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Reproduction by ergatoid queens in the myrmicine ant *Monomorium brocha* (Bolton) (Hymenoptera: Formicidae) in West Java, Indonesia, with a description of the male

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ABSTRACT. This study reports on reproduction by ergatoid queens of *Monomorium brocha* (Bolton) collected in the Bogor Botanic Garden, West Java, Indonesia. One colony fragment comprised 20 ergatoid queens that showed variable ovariole numbers. All but one of the dissected queens had mated, but the ovarian condition varied among individual queens. Ergatoid queens can be easily distinguished from workers by morphological characteristics such as large compound eyes and a suture between the pronotum and mesonotum. The development of the mesonotum varies among ergatoid queens, but has no correlation with ovariole number. Comparison of queen-worker dimorphism in body size and ovariole number among 11 *Monomorium* species indicates that the present species shows smallest caste dimorphism among the known species of this genus. A description of the male is given.

INTRODUCTION

The evolution of wingless reproductive females in ants is one of the most important features underlying the diversity of ant life history strategies (Heinze & Tsuji 1995; Peeters & Ito 2001; Peeters & Molet 2010). However, our knowledge of wingless reproductive females is still restricted to certain genera only. Therefore, biological information on other ant genera with this type of caste is undoubtedly important to understand the significance of reproduction by wingless reproductive females.

Epelysidris was described as a monotypic genus from Sarawak, Borneo by Bolton (1987) based on nine workers collected in 1932. Only one species, *E. brocha* Bolton, has been described. Ants of this genus are considered rare, and no data are available from recent surveys in Southeast Asia except from Ito *et al.* (2001), who reported *E. brocha* from Bogor Botanic Garden, West Java, Indonesia based on a small fragment of a colony. At present, nothing of their biology is known. Recent review of the genus *Monomorium* by Fernández (2007) treated *Epelysidris* as a junior synonym of *Monomorium*. However, *Epelysidris* has some peculiar morphological features (Bolton, 1987) as mentioned by Fernández (2007). Thus biological information would surely contribute to a better understanding of *Monomorium* and allied genera. In this paper we follow the taxonomic treatment by Fernández (2007).

Fortunately, one additional colony of *Monomorium brocha* was collected in the botanical garden in Indonesia in August of 2001with mated and egg-laying wingless reproductive females.

The biological information on this rare ant species is reported herewith. The terminology describing wingless reproductive females has been controversial (Peeters, 1991; Heinze, 1998). For wingless reproductive females with variable morphology, e.g. some species of *Leptothorax*, some authors use intermorphs, whereas such females without a remarkable variation, as seen in the ponerine genus *Leptogenys*, are always described as ergatoid queens (e.g. Peeters 1991; Heinze 1998). Species with “intermorphs” and species with “ergatoids” show different life history patterns, i.e., the majority of the former type coexists with alate queens in a population, while the latter have permanently lost alate queens (Peeters, 1991). However, there are several exceptions, and the distinction between the two types is largely semantic (Molet *et al.* 2009). In this paper, we use the term “ergatoid queens” for the wingless reproductive females, which can be morphologically distinguished from workers. A description of the male of this species is given in the Appendix.

MATERIALS AND METHODS

The colony (code FI01-151, Fig. 1) of *M. brocha* was found underground in the *Shorea* forest of Bogor Botanic Garden (6˚35’S, 106˚47’E, and ca 240 m alt.), West Java, Indonesia, on 10 August 2001. Almost half of the colony was collected with an aspirator. Some individuals were dissected under a binocular microscope immediately after collection. The remaining individuals were kept in a container measuring 20 × 10 × 5 cm, which contained a small artificial nest (5 × 5 × 2 cm) as a nest chamber. The floor of the container was covered with plaster to maintain humidity. In the laboratory, the colony was provided with several kinds of dead arthropods including termites, mealworms, crickets, and particles of sweet cookies. Workers also took honey water. A small sub-colony composed of ten queen pupae, about ten male pupae and 30 adult workers were divided from the original colony and kept in another artificial nest. Sexuals emerged from these pupae within a few weeks. After two months, all wingless queens in the isolated sub-colony (number of emerged individuals = 6) were dissected to check their reproductive status. Head width and head length of 17 queens and 20 workers were measured to the nearest 0.02 mm under a binocular microscope. Maximum width of the compound eye was measured to the nearest 0.005 mm under a light microscope for 14 workers and 13 queens. Head width of queens and workers of ten additional *Monomorium* species collected in the Oriental tropics and Japan was also measured for comparison of size dimorphism between queens and workers. Species codes given to unidentified species are personal species codes used by one of the authors (FI). Male morphology was compared with other *Monomorium* species from the SKY collection, Kagoshima. Voucher specimens are deposited in Bogor Zoological Museum.

RESULTS

Colony composition

The colony was collected from hard soil on the forest floor. The colony fragment contained ca 220 wingless females, 40 males, and several immatures. The wingless females were of two types: one with a large abdomen, and one with a small abdomen (Fig. 1). Dissection of some individuals of both types showed that the former had a spermatheca and 6 to 14 ovarioles per individual (average ± SD, 9.2 ± 2.1, N = 17), while the latter had two ovarioles and lacked a spermatheca (N = 20), indicating that the former type are ergatoid queens and the latter are workers. The overall body size of workers was slightly smaller than that of ergatoid queens [head width: 0.73 ± SD 0.025 mm in queens (N = 17), 0.64 ± 0.023 mm in workers (N = 20), Welch two sample t-test, $t = 11.3$, $df = 31$, $P < 0.0001$] (Fig. 2). Furthermore, both female types can be distinguished by the following morphological characteristics: the compound eyes of ergatoid queens were remarkably larger than those of workers in the long axis [0.12 ± 0.011 mm in queens (N = 13), 0.05 ± 0.004 mm in workers (N = 13), Welch two sample t-test, $t = 18.3$, $df = 15$, $P < 0.0001$], while workers had a slightly elongated heads [proportion of head length to head width: 1.05 ± 0.028 in queens (N = 16), 1.12 ± 0.032

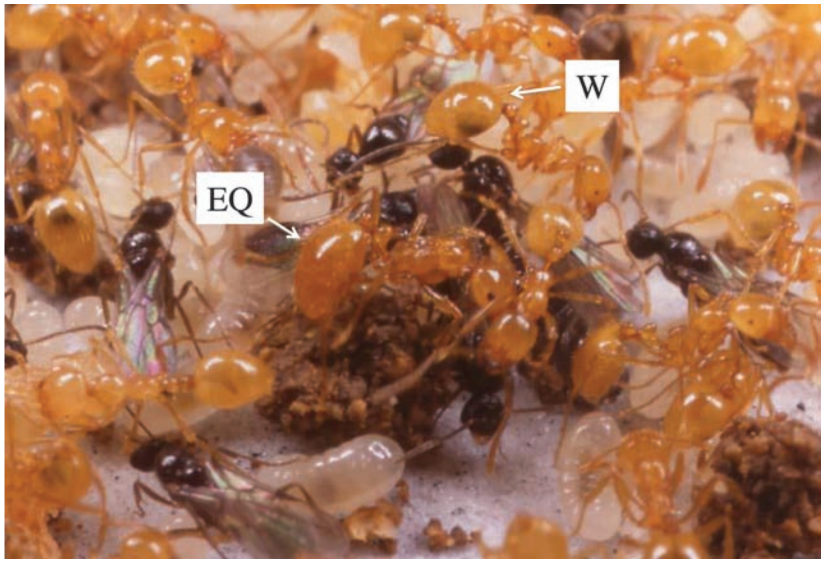

Fig. 1. Colony fragment of *Monomorium brocha* collected in the Bogor Botanic Garden. EQ: ergatoid queen, W: worker

in workers (N = 20), Mann-Whitney U-test, Z = −4.89, P < 0.0001]. Representative specimens are shown in Fig. 3. The structure of the thorax, especially the development of the mesonotum, varied among ergatoid queens (Fig. 3A~C); some of them were very similar to workers but the pronotum was separated from the mesonotum by a suture in all ergatoid queens while the pronotum was fused with the mesonotum without a suture in workers (Fig.3 D). Four ergatoid queens had a remarkably developed thorax with a "wing base" (Fig. 3 A): however, their mesonotum was not well developed compared to that of alate queens of other *Monomorium* species. The ovariole number of these four ergatoid queens with wing bases was nine (3 queens) or 11 (one queen), being not significantly different from that of queens without a wing base (Welch two sample t-test, t = 0.67, df = 10, P =0.71). This indicates that the development of the thorax is not positively correlated with ovariole number. The majority of ergatoid queens had two degenerated ocelli, while workers completely lacked ocelli. Based on this difference, 20 ergatoid queens and 200 workers were recognized among the females in this colony fragment. Details of brood composition were not examined, but the sex and caste of 67 randomly selected pupae collected in the field were checked: these included 33 workers, nine ergatoid queens, and 21 males.

Reproduction by ergatoid queens

All but one of the ergatoid queens had mated (N = 17). Ovary development of ergatoid queens dissected immediately after collection varied greatly: two had well developed ovaries, one had only two developing oocytes without yellow bodies, and another two mated queens and one virgin queen had no developing oocytes. These results indicate that this species exhibits polygyny with variation in queen fecundity. The relationship between the fecundity of queens and their age was unclear, because there were no indications of age difference among queens. Under laboratory conditions, many queens held eggs in their mandibles, and carried eggs inside the nest chamber. Queens without eggs in their mandibles often tried to pick up eggs held by other queens, though this was rarely successful. Any clear dominance behavior was not observed among ergatoid queens. Most workers had a few developing oocytes.

Three of six ergatoid queens that emerged in an isolated colony had mated, indicating that intracolonial mating occurred, even though mating behaviour was not observed.

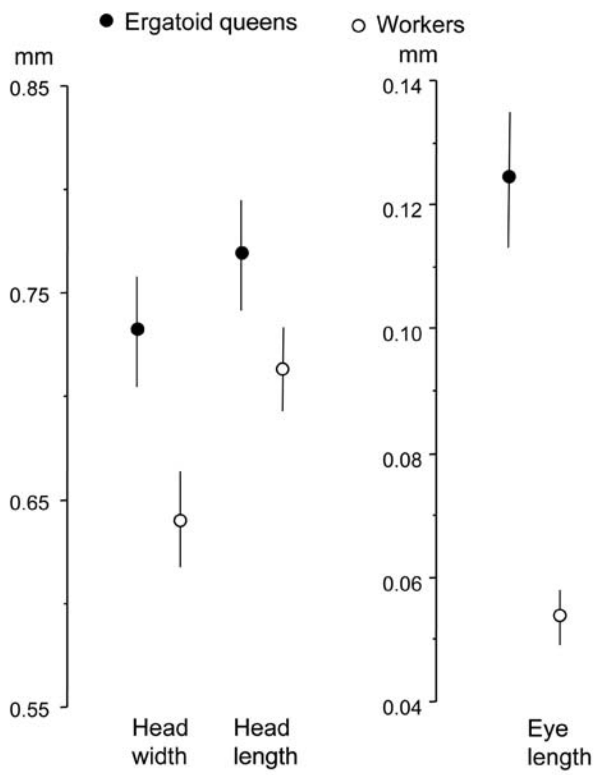

Fig. 2. Head width, head length and eye length of queens and workers.

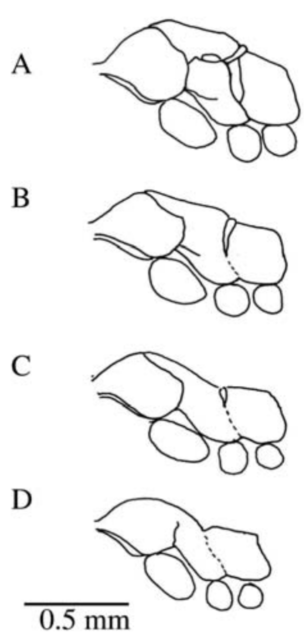

Fig. 3. Thorax structure of ergatoid queens (A ~ C) and worker (D).

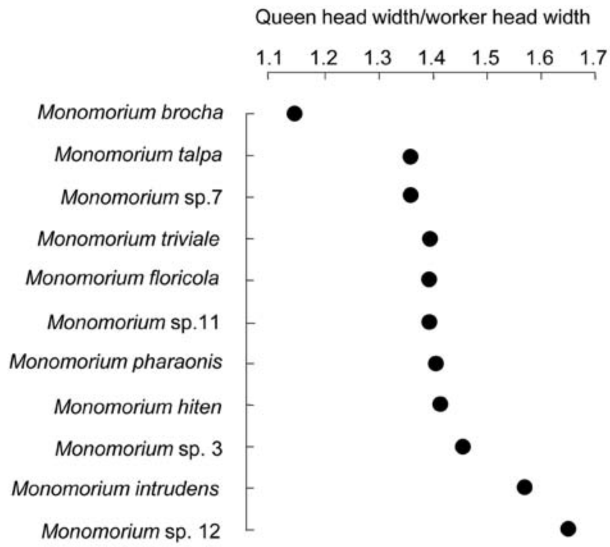

Fig. 4. Size dimorphism between queens and workers in the Oriental *Monomorium* ants. Localities of specimens and number of individuals measured (shown in parenthesis) are as follow: *M. brocha* (17Q, 20W), *M. talpa* (2Q, 6W), *Monomorium* sp. 3 (2Q, 3W), *Monomorium* sp. 7 (1Q, 5W), *M. floricola* (1Q, 5W), and *M. pharaonis* (1Q, 5W) from Bogor Botanic Garden, West Java; *M. intrudense* (3Q, 5W) from Miki, Kagawa Pref., Japan; *M. triviale* (3Q, 5W) from Ibaraki Pref. Japan; *M. hiten* (3Q, 5W) from Kunigami-son, Okinawa Pref., Japan; *Monomorium* sp. 11 (1Q, 5W) from Puruwodadi Botanical Gardens, East Java, Indonesia; *Monomorium* sp. 12 (1Q, 5W) from Ulu Gombak, West Malaysia. *M. triviale* and *M. brocha* have ergatoid queens, and queens of the other species have well-developed thorax with wing base, thus they are alates.

Fig. 5. Lateral and full-face view of *M. brocha* male. Bar = 1 mm

Table 1. Ovariole number per individual (mean±SD) in *Monomorium* ants. Collection localities are shown in the legend of Figure 4. Figures in parentheses are numbers of dissected individuals.

	Queens	Workers	Data source
Momomorium intrudense	30 ± 4 (8)	0 (6)	Ito,unpub.
Monomorium triviale	15, 20, 22 (3)	0 (6)	Ito,unpub.
Monomorium hiten	20 (1)	0 (6)	Ito,unpub.
Monomorium sp. 12	8, 8, 13 (3)	0 (6)	Ito,unpub.
Monomorium brocha	9.2 ± 2.1 (17)	2 (20)	The present study

DISCUSSION

Several ergatoid queens reproduced in the colony of *Monomorium brocha*. The majority of *Monomorium* species have alate queens, though ergatoid queens are known from some species (e.g. Bolton 1986, Dubois 1986), and the coexistence of both alate and ergatoid queens has been documented in *M. vilidum* in the USA (Dubois 1986) and one species of Australian *Monomorium* (Fersch *et al.* 2000). Furthermore, some species of the related genus *Megalomyrmex* also have ergatoid queens (Brandão 1990). Modification of the thorax structure of ergatoid queens in *Monomorium* varies greatly among species, but no variation within species has been reported (Bolton 1986, Dubois 1986). In this respect, the remarkable diversity in the thorax morphology exhibited by ergatoid queens in the colony of *M. brocha* in this study is exceptional. In ants in general, ergatoid queens coexisting in a population with alate queens show variable thorax morphology, while ergatoid queens exhibit less variation in the absence of alate queens, as shown in the genus *Myrmecina* (Buschinger and Schreiber 2002; Ito 1996 and unpublished). As only a fragment of a colony was collected in the present study, the possibility that some alate queens were missed cannot be ruled out. Dubois (1986) described ergatoid queens of six species of the *M. minimum* species group, all of which had developed mesonotum and mesoscutellum, and reduced pronotum as in alate queens. These characteristics were also found in ergatoid queens of four species of the *M. salomonis* -group (Bolton 1986). Ergatoid queens such as this were not found in our colony of *M. brocha*. Even if [?]queens had “wing base”, the mesonotum and mesoscutellum were reduced, and pronotum developed as in *M. advena*, as shown by Bolton (1986).

In *Monomorium brocha* ergatoid queens are similar to workers in body size, and workers retain ovaries. The majority of *Monomorium* ants so far studied show a huge size dimorphism between queens and workers (e.g. Dubois, 1986). Figure 4 shows queen-worker dimorphism of the Oriental and Japanese *Monomorium* species including a few tramp ants. Compared to the other *Monomorium* species, size dimorphism between the two castes is less pronounced in the present species. Although our knowledge of ovarian dimorphism between queens and workers in *Monomorium* is limited, specialization of the reproductive apparatus is known in some species. For example, workers have lost ovaries, while queens have ca 20 to 30 ovarioles in three Japanese species (Table 1). Alate queens of the Malaysian species *Monomorium* sp.12 have comparable ovariole numbers to the present species. Another example is known from Australian *Monomorium*: workers of *Monomorium* sp. 10 have 3 - 5 ovarioles while ergatoid queens (intermorphic queens) and dealate queens (gynomorphic queens) have 6 to 11 (Fersch *et al.* 2000), although the overall body size difference was not reported. Besides *Monomorium*, many other species of the tribe Solenopsidini (e.g. species which belong to *Pheidologeton* and *Solenopsis*), have workers without ovaries (Hölldobler and Wilson 1990), and queen-worker dimorphism in body size is generally remarkable (e.g. Moffett 1988). An extreme size difference is found in *Carebara* spp. (e.g. Fernández 2004). In this respect, *Monomorium brocha* is an unusual species among the tribe Solenopsidini. Therefore, further investigations of the biology and ecology of *Monomorium* and related genera seems to be important for understanding the evolution of queen-worker dimorphism and obligate worker sterility.

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APPENDIX

Description of male

Measurements (n = 4). Head width including eye 0.64 – 0.67 (mean: 0.66), head length 0.56 – 0.58 (0.57), eye width 0.22 – 0.23 (0.23), eye length 0.28 – 0.30 (0.29), scape length 0.17 – 0.18 (0.18), mesonotal width in dorsal view 0.60 – 0.63 (0.62).

Structure. Head, excluding eyes, as long as broad, much narrower at mandibular bases than at the level behind eyes, with evenly rounded posterior margin. Occipital carina recognizable as a blackened low keel in median portion of posterior margin of occiput. Clypeus clearly demarcated from frons, medially strongly convex dorsad, with straight anterior margin. Mandible moderately developed; masticatory margin with 3 teeth; first (apical) longest and third (basal) shortest or subequal to second; first and second sharply pointed at apex, close to each other; basal margin with a denticle located close to basal tooth of masticatory margin (the denticle looks a fourth tooth). Eye very large, distinctly protruding from outer margin of cranium; malar space (distance between mandibular base and anterior margin of eye) short. Ocelli rather large; their diameter as long as antennal pedicel; distance between lateral ocelli larger than that between median ocellus and lateral ocellus, 1.5 times as long as ocellar diameter. Antennal socket close to posterior margin of clypeus; frontal lobe poorly developed, not covering antennal socket; frontal carina almost absent. Antenna 13-segmented; scape cylindrical, when laid back not extending beyond the level of the anterior margin of median ocellus, as long as segments 2 (pedicel) and 3 combined; segments 3 to 13 gradually becoming longer toward antennal apex; apical segment twice as long as segments 11 and 12 combined. Mesosoma massive, broader than head excluding eyes. Seen from above pronotum reduced to a narrow belt; lateral face posterovetrally sloping steeply to anterior margin of anepisternum. Mesoscutum huge, with weak median suture and notaulices that are often evanescent, seen from above as broad as long, and seen in profile roundly convex dorsad; mesoscutellum separated from mesoscutum by a deep furrow with the bottom provided with short keels, broader than long, strongly convex dorsad; anepisternum well differentiated from katepisternum by a suture (or a series of punctures), dorsally margined with a carina. Metanotum a very narrow zone, well defined between mesoscutellum and propodeum; metapleuron differentiated from mesopleuron, but completely fused with propodeum in lower half. Propodeum weakly convex posterodorsad; dorsal and posterior faces poorly differentiated; weak lateral carinae present on posterior face; with propodeum in full-face view spiracle located high on lateral face, at some distance from both dorsal and posterior margins of propodeum. Petiole with a distinct peduncle; petiolar node in dorsal view broader than long, in profile as long as high, apically narrowed with round apex; postpetiole as high as petiole, but more globular than the latter, with more rounded apex. First gastral tergite large, slightly shorter than the remaining tergites combined, seen from above with almost parallel sides.

Sculpture. Head extensively covered with dense sculpture and mat; frons and area behind ocelli with weaker sculpture and somewhat shiny; mandible superficially sculptured and shiny; antennal scape and pedicel smooth and shiny; other segments densely and minutely sculptured. Pronotum, mesoscutellum and metanotum, and meso- and metapleura smooth and shiny; mesoscutum and propodeum weakly sculptured. Petiolar and postpetiolar nodes and gastral tergites and sternites smooth and shiny; petiolar peduncle densely punctate.

Pilosity. Dorsa of head, mesosoma and waist, and gastral tergites and sternites with many erect hairs that are longer than antennal pedicel; clypeus with a long median seta; antennal scape with erect hairs that are shorter than diameter of scape; tibiae of all legs with numerous obliquely standing hairs on outer faces.

Wing venation. The terminology follows the system adopted by Hölldobler and Wilson (1990, Figs. 2 – 11). Forewing: costal vein almost fused with subcostal vein half way from wing base; pterostigma distinct and large; marginal cell open apically; submarginal cell open near pterostigma; first discoidal cell small, closed; cubito-anal crossvein (cu-a) complete or not reaching anal vein (as in Fig. 5); cubital vein and median vein short, not reaching outer margin of wing. Hindwing: venation reduced; only median cell enclosed with strong veins.

Remarks. We compared the male of *Monomorium brocha* with those of *M. floricola* (Jerdon), *M. chinense* Santschi and three unidentified Asian species. It is in most characters very similar to the males of above-mentioned species and those of the *Monomorium* species for which the male sex has been described (Smith, 1943; Ettershank, 1966; Bolton, 1987; Ogata, 1991). The following conditions may be noted: occipital carina distinct on the median portion of posterior margin of occiput; costal and subcostal veins of forewing almost fused in basal half; first discoidal cell present (this condition is also seen in some African species; Bolton, 1987). As a whole we did not find a strong reason to separate this species in male morphology from other species of *Monomorium*.