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Chalicodoma pluto: The World's Largest Bee Rediscovered Living Communally in Termite Nests (Hymenoptera: Megachilidae)

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ABSTRACT: The long-lost bee *Chalicodoma pluto* was found in the North Moluccas of Indonesia, and was discovered nesting communally in association with a tree-dwelling termite. Using their extraordinary mouthparts, females gather resin and wood and fashion these materials into galleries resistant to termite invasion. The first males known of the species were taken, and male territoriality was observed.

Alfred Russel Wallace collected the female type of *Chalicodoma pluto* (Smith) (Hymenoptera: Megachilidae) in 1859, on Bacan, in the North Moluccas of Indonesia (Smith, 1861). The species, which is the world's largest bee (Michener, 1965), was previously known from only two specimens (Friese, 1909), and presumed extinct (Wells et al., 1983). In addition to their 39 mm length (Fig. 1), females are remarkable for their enormous, stag beetle-like mandibles and expanded labrum (Fig. 2), structures which have puzzled entomologists since the species was described, and which are shared with the few other members of the subgenus *Eumegachilana* (Michener, 1965).

I rediscovered *C. pluto* on three Indonesian islands and found that it nests communally, apparently always within the inhabited nests of a tree-dwelling termite. The use of the huge female mouthparts was observed, males were taken, and male territorial behavior was recorded.

I first located *C. pluto* on Halmahera in February 1981, in primary lowland forest about 8 km SE of Kampung Pasir Putih (0°57'N, 127°42'E). There I saw females repeatedly returning to a tree to gather resin. Field assistants helped me to follow *C. pluto* to its tunnels in the nest of a common arboreal termite, *Microcerotermes amboinensis* Kemner (Termitidae) (J. A. L. Watson, pers. comm.). Surveys for other nests were then carried out, and additional nests were located on Bacan, Halmahera, and Tidore, mountainous islands near the Equator in the North Moluccas. Despite an abundance of potential nesting sites, the bee appears to be rare. Local informants had never seen the bee prior to its rediscovery, although a specific folk epithet, *o ófungu ma kóana,* "king bee," is based on it. Intensive searches failed to locate *C. pluto* in substrates other than the termite nests, and it seems possible that the association is an obligate one.

Chalicodoma pluto females harvest resin from vertical trunk fissures of a primary forest dipterocarp, which is probably *Anisoptera thurifera* Blanco (Bl.) (Taylor, 1980). The resin-collecting behavior provided an explanation for the bizarre structure of the labrum and mandibles. Facing upward, a female loosened resin with the mandibles, then scraped it up using the elongate labrum in the manner of a bulldozer blade. The ball of resin which formed was held in place between the tree and the labrum while being progressively enlarged. The process was repeated until a ball approximately 10 mm in diameter had been amassed.

In addition to providing a surface against which resin was held as it was gathered, the labrum was observed to act as a lever, applying tension to a load in the mandibles and possibly helping to secure it during flight.

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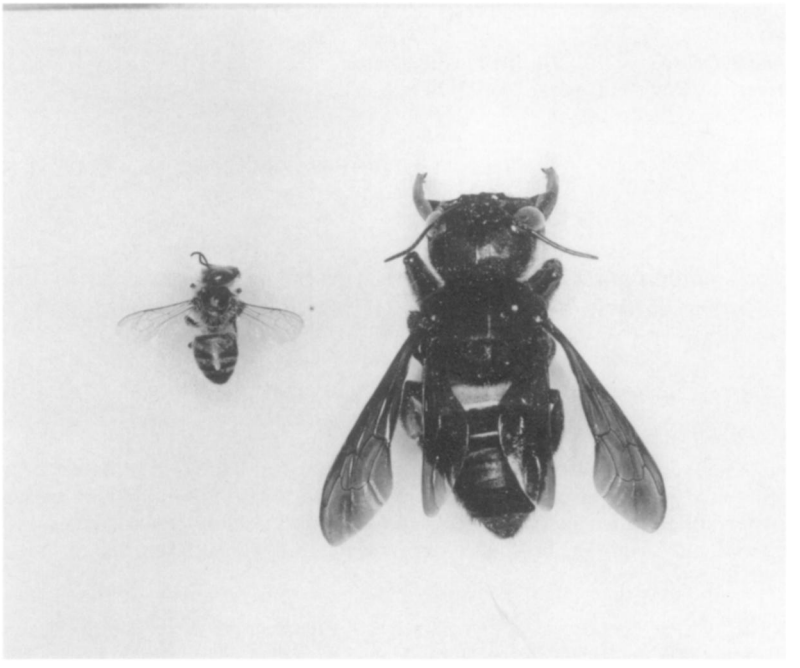

Fig. 1. Dorsal view of a common honeybee worker, *Apis mellifera* L. (left) compared to *C. pluto.* The tridentate clypeus, white band on the abdomen, enormous mandibles and body size serve to distinguish the latter species. (Photographs by J. W. Porter.)

Females brought wood to the nest in the form of cylindrical bundles of dried fibers, also carried between the labrum and mandibles. A waterproof mixture of wood fibers and resin, which hardens with time, was used to construct cells and tunnels. The termitary with which the bee is associated is made of carton, and completely conceals the bee nest. A single entrance hole provides access to the tunnels.

When nests were dissected, no connections between *C. pluto* and termite tunnels were found. Moreover, the volatile poisons ether, ethyl acetate, and paradichlorobenzene that were introduced into the bee galleries did not kill the termites.

Male bees are smaller (mean length = 23.4 mm, SD = 1.2 mm, $n = 6$) than females, lack large mouthparts (Fig. 2), and have rufous, instead of white, pubescence. They were never seen gathering resin or wood, nor were they found within nest tunnels. Male territorial behavior was observed near the resin source and in the vicinity of a nest. Males perched head-up on a vine, and darted off to chase away an intruding male or to pursue a female. After such encounters the male returned to the vine.

Males developed in smaller cells (approx. 15 × 27 mm) than did females (cell size approx. 19 × 41 mm). Cells were lined with a continuous layer of wood fiber prior to pollen and egg deposition, and were reused after a new lining of resin and wood was installed over larval and adult excreta. Female cells were frequently but not always converted into male cells by the addition of a thick layer of resin and wood fiber to the inside. Since cell diameter decreased with each reuse, cells were ultimately abandoned, as they became too small for brood rearing. Hence, in four nests, an average of only 24% (range 15%–34%) of the cells contained live forms. The remainder, containing frass and excreta, were sealed with resin plugs.

Chalicodoma pluto packs a moist mass of pollen and nectar at the base of the cell and lays the 9 mm long egg horizontally on the pollen surface. The species is polylectic, gathering pollen from several plant species. Laboratory analysis of pollen taken from nests showed Myrtaceae to be the dominant type, with smaller percentages of other forms present (J. Muller, pers. comm.).

Nest architecture was of the progressive form, with the youngest cells furthest from the entrance

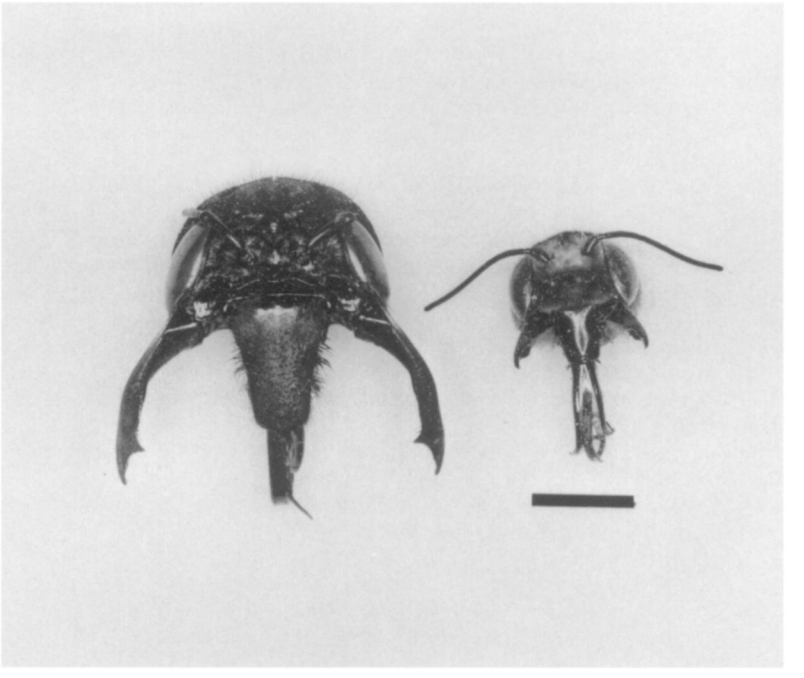

Fig. 2. The gape of the mandible and the size of the labrum are considerably greater in females (left). Males of *C. pluto* do not gather resin or participate in nest building. The long tongue (ca. 25 mm in females) is visible below the labrum. Bar = 5 mm.

(Stephen et al., 1969). The largest nest found contained 157 cells radiating horizontally from the more or less vertical central tunnel. This tunnel was 20–24 mm wide and spiralled vertically, both above and below the single entrance hole. There were 22 active cells, 3 open cells with pollen, and 132 sealed cells containing refuse. Six adult females were taken from this nest.

Four smaller nests, of similar architecture, contained 4–49 cells ($\bar{x}$ = 28, SD = 20). Two of the four contained at least two adult females; the other two contained one female each. Seven nests were located in the course of the study and five were dissected. Because 2 of those 5 were taken in daylight, it is possible that some resident females were not in the nests.

Although most other megachilids are solitary, the level of sociality attained by *C. pluto* is unclear; it is probably communal (Michener, 1974). Dissection of 4 females from the largest nest revealed that each ovary contained 3 ovarioles (as in all Megachilidae) and each bee had at least one maturing oocyte (mean oocyte length = 4.9 mm, SD = 2.1, n = 6). Thus, reproductive division of labor does not appear to be a characteristic of this species.

Other nesting associations between bees and termites are known. For example, several stingless bees (Meliponinae) nest with termites (Wille and Michener, 1973), the euglossine bee *Eufriesea laniventris* builds resin within termite nests in Trinidad (Kimsey, 1982), and a solitary anthophorine bee, *Centris derasa* is associated with a West Indian *Microcerotermes* species (Bennett, 1964; Callan, 1977). *C. derasa* suffers considerable mortality due to termite invasion of brood cells, a liability which the hardened resin of *C. pluto* resists. What advantage *C. pluto* derives from termite nest association is not yet understood, but it may be related to microclimate or protection from predators and parasites.

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