, HL 1.60–1.64, HW 1.20–1.30, EL 0.50–0.54, SL 0.76–0.80, CI 74–80, EI 62–65, SI 40–43 (n = 4). Clypeus smoothly rounded with middle part shining; head elongate in frontal view; genae, just above the mandibles, slightly reddish, head otherwise blackish; head surface shining and smooth, very widely scattered punctulation between clypeus and the ocelli; dorsal part of katepisternum shining and with a distinct pubescence; metapleural gland orifice medium sized and open, in front a bunch of long, erect hairs; petiole in lateral view squamiforme, in hind view dorsally truncated; whole body covered with long, erect, golden hairs; on gastral tergites 2 and 3 erect hairs only at posterior margin; gaster tergites 2 and 3 at most with short, widely set appressed pubescence; gaster tergite 1 with long, backward curved hairs; gaster brilliantly shining; head and alitrunk evenly blackish; large body size. HOLOTYPE: Queen AL 2.72, HL 1.64, HW 1.30, EL 0.52, SL 0.80, CI 79, EI 40, SI 62.

COMMENTS: The worker series was collected from a very small colony containing only 22 workers. Therefore, it is likely that the extremely small soldiers and workers are the product of an early phase of colony foundation (= nanitics). This species is easily recognized by the queen's blackish and extremely shining body surface, and the distribution of erect hairs restricted to the posterior margin

of the gastral tergites (dorsal part of gastral tergites 2 and 3 lacks setae).

BIOLOGY AND DISTRIBUTION: Collected only from an unidentified *Neonauclea* species and *N. gigantea* in the Hose Mountains, Sarawak, East Malaysia. The natal colony inhabited the first, single domatium of a *N. gigantea* sapling 0.42 m in height.

MATERIAL EXAMINED: HOLOTYPE: E-MALAYSIA, Sarawak, Kapit, SE side Hose Mountains, 2/3/1997, Joachim Moog, 97-082, ex: *Neonauclea gigantea*, colony size small (worker = nanitics), AMNH. PARATYPE: E-MALAYSIA, Sarawak, Kapit, SE side Hose Mountains, 2/3/1997, Joachim Moog, 97-088, ex: *Neonauclea* sp. AMNH, FRIM, NHM. OTHER SPECIMENS: E-MALAYSIA, Sarawak, Kuching, Kubah NP, 2/8/1997, Joachim Moog, 97-093, ex: *Neonauclea* sp.

Cladomyrma crypteroniae, new species

Figures 20, 32

DIAGNOSIS: **Major worker.** AL 1.12–1.28, HL 1.20–1.28, HW 1.06–1.13, EL 0.18–0.20, SL 0.48–0.58, CI 88–92, EI 17–19, SI 46–52 (n = 8). Clypeus smooth, not longitudinally striate; body color yellow; long erect hair all over alitrunk; appressed, dense gastral pubescence; large ants. **Minor worker.** AL 0.76–0.88, HL 0.68–0.80, HW 0.66–0.74, EL 0.14–0.16, SL 0.34–0.42, CI 87–95, EI 19–23, SI 53–61 (n = 8). Whole body evenly yellowish; dorsum of mesonotum with many erect hairs. **Queen.** AL 2.40–2.72, HL 1.60–1.74, HW 1.34–1.52, EL 0.54–0.58, SL 0.78–0.84, CI 85–87, EI 37–40, SI 52–58 (n = 8). Clypeus smoothly rounded; head slightly elongate with rounded sides in lateral view; genae same color as remainder of head; dorsal part of katepisternum punctulate and with pubescence; metapleural gland orifice large; petiole in lateral view high, dorsally truncated with the posterior face meeting the dorsal in an angle; whole body covered with long, erect hairs; gaster with long semidecumbent pubescence, space between hairs as long as hairs; whole body evenly yellowish, sometime with gaster slightly darker. HOLOTYPE: Queen AL 2.64, HL 1.72, HW 1.48, EL 0.58, SL 0.78, CI 86, EI 39, SI 53.

COMMENTS: The combination of yellow

body color and smooth clypeus surface is unique among *Cladomyrma* workers. *Crypteroniae* workers are distinguished from *maschwitz* workers by the smooth clypeus, more numerous and smaller ommatidia, more densely set, long pubescence on alitrunk and along posterior margins of gastral tergites, darker yellow golden body color, and larger size of both workers and queens. As in *maschwitz*, the Sumatran material differs from the rest by having somewhat smaller and darker-colored queens with slightly longer heads (CI 82–84), showing otherwise the typical character set of *crypteroniae*.

BIOLOGY AND DISTRIBUTION: This species was collected from *Crypteronia griffithii* in Borneo (Lambir NP, Sarawak, Danum Valley, Sabah) and from Muarabungo district in Sumatra. Both ant partners associated with *Crypteronia* (*maschwitz* and *crypteroniae*) are the only *Cladomyrma* species extending to Sumatra. *C. crypteroniae* shares its host with *maschwitz*, and preliminary data suggest *crypteroniae* to be a competitor for the host plant (see above). In Borneo, as indicated by herbarium material, *crypteroniae* (or *maschwitz*) appears to be associated with another *Crypteronia* species, *C. macrophylla*, but field data are lacking. *C. macrophylla* is restricted to the central part of Sarawak and field trips to the collecting sites known from herbarium specimens have not been successful due to the rapid and destructive exploitation of formerly untouched primary forest. Two collections (#0022, #0032) by Diane Davidson were made from a *Crypteronia* species supposed to be different from *C. griffithii* and *C. macrophylla* (D. Davidson, personal commun.). However, all *Crypteronia* specimens, other than *griffithii* and *macrophylla*, seen by JM in several herbaria did not show signs of former ant occupation, but sample size for some species was low. Lack of ant occupation, as indicated by herbarium studies, may not reflect the proportion of occupied trees in the field. For instance, the very high proportion of ant habitation in young *C. griffithii* trees is not seen in herbarium specimens because botanists usually collect plant parts from adult, flowering trees (Moog et al., 1998). Thus, we cannot yet exclude or verify a third *Crypteronia* species as host plant of *C. crypteroniae*.

MATERIAL EXAMINED: HOLOTYPE: E-MALAYSIA, Sarawak, Lambir NP, Miri, 1/30/1997, Joachim Moog, 97-073, ex: *Crypteronia griffithii*, queen, AMNH. PARATYPES: E-MALAYSIA, Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 6/24/1991, Diane Davidson, 91-003; Sarawak, Lambir NP, Miri, 2/23/1995, Joachim Moog, 95-083, ex: *Crypteronia griffithii*, mature colony; Sarawak, Lambir NP, Miri, 2/23/1995, Joachim Moog, 95-086, ex: *Crypteronia griffithii*; Sarawak, Lambir NP, Miri, 2/25/1995, Joachim Moog, 95-090, ex: *Crypteronia griffithii*, mature colony; Sarawak, Lambir NP, Miri, 2/26/1995, Joachim Moog, 95-091, ex: *Crypteronia griffithii*; Sarawak, Lambir NP, Miri, 2/27/1995, Joachim Moog, 95-093, ex: *Crypteronia griffithii*; Sarawak, Lambir Hills NP, Miri, 1/31/1997, Joachim Moog, 97-078, ex: *Crypteronia griffithii*. AMNH, FRIM, LACM, MCSN, MCZ, MHNG, Collections of Agosti and Maschwitz. **OTHER SPECIMENS:** E-MALAYSIA, Sabah, Ulu Segama FR, near Bole River, 10/1994, Diane Davidson, #0022, ex *Crypteronia* sp.; Sabah, Ulu Segama FR, near Bole River, 10/1994, Diane Davidson, #0032, ex *Crypteronia* sp.; SUMATRA, Jambi Province, Muarabungo, Muar Buat, 3/18/1998, Joachim Moog, 98-047, ex: *Crypteronia griffithii*, alt.: ca. 180 m; Jambi Province, Muarabungo, Muar Buat, 3/18/1998, Joachim Moog, 98-048, ex: *Crypteronia griffithii*, alt.: ca. 180 m.

Cladomyrma dianeeae, new species

Figures 21, 33

DIAGNOSIS: **Major worker.** AL 0.89–1.29, HL 0.90–1.42, HW 0.85–1.08, EL 0.14–0.22, SL 0.42–0.58, CI 76–90, EI 16–24, SI 49–61 (n = 8). Medium to large sized ants; alitrunk color yellowish brown, with metapleuron, petiole, gaster, and head dark brown; gastral pubescence short and space between hairs longer than hair; clypeus in lateral view rounded; erect hairs on clypeus very short; head rather short; metapleural gland orifice covered with long erect setae. **Minor worker.** AL 0.76–0.84, HL 0.70–0.89, HW 0.60–0.86, EL 0.13–0.18, SL 0.36–0.46, CI 84–93, EI 19–25, SI 53–66 (n = 8). Medium to larger sized ants; body color dark brown with genae and pronotum yellowish brown; gastral pubes-

cence short, dense, hairs of about same length as distances between their insertions. **Queen.** AL 2.06–2.22, HL 1.32–1.44, HW 1.12–1.18, EL 0.4–0.48, SL 0.64–0.72, CI 82–86, EI 38–41, SI 58–60 (n = 8). Clypeus smoothly rounded, almost flat, in lateral view, matte, longitudinally finely striate; head elongate in frontal view; clypeus and frontal part of head reddish, head otherwise dark brown; head surface shining; dorsal part of katapisternum matte and with a distinct pubescence; metapleural gland orifice large and open, with bunch of long, erect hairs in front; petiole in lateral view nodiform to squamiform; whole body covered with long erect, golden hairs, including all gastral tergites; gastral tergites 2 and 3 with short, widely set semidecumbent pubescence; gastral tergite 1 with erect, golden hairs; gaster somewhat shining; head and alitrunk evenly dark brown to brown to light brown; large body size. **Male.** Subgenital plate long and slender, apically bicornuate; small body size. **HOLOTYPE:** Queen: AL 2.20, HL 1.40, HW 1.18, EL 0.48, SL 0.71, CI 84, EI 41, SI 60.

COMMENTS: This species is easily distinguished by the combination of nodi- to squamiform petiole and an abundant pilosity of erect hair on all gastral tergites. However, it shows a considerable variation in coloration, shape of petiole, width of alitrunk, and to a lesser extent pilosity. At the present time it is impossible to find characters that would allow segregating this species into more than one species. Here again, all the colonies collected included only a limited number of specimens, and it is thus difficult to judge whether the workers are small or just at the beginning of the colony cycle.

BIOLOGY AND DISTRIBUTION: All specimens (except the holotype) were collected from several *Neonauclea* species: *N. borneensis*, *N. gigantea*, *N. longipedunculata*, *N. sp. E* (J. Moog), *N. sp. 2* and *3?* (D. Davidson), and two unidentified *Neonauclea* species (probably including *N. paracyrtopoda*). Doubtful records, which have to be verified, are from *N. sp. C* (J. Moog). *Dianeeae* appears to be a specialized ant associate of *Neonauclea*. It has been collected from at least five different *Neonauclea* species and probably colonizes in Borneo the three other known domatia-bearing *Neonauclea* as well

(*N. artocarpoides*, *N. calcarea*, *N. excelsioides*). The holotype queen has probably been collected from an unknown Bornean *Fagraea* species (D. Davidson, personal commun.). All known myrmecophytic *Fagraea* species bear at the base of the petiole auriclelike scales which clasp the stem. The cavities thus formed are occupied by ants that close the entrances with carton material (Bequaert, 1992), a behavior not displayed by *Cladomyrma* ants. However, if this finding can be verified in future field studies, it would increase the number of known host plant genera of *Cladomyrma* to ten. We predict either that this *Fagraea* species is different from the species having ant-occupied auricles or that the colonization by a *Cladomyrma* queen occurred "erroneously" (compare below: *Cladomyrma hewitti* ex *Myrmeconuclea strigosa*). *C. dianeae* is recorded only from Sabah and Sarawak but increased sampling efforts are likely to extend its known distribution.

MATERIAL EXAMINED: HOLOTYPE: E-MALAYSIA, Sabah, Ulu Segama FR, 10/1994, Diane Davidson, 0023 (queen), ex ?*Fagraea* sp. (Loganiaceae), AMNH. PARATYPES: E-MALAYSIA, Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 6/29/1991, Diane Davidson, 91-012, ex: *Neonauclea* sp.; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/3/1991, Diane Davidson, 91-015, ex: *Neonauclea* sp. 3?; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/6/1991, Diane Davidson, 91-030, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 6/24/1991, Diane Davidson, 91-002, ex: *Neonauclea* sp., AMNH, FRIM, LACM, MCSN, MCZ, MHNG, NHM, collections of Agosti and Maschwitz. OTHER SPECIMENS: E-MALAYSIA, Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 6/27/1991, Diane Davidson, 91-004, ex: *Neonauclea* sp.; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 6/27/1991, Diane Davidson, 91-007, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/8/1991, Diane Davidson, 91-032, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/16/1991, Diane Davidson, 91-051,

ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/16/1991, Diane Davidson, 91-052, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/16/1991, Diane Davidson, 91-053, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/16/1991, Diane Davidson, 91-054, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/16/1991, Diane Davidson, 91-056, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/16/1991, Diane Davidson, 91-058, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/16/1991, Diane Davidson, 91-059, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 7/22/1991, Diane Davidson, 91-063, ex: *Neonauclea* sp. 1; Sabah, Ranau, Poring Hot Springs, 1/24/1993, Joachim Moog, 93-048, ex: *Neonauclea* sp. ?C; Sabah, Ranau, Poring Hot Springs, 1/28/1993, Joachim Moog, 93-064, ex: *Neonauclea gigantea*, young colony: 36 workers in total; Sabah, Ranau, Poring Hot Springs, 1/28/1993, Joachim Moog, 93-066, ex: *Neonauclea gigantea*, mature colony; Sabah, Ranau, Poring Hot Springs, 1/28/1993, Joachim Moog, 93-067, ex: *Neonauclea gigantea*, colony size: ca. 1500 workers in total; Sabah, Ranau, Poring Hot Springs, 1/29/1993, Joachim Moog, 93-071, ex: *Neonauclea gigantea*, young colony: 22 workers in total; Sabah, Ranau, Poring Hot Springs, 1/29/1993, Joachim Moog, 93-072, ex: *Neonauclea gigantea*, young colony: 14 workers in total; Sabah, road Ranau (63.5 km); Telupid, 1/27/1995, Joachim Moog, 95-030, ex: *Neonauclea longipedunculata*, mature colony; Sabah, Ranau, Poring Hot Springs, 3/9/1995, Joachim Moog, 95-110, ex: *Neonauclea gigantea*; Sarawak, Lambir NP, Miri, 2/26/1992, Brigitte Fiala, 92-216 (a & b), ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 2/22/1995, Joachim Moog, 95-081, ex: *Neonauclea paracyrtopoda*?; Sarawak, Niah Cave NP, Miri, 2/24/1995, Joachim Moog, 95-088, ex: *Neonauclea* sp. E; Sarawak, Kapit, SE side Hose Mountains, 2/3/1997, Joachim Moog, 97-084, ex: *Neonauclea borneensis*.

Cladomyrma hewitti (Wheeler), rev. stat.

Figures 22, 34

Aphomomyrmex hewitti Wheeler, 1910: 132. Lectotype major worker. BORNEO: East Malaysia, Sarawak, 1st Division, Bidi, .viii. 1907, John Hewitt [lectotype designated by Agosti, 1991: 303; combination in *Cladomyrma hewitti*, Wheeler, 1920: 53; synonym of *C. andrei*, Agosti, 1991: 303.]. Rev. stat.

DIAGNOSIS: Major worker. AL 0.98–1.23, HL 0.95–1.26, HW 0.84–1.06, EL 0.16–0.23, SL 0.44–0.52, CI 86–90, EI 19–23, SI 47–55 (n = 8). Elongate head with subparallel sides; clypeus, in lateral view, rounded; large metapleural gland orifice; body dark brown with gaster and head distinctly darker; genae lighter brown; body surface shining; gastral pubescence sparse, widely set, so that pubescence hairs do not overlap; medium to large sized ants. **Minor worker.** AL 0.70–0.90, HL 0.66–0.84, HW 0.58–0.74, EL 0.13–0.18, SL 0.32–0.45, CI 87–88, EI 22–25, SI 55–61 (n = 4). Body color dark brown with gaster and head darker; metapleural gland orifice large; medium sized ant; gastral pubescence on tergites widely set and short; hairs not longer than the space in-between them. **Queen.** AL 2.32–2.92, HL 1.60–1.80, HW 1.32–1.36, EL 0.52–0.60, SL 0.80–0.92, CI 77–83, EI 37–45, SI 60–68 (n = 6). Clypeus slightly angulate with anterior face straight; head long in full frontal view, with parallel sides; genae same color as remainder of head; dorsal part of katapisternum punctulate and with thin pubescence; metapleural gland orifice large and open; petiole in lateral view high, dorsally truncated with the posterior face gently sloped; whole body covered with long, erect hairs; gaster with short, widely set subdecumbent pubescence; gaster surface with silky shine; head and alitrunk (dark) brown, gaster with at least posterior parts of tergites darker; large body size. **LECTOTYPE:** Soldier AL 1.18, HL 1.22, HW 1.06, SL 0.50, EL 0.22, CI 87, EI 21, SI 47. Queen from same series as lectotype: AL 2.92, HL 1.8, HW 1.32, EL 0.60, SL 0.84, CI 73, EI 45, SI 54.

COMMENTS: After examining the type again and remounting the queen, it became obvious that the extremely long head of the worker is correlated with a unique, long, par-

allel-sided head of the queen, and a nodiform petiole, which is not present in *andrei* or indeed any other species. In lateral view the queen head of the lectotype specimen is rather elongated, correlated with an exceptionally long alitrunk. In these respects the type thus differs from all other *Cladomyrma* species. None of the additional specimens has this elongated head or AL size. However, in the nontype specimens the character combinations of a long head, together with the raised petiole, make it most likely that they belong to the same species.

BIOLOGY AND DISTRIBUTION: The type specimen was collected in Bidi (SW of Kuching, near Bau), Sarawak, in the “swollen internodes of a shrub” (label information). Based on current knowledge, the shrub might be a representative of one of eight domatia-bearing Bornean *Neonauclea* species, the only host tree genus of *Cladomyrma* with distinct swollen internodes whose species locally grow as shrubs (the other Bornean hosts are either understory treelets or climbers). Indeed, new collections of this species were made only from domatia of two *Neonauclea* species. However, it cannot be excluded that the “shrubs” may belong to *Myrmeconuclea strigosa*, a small rheophytic treelet or shrub with spontaneously opening domatia. This species, regularly colonized by a variety of facultative stem-nesting ant species (Maschwitz et al., 1989), was never found to be inhabited by *Cladomyrma* in Sabah and Sarawak (n > 50), but recent collections in Brunei revealed that colony-founding queens rarely colonize the domatia of *Myrmeconuclea strigosa* (C. Brouat and D. McKey, personal commun.). It is not known if neighboring *Neonauclea* trees, which often grow in *Myrmeconuclea* habitat, are the source plants of these foundress queens. A second trip to the collecting site revealed that *Neonauclea*, inhabited by *Cladomyrma* ants, grow in close vicinity to *M. strigosa* (D. McKey, personal commun.). We suspect that only a very low frequency of *Cladomyrma* queens occupy the latter plant species, presumably due to high intraspecific competition for regular host plants in the vicinity. Mature colonies or alates of *Cladomyrma* were not found in *M. strigosa*. Nevertheless, this phenomenon needs to be studied in detail.

MATERIAL EXAMINED: HOLOTYPE: E-MALAYSIA, Sarawak, 1st Division, Bidi, 8/1907, John Hewitt, MCZ. OTHER SPECIMENS: E-MALAYSIA, Sabah, road Ranau (60.5 km)—Telupid, 1/27/1995, Joachim Moog, 95-027, ex: *Neonauclea longipedunculata*, mature colony; Sabah, Tambunan, Crocker Range, 2/1/1995, Joachim Moog, 95-042, ex: *Neonauclea pseudocalycina*; Sabah, road Kota Kinabalu—Tambunan (33.5 km), Crocker Range, 2/1/1995, Joachim Moog, 95-047, ex: *Neonauclea pseudocalycina*, colony size small: 42 worker in total; Sabah, Tambunan, Crocker Range, 1/1/1995, Joachim Moog, 95-050, ex: *Neonauclea pseudocalycina*; Sabah, road Kota Kinabalu—Tambunan (39.5 km), Crocker Range, 2/1/1995, Joachim Moog, 95-035, ex: *Neonauclea pseudocalycina*, mature colony.

Cladomyrma maryatiaae, new species

Figures 9, 11, 23, 35

DIAGNOSIS: **Major worker.** AL 1.02–1.22, HL 0.98–1.08, HW 0.84–0.96, EL 0.20–0.22, SL 0.45–0.52, CI 85–89, EI 21–24, SI 51–56 (n = 8). Small body size; coloration reddish brown; clypeus in lateral view smoothly curved; metapleural gland orifice large; gaster matte; gastral pubescence widely set (hairs of about same length as distance between their insertions). **Minor worker.** AL 0.72–0.90, HL 0.70–0.80, HW 0.59–0.67, EL 0.14–0.16, SL 0.34–0.40, CI 83–87, EI 22–29, SI 58–61 (n = 8). Small body size; body color dark brown, with head and gaster darker and genae slightly lighter colored; metapleural orifice covered with some long, erect setae; gastral pubescence very short and dense, hair longer than the space between them. **Queen.** AL 2.10–2.28, HL 1.30–1.52, HW 1.06–1.14, EL 0.46–0.50, SL 0.64–0.74, CI 79–82, EI 42–45, SI 58–64 (n = 8). Clypeus slightly angulate in lateral view, matte; head elongated in frontal view; clypeus and frontal part of head reddish, head otherwise dark brown; head surface slightly shining; dorsal part of katapisternum matte and with a distinct pubescence; metapleural gland orifice large and open, in front a bunch of long erect hairs; petiole in lateral view squamiform, in hind view dorsally truncated; whole body covered with long, erect, golden hairs; on gastral tergites 2 and 3 erect

hairs only at posterior margin and lateral parts; gastral tergites 2 and 3 with short, widely set appressed to semidecumbent pubescence; gastral tergite 1 with erect, golden hairs; gaster somewhat shining; head and alitrunk evenly dark brown to brown; medium to small body size.

HOLOTYPE: Queen: AL 2.20, HL 1.43, HW 1.14, EL 0.48, SL 0.68, CI 80, EI 42, SI 60.

COMMENTS: The coloration of the queen is variable, from dark brown to a lighter brown. However, this species is distinct from most others by the combination of the following characters: (1) absence of erect hairs on second and third gastral tergite, (2) raised petiole, (3) large metapleural gland orifice, and from the very similar *aurochaetae* by the absence of the long curved hairs on the gastral tergite 1, and the matte clypeus. All workers seen were small.

BIOLOGY AND DISTRIBUTION: This species was collected from *Neonauclea* species (sp. C of J. Moog; sp. 2 of D. Davidson) in Sabah and Sarawak. Specimens are recorded as displaying an aggressive behavior (Davidson, label information), a trait which it shares with most other *Cladomyrma* species (see above). [Two dubious records exist for *Spatholobus oblongifolius*, but those determination are based solely on workers and should be regarded with some caution.]

MATERIAL EXAMINED: HOLOTYPE: E-MALAYSIA, Sabah, Ranau, Poring Hot Springs, 3/14/1995, Joachim Moog, 95-123, ex: *Neonauclea* sp., altitude ca. 700 m, mature colony, AMNH. PARATYPES: E-MALAYSIA, Sabah, Ranau, Poring Hot Springs, 3/12/1995, Joachim Moog, 95-119, ex: *Neonauclea* sp. C, altitude ca. 600 m, young colony: 195 workers in total; Sabah, Ranau, Poring Hot Springs, 3/12/1995, Joachim Moog, 95-120, ex: *Neonauclea* sp. ?C, colony size: ca. 760 workers in total; Sabah, vic. Danum Valley Res. Center, 85 km W Lahad Datu, 8/7/1991, Diane Davidson, 91-031, ex: *Neonauclea* sp. 2; AMNH, FRIM, LACM, MCSN, MCZ, MHNG, NHM, and collections of Agosti and Maschwitz. OTHER SPECIMENS: E-MALAYSIA, Sabah, Ranau, Poring Hot Springs, 1/24/1993, Joachim Moog, 93-045, 93-045a, ex: *Neonauclea* sp. ?C; Sabah, Ranau, Poring Hot Springs, 1/26/1993, Joachim Moog, 93-052, ex: *Neonauclea* sp. ?C, colony size: 180

TABLE 1
Host Plant Species versus *Cladomyrma* Species

Host plant	Ant species	Location
<i>Callerya nieuwenhuisii</i>	<i>andrei</i>	Borneo
<i>Crypteronia</i> sp. ^a	<i>crypteroniae</i>	Borneo
<i>Crypteronia griffithii</i>	<i>crypteroniae</i> , <i>maschwitzii</i>	Borneo
<i>Crypteronia macrophylla</i>	herbarium ^b	Borneo
<i>Drypetes longifolia</i>	<i>andrei</i> , <i>hobbyi</i> , <i>yongi</i>	Borneo
? <i>Fagraea</i> sp.	<i>dianeae</i>	Borneo
<i>Neonauclea borneensis</i>	<i>dianeae</i>	Borneo
<i>Neonauclea gigantea</i>	<i>aurochaetae</i> , <i>dianeae</i>	Borneo
<i>Neonauclea longipedunculata</i>	<i>dianeae</i> , <i>hewitti</i>	Borneo
<i>Neonauclea paracryptopoda</i>	<i>dianeae</i> ?	Borneo
<i>Neonauclea pseudocalycina</i>	<i>maryatiae</i> , <i>hewitti</i>	Borneo
<i>Neonauclea</i> sp. C (JM)	<i>dianeae</i> , <i>maryatiae</i>	Borneo
<i>Neonauclea</i> sp. D (JM)	unidentified	Borneo
<i>Neonauclea</i> sp. E (JM)	<i>dianeae</i>	Borneo
<i>Neonauclea</i> sp. 1 (DD)	<i>dianeae</i>	Borneo
<i>Neonauclea</i> sp. 2 (DD)	<i>dianeae</i> , <i>maryatiae</i>	Borneo
<i>Neonauclea</i> sp. 3? (DD)	<i>dianeae</i>	Borneo
<i>Neonauclea</i> sp. (unident.)	<i>aurochaetae</i> , <i>dianeae</i> , <i>maryatiae</i>	Borneo
<i>Spatholobus oblongifolius</i>	<i>andrei</i> , <i>hobbyi</i> , <i>maryatiae</i>	Borneo
<i>Crypteronia griffithii</i>	<i>maschwitzii</i>	Malay Pen.
<i>Drypetes longifolia</i>	<i>nudidorsalis</i> , <i>petalae</i>	Malay Pen.
<i>Luvunga</i> sp.	<i>petalae</i>	Malay Pen.
<i>Ryparosa fasciculata</i>	<i>nudidorsalis</i> , <i>petalae</i>	Malay Pen.
<i>Saraca thaipingensis</i>	<i>petalae</i>	Malay Pen.
<i>Spatholobus bracteolatus</i>	<i>petalae</i>	Malay Pen.
<i>Strychnos vanprukii</i>	<i>petalae</i>	Malay Pen.
<i>Crypteronia griffithii</i>	<i>crypteroniae</i> , <i>maschwitzii</i>	Sumatra

^a Possibly a *Crypteronia* species new as host plant (not *griffithii* or *macrophylla*).

^b Herbarium specimens of *Crypteronia macrophylla* show typical signs of regular *Cladomyrma* occupation, but ants not collected (plants not found in the field). JM = Joachim Moog, DD = Diane Davidson. ? indicates that identification is based on workers only. Note that *Neonauclea* species of DD are most likely identical to some of the other eight listed species, since only eight myrmecophytic *Neonauclea* are known to occur in Borneo. [The table lists all records of colonization without noting the frequency of occupation.]

workers in total; Sabah, Ranau, Poring Hot Springs, 3/10/1995, Joachim Moog, 95-114, ex: *Neonauclea* sp. C, colony size small (nanitic workers); Sarawak, Lambir NP, Miri, 2/26/1992, Brigitte Fiala, 92-211 a-b, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 2/26/1992, Brigitte Fiala, 92-212, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 2/27/1992, Brigitte Fiala, 92-213, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 2/27/1992, Brigitte Fiala, 92-215b, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 2/28/1992, Alfred Buschinger, 92-223, ex: *Spatholobus oblongifolius*; Sabah, Ranau, Poring Hot Springs, 3/24/1995, Joachim Moog, 95-151, ex: *Neonauclea* sp. C, colony size small (workers = nanitics).

CONCLUSIONS

This taxonomic study is a first attempt to clarify the species identities of certain, newly discovered *Cladomyrma* species and particular host plants, although limited data and taxonomic uncertainties give a rather provisional picture to date. We are still far from understanding the factors leading to some apparent species pairings (table 1), which will be part of a broader study by one of us (JM). However, both the extremely diverse host plant taxa (with apparently different degrees of myrmecophytism) and specific ant traits, indicating a predisposition for symbiosis with "preadapted" plants, point to frequent

TABLE 2
Coordinates of Important Collecting Sites

Lambir NP, Miri, 4th Div., Sarawak, East Malaysia	4°12'N 114°01'E
Danum Valley, Lahad Datu, Sabah, East Malaysia	4°55'N 117°45'E
Poring Hot Springs, Ranau, Sabah, East Malaysia	6°03'N 116°41'E
Ulu Gombak, Selangor, West Malaysia	3°19'N 101°45'E
Fraser's Hill, Raub, Pahang, West Malaysia	3°43'N 101°44'E
Maxwell Hills, Taiping, Perak, West Malaysia	4°51'N 100°48'E
Belum (Camp Halong), Gerik, Perak, West Malaysia	5°31'N 101°25'E
Sg. Busaha, Muarabungo, Jambi, Sumatra	1°41'S 101°49'E

host shifts and host additions and thus corroborate the findings of previous studies stating that ant-plant symbioses diversify primarily through processes of host shifts and ecological fitting (Davidson and McKey, 1993, Chenuil and McKey, 1996, Yu and Davidson, 1997). However, at present, it is premature to exclude periods of pairwise coevolution, e.g., in the rubiaceous genus *Neonauclea* in which a small radiation of myrmecophytic species occurred. It should be noted that all eight Bornean domatia-bearing species seem to be regular host plants of *Cladomyrma* (despite the local inhabitation of *Neonauclea* by some facultative *Crematogaster* species [unpubl. results]), whereas the nine known myrmecophytic *Neonauclea* species outside Borneo—in Sumatra (2), Sulawesi (6), and the Philippines (1)—are colonized by obligate *Crematogaster* (subgenus *Decacrema* and *Physocrema*) species (Maschwitz and Fiala, 1995; unpubl. results). This interesting pattern is correlated with differences in the formation of ant domatia. In Bornean *Neonauclea* inhabited by *Cladomyrma*, the young swollen internodes are filled with a soft pith, whereas the domatia of *Crematogaster*-inhabited *Neonauclea* are characterized by a distinct pith degeneration. Furthermore, it will be of great interest to compare the *Cladomyrma*-plant relationships with the best-known Southeast Asian ant-plant system, the *Crematogaster*-*Macaranga* mutualism, and the New World *Myrmelachista*-plant associations. A set of *Myrmelachista* species exhibits striking ecological similarities with *Cladomyrma*; these similarities include (1) a range of (often sympatric) host plants extending over several plant families with one plant genus as a dominant partner group (*Ocotea* and *Neonauclea*, respec-

tively), (2) apparently different degrees both of host specificity by the ants and host-plant adaptations to the ant partners, and (3) the regular use of coccoid trophobionts inside the stem hollows. However, the formicine genus *Myrmelachista* not only includes obligate plant-ant species inhabiting live stems of a particular set of host plants (e.g. *Licaria*, *Guaireia*) but also opportunistic arboreal species that nest in various plant cavities such as dead stems or leaf pouches, e.g., of *Clidemia*, *Maieta*, *Tococa* (Wheeler, 1942; Tennant, 1994). These latter *Myrmelachista* species often have large polydomous colonies, forage off their host, and can be common at extrafloral nectaries in the vegetation (Longino and Hanson, 1995). If the obligate plant-ant habit is a derived character from generalized arboreal nesting by *Myrmelachista* species, it may illustrate the potential for multiple independent evolutionary colonizations of ant-plants (although a study of their phylogeny is lacking). In contrast, the genus *Cladomyrma* consists only of morphologically and behaviorally similar species that inhabit live stems of specific host plants. Therefore, it is assumed that a monophyletic origin of the plant-ant habit in *Cladomyrma* is likely.

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