MIMICRY OF THE WEAVER ANT, OECOPHYLLA SMARAGDINA BY THE MOTH CATERPILLAR, HOMODES BRACTEIGUTTA, THE CRAB SPIDER,AMYCIAEA LINEATIPES, AND THE JUMPING SPIDER, MYRMARACHNE PLATALEOIDES

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ABSTRACT. — Amazing and amusing examples of three different mimics of the same species of ant (Oecophylla smaragdina Fabricius) are described and discussed, based on observations in Singapore. These include: (i) the caterpillar of the erebid moth, Homodes bracteigutta (Walker), (ii) the thomisid spider, Amyciaea lineatipes Pickard-Cambridge, and (iii) the salticid spider, Myrmarachne plataleoides (Pickard-Cambridge). A possible fourth candidate as a mimic of this weaver ant is a micropezid fly.

KEY WORDS. — weaver ant, mimicry, Oecophylla smaragdina, Homodes bracteigutta, Amyciaea lineatipes, Myrmarachne plataleoides

INTRODUCTION

The adoption of ant-like characters by other organisms, especially morphological and behavioural, has been referred to as myrmecomorphy (McIver & Stonedahl, 1993; Cushing, 1997; Maderspacher & Stensmyr, 2011). These ant-mimics are thus known as myrmecomorphs, and mostly comprise spiders and certain groups of insects. Worldwide, the diversity of myrmecomorphic arthropods has surpassed 2,000 described species, belonging to more than 200 genera in 54 families (McIver & Stonedahl, 1993). Another category of arthropods are known as myrmecophiles, which also demonstrate a close association with ants, but do not necessarily resemble them. More often, myrmecophiles adopt convergent chemical and/or textural cues that allow an intimate relationship with the ants. Here, we highlight three classic examples of myrmecomorphs found in Singapore: a moth caterpillar and two species of spiders from different lineages. Their continued survival has both evolved and revolved around the same species of ant: the Asian weaver ant, Oecophylla smaragdina Fabricius.

Fig. 1. Typical defensive posture of the weaver ant, Oecophylla smaragdina Fabricius (Formicidae: Formicinae) with head raised and mandibles wide open.
Fig. 2. An aerial nest of a weaver ant colony, elegantly constructed by folding and weaving the leaves of a fish-tail palm (*Caryota mitis*, Arecaceae) together. Photographed at edge of scrubland in Pasir Ris (Jul.2011).
THE MODEL — *OECOPHYLLA SMARAGDINA*

The Asian weaver ant, *Oecophylla smaragdina* Fabricius (family Formicidae, subfamily Formicinae) has a widespread Australasian distribution (Azuma et al., 2006; Chadwick, 2011). In Singapore, it is commonly encountered in gardens, parks, scrubland and along forest edges. These ants are highly visible and readily recognisable by their reddish to orange-brown bodies. The major workers on sentry duty are constantly alert for signs of intrusion to their respective colonies. Upon sensing danger, they face the potential threat with heads raised and mandibles wide open (Fig. 1). Oftentimes, their abdomens may also be arched upwards. Weaver ant colonies reside in a widely dispersed network of aerial nests, which are constructed from leaves carefully woven together. Usually, plants with medium to large leaves are employed, such as the fish tail palm, *Caryota mitis* (family Arecaeeae), which have broad and flexible leaves to provide shade and shelter (Fig. 2).

During the initial phase of nest construction, adjacent leaves at a selected site are drawn close together by the unified team efforts of major workers, with their strong mandibles clamped onto the leaf margins (Fig. 3). Thereafter, the narrow gaps are sealed off and the leaves fastened in place by silken threads, secreted upon instruction by their own ant larvae that are being manipulated by the workers (Chadwick, 2011). The weaver ant’s reputation as an aggressive species may be testified by many who have been inadvertently bitten by them in the field, experiencing sharp, localised pain in the process (Fig. 4). Prominent ant biologist, Mark W. Moffett (Smithsonian Institution) has described its bite to be “like lemon juice rubbed into abraded skin”, owing to acidic secretions which accentuate the agony (Moffett, 2010). Kalshoven (1961) reported that the weaver ants “are particularly apt at taking hold of hairs or feathers of animals (and men!) that come too near to their mandibles, tenaciously cling to them and pull them.”

Weaver ants also have the reputation of being efficient predators within their territorial domain and feed opportunistically on a wide variety of animals, mostly insects (Offenberg et al., 2004; Duangphakdee et al., 2005; Azuma et al., 2006; Chadwick, 2011). Prey, which may often be larger than the ants themselves, are always subdued by cooperative efforts (Moffett, 2010). In Singapore, an example of this group-hunting technique was witnessed in a garden at Kew Drive in Jun.2011. Among the white inflorescence of a Crown Flower, *Calotropis gigantea* (family Asclepiadaceae), a caterpillar of the plain tiger butterfly, *Danaus chrysippus* (Nymphalidae: Danainae) had become overpowered by a group of weaver ants and was being progressively carried away (Fig. 5). In Jul.2011, an entourage of weaver ants was observed as they were returning to their aerial nest with a freshly captured, green noctuid caterpillar prey (Fig. 6). The caterpillar was then transferred to the inner chamber of the nest via an elliptical entrance between the leaves. Weaver ants are also capable of overcoming and bringing down potentially dangerous prey, including scorpions (Chadwick, 2011).
Fig. 4. An aggressive weaver ant digging its sharp, serrated mandibles into the skin of T. M. Leong’s leg. Its characteristic bite has previously been described as feeling “like lemon juice rubbed into abraded skin” (Moffett, 2010).

Fig. 5. A group of weaver ants attack and subdue a caterpillar of the plain tiger butterfly, Danaus chrysippus (Nymphalidae: Danainae) on its hostplant, the crown flower, Calotropis gigantea (Asclepiadaceae). Photographed by Vilma D’Rozario at Kew Drive (Jun.2011).
The regular patrolling and scouting for prey among the foliage has also been demonstrated to reduce the incidence of folivory in these plants. In an ecological study within mangrove forest in Thailand, it was found that *Rhizophora mucronata* trees harbouring populations of *Oecophylla smaragdina* ants were less susceptible to folivory by chrysomelid beetles and sesarmid crabs, in comparison with other trees that were not frequented by weaver ants (Offenberg et al., 2004).

**MIMIC 1 — HOMODES BRACTEIGUTTA**

Caterpillars in the moth genus, *Homodes* Guenée have been documented to be closely associated with weaver ants, as well as resembling them in terms of morphology and behaviour (Shelford, 1902, 1916; Kalshoven, 1961; Common, 1990; Holloway, 2005). Previously in Noctuidae: Catocalinae (Holloway, 2005), *Homodes* is presently under Erebidae: Boletobiinae (Holloway, 2011). In Singapore, at least two species have been previously recorded, namely *Homodes iomolybda* Meyrick and *Homodes vivida* Guenée (Holloway, 2005). Here, a third species, *Homodes bracteigutta* (Walker) is documented for Singapore, based on the successful rearing of a final instar caterpillar.

This caterpillar was found to be feeding on the leaves of *Clerodendrum inerme* (family Verbenaceae) at Kew Drive on the night of 25 Mar. 2011 (Fig. 7). The caterpillar had a body length of 18 mm, and was light olive green with faint white mottling between A1 to A7. Its front and rear ends were a darker orange brown. The abdominal prolegs of A3 are absent, while those of A4 are slightly reduced. Rounded, mid-dorsal humps are present at A5 (dark brown) and A8 (honey coloured, encircled with dark brown). At its anterior, an intricate arrangement of slender, elongated setae arises from dorsal and dorsolateral verrucae of the thoracic segments (Fig. 8). The most prominent pair rises over the caterpillar’s head and terminates in a purplish brown, bulbous tip. The other setae are orange brown and blade-like, radiating from the thoracic region and extending beyond the head.

When alarmed, the caterpillar does not hesitate to vibrate its setae in almost rhythmical fashion, with abrupt and alternate raising/lowering of the structures. This is accompanied by the elevation of its posterior-most segments, as well as the parting of its anal prolegs (Figs. 7, 9). A pair of strategically placed black dots on the anal segment resembles the eyes of a weaver ant, while the parted prolegs simulate its wide open jaws (compare with Fig. 1). Immediately above the pair of false eyes are shorter setae that resemble the antennae of the ant. Other lateral setae along the posterior segments are equally mobile and provide the illusion of jerky ant limbs.
Fig. 7. The final instar caterpillar of *Homodes bracteigutta* (head towards right, body length: 18 mm) on its hostplant, *Clerodendrum inerme* (Verbenaceae), found at Kew Drive in Mar. 2011. It was in the process of biting out a semi-circular slice of the leaf to close over itself for the pupation process (see Fig. 10a).

Fig. 8. Frontal view of the caterpillar’s head. Note prominent pair of bulbous tipped setae positioned over the head, as well as arrangement of elongated setae arising from its thoracic segments.
On the night of 27 Mar. 2011, the caterpillar began to cut out a curved flap from the leaf margin inwards. It subsequently connected both margins of the leaf with silk, thus curling the leaf upwards. By the morning of 28 Mar. 2011, it had already sealed itself within the tightly curled leaf, using the cut-out leaf flap to close itself in (Fig. 10a). On the morning of 6 Apr. 2011, an adult moth emerged and was confirmed to be a female *Homodes bracteigutta* (Fig. 10b), resembling a published illustration of the species (Holloway, 2005: pl. 19 – moth 22). The moth was then preserved as a voucher specimen and deposited at the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research (RMBR), National University of Singapore (ZRC.LEP.350, body length: 9 mm, forewing: 9 mm). Its corresponding pupal case (8 × 3 mm) was carefully extracted from within the leaf curl and preserved as well (Fig. 10c).

The larvae of *Homodes bracteigutta* may be regarded as polyphagous, as they have been documented to feed on a wide variety of hostplants, including: *Mangifera* (Anacardiaceae), *Hevea* (Euphorbicaceae), *Cinnamomum* (Lauraceae), *Amyema* (Loranthaceae), *Pithecellobium* (Fabaceae), *Melaleuca* (Myrtaceae), *Coffea* (Rubiaceae), *Cupaniopsis*, *Dimocarpus*, *Nephelium* (Sapindaceae) (Common, 1990; Holloway, 2005; Robinson et al., 2011). The present record of *Clerodendrum* (Verbenaceae) adds an additional plant genus (and family) to this list.

**MIMIC 2 — AMYCIAEA LINEATIPES**

The crab spider, *Amyciaea lineatipes* Pickard-Cambridge (family Thomisidae) was first described from Singapore, based on a specimen collected by H. N. Ridley (first Director of Singapore Botanic Gardens: 1888–1912) and subsequently sent to R. Shelford, who forwarded it to O. Pickard-Cambridge. The original description was accompanied by excellent colour lithographs of the species (Pickard-Cambridge, 1901: pl. V, Figs. 4–4d), as well as its model – *Oecophylla smaragdina* (Pickard-Cambridge, 1901: pl. V, Fig. 5). Recent encounters with this spider in Singapore were in the vicinity of the weaver ant colony at Pasir Ris (Fig. 2). In Jul. 2011, a number of individual crab spiders were observed on vegetation that was patrolled by weaver ant scouts. On 6 Jul. 2011, a crab spider (6 mm) was sighted at knee-level, dangling by a single silk strand and grasping onto a weaver ant by the back of its neck (Fig. 11). The spider was waiting for its venom to take full effect and immobilise the ant, after which it carried the ant to the nearest leaf to begin consumption. While consuming the ant, the spider would constantly wave its first two pairs of limbs along a flat plane perpendicular to its body axis (Fig. 12).
Fig. 10. By 28 Mar. 2011, the caterpillar had securely enclosed itself within a curled leaf (a), lined internally with silk. The adult moth (b) eclosed on the morning of 6 Apr. 2011 and was determined to be a female specimen (ZRC.LEP.350, body length: 9 mm, forewing: 9 mm). Its pupal case (c) was also preserved (8 × 3 mm).
Fig. 11. A crab spider, *Amyciaea lineatipes* (6 mm) is suspended by its own silk, while maintaining a firm hold onto the neck of a subdued weaver ant. Encountered just below the aerial nest at Pasir Ris (as in Fig. 2) in Jul. 2011.

Fig. 12. When the weaver ant prey (as in Fig. 11) had succumbed to the crab spider’s venom, it was then transferred to a nearby leaf for subsequent consumption. Its first two pairs of limbs would be regularly waved in an entrancing ‘dance’. From the posterior, the prominent pair of black dots on its abdomen bears resemblance to the eyes of a weaver ant.
On 8 Jul.2011, a sub-adult crab spider (4 mm) was found to have subdued a weaver ant (Fig. 13) with the same strategy as previously observed – gripping the ant’s neck and suspended by silk. By approaching from the back of the ant’s neck, the crab spider stays clear of the menacing mandibles of the ant, even though the ant was double the size of the immature spider. By suspending the ant in mid-air, the ant is deprived of any foothold to grip onto and retaliate. On 9 Jul.2011, an adult female (7 mm) was observed with an immobilised weaver ant prey at eye-level on a cinnamon bush, *Cinnamomum iners* (family Lauracea). It was in the process of consuming its ant prey (Fig. 14), but was visibly bothered by a small group of freeloader flies (Diptera: Milichiidae) that were attempting to siphon off leaked body fluids from the ant. With regular swipes from its front two pairs of limbs, the spider would strive to keep these flies at bay. A brief video clip of this female crab spider with subdued weaver ant prey, and displaying characteristic waving motions of its first two pairs of limbs was recorded and subsequently uploaded (http://www.youtube.com/watch?v=3IrT0auASi4).

An example of a male *Amyciaea lineatipes* was also sighted on 9 Jul.2011. It was perched on a leaf of a fish tail palm and waving its front four limbs in characteristic fashion (Fig. 15). On closer inspection, its enlarged male palps could be discerned. Its abdomen, however, was noticeably shrunken—indicative that it was most probably in search of a next ant meal.

One of the earliest published accounts of the mimicry of weaver ants by the *Homodes* caterpillar and crab spider, *Amyciaea lineatipes* was by R. Shelford, in his comprehensive comparison of mimetic insects from Borneo and Singapore (Shelford, 1902). Subsequently, line illustrations of these two mimics and the ant model were published (Shelford, 1916: pl. XVI – facing p. 230), in which the prominent false eyes on the spider’s abdomen and caterpillar’s anal segment were accurately depicted (Fig. 16). The illustration of the caterpillar was reproduced in Kalshoven (1961: 44 – Fig. 1). Recent publications on *Amyciaea lineatipes* featured specimens from Singapore (Koh, 1989: 150), and Johor, Peninsular Malaysia (Murphy & Murphy, 2000: 427 – Family 63, Fig. 1; pl. 26.3 & 26.4). The genus *Amyciaea* Simon is currently represented by five species, occurring in Africa (one species) and Australasia (Platnick, 2011).

Fig. 13. Lateral view of a sub-adult *Amyciaea lineatipes* (4 mm) with a secure neck-hold of its weaver ant prey. Encountered at Pasir Ris in Jul.2011.
Fig. 14. An adult female *Amyciaea lineatipes* (7 mm) commences feeding on the fluids of a weaver ant. Its prey had been captured on a cinnamon bush (*Cinnamomum iners*, Lauraceae) that was adjacent to the fish tail palm (as in Fig. 2) at Pasir Ris. The crab spider would frequently use its front two pairs of limbs to brush away freeloader flies (Milichiidae) that were scavenging on leaked fluids from the ant prey.

Fig. 15. Anterior (a) and posterior (b) views of a male *Amyciaea lineatipes* (5 mm) on the prowl for weaver ant prey. Its shrunken abdomen is a possible indication that it has not had a meal in a while.
Fig. 16. Early illustrations of the crab spider, *Amyciaea lineatipes* (a), the weaver ant, *Oecophylla smaragdina* with silk-secreting larva in mandibles (b), and the caterpillar of *Homodes* species with raised posterior segments (c). After Shelford (1916: Pl. XVI).

**MIMIC 3 — MYRMARACHNE PLATALEOIDES**

The jumping spider, *Myrmarachne plataleoides* (Pickard-Cambridge) (family Salticidae) has been previously recorded for Singapore, and is also known to occur in Sri Lanka, India, and Thailand (Koh, 1989: 132; Murphy & Murphy, 2000: 305 – Family 51, Fig. 29). Accompanying its original description were detailed line drawings of a male specimen (Pickard-Cambridge, 1869: Pl. VI, Figs. 61–65a). Locally, we encountered this species in close proximity to the weaver ant colony at Pasir Ris (Fig. 2). Adults and sub-adults of both male and female spiders were seen walking around leaves that were easily accessible by the weaver ants and most likely to be within the territory of the colony. The spiders predominantly moved about individually and cautiously, regularly raising their first pair of limbs to resemble the antennae of the ant (Fig. 17). Furthermore, their cephalothorax and abdomen are elongated, with distinct constrictions, to create the ant-like illusion of having a narrow waist (petiole). The reddish brown colour of these spiders is almost an identical tone to that of the weaver ants.

At the weaver ant colony monitored in Pasir Ris, an adult male *Myrmarachne plataleoides* (11 mm) was sighted on 9 Jul. 2011. It was perched on a translucent sheet of silk which had been constructed over the leaf of a vine (Fig. 18). Beneath this silk sheet was a conspecific female (6 mm), which was probably a mate that was being guarded by the male. Mere millimetres away, along the main stem of the vine, was an actively used trail with constant weaver ant traffic. On closer inspection, the greatly enlarged chelicerae of the male spider were noticeable, as they protruded beyond its head. The apices were bulbous and bore a pair of black dots at the tip (Fig. 19). These black dots potentially mimic the eyes of the weaver ant and when viewed in its entirety, the male spider may be perceived as a dead/injured weaver ant being carried by another (Maderspacher & Stensmyr, 2011: R293 – structures incorrectly referred to as 'pedipalps', rather than chelicerae; Nelson & Jackson, 2006).
Fig. 17. A female jumping spider, *Myrmarachne plataeoides* (6 mm) with first pair of limbs elevated to resemble the antennae of a weaver ant. Note also the elongated and constricted abdomen.

Fig. 18. A male *Myrmarachne plataeoides* (11 mm) watching over its female mate (6 mm) beneath a silk sheet, in close proximity to a busy weaver ant trail along the stem of a vine.
The marked sexual dimorphism witnessed in *Myrmarachne plataleoides* prompted an earlier investigation into the comparative feeding strategies between male and female spiders (Pollard, 1994). It was found that males lack a fang duct and do not envenom their prey. Instead, they use their spear-like fangs to skewer prey, and then extract its contents through puncture holes created on the prey’s cuticle. Females typically pierce the prey with their fangs and introduce venom through fang ducts (Pollard, 1994). In another study focused on *Myrmarachne plataleoides*, investigations were conducted on the reproductive isolation mechanisms between sympatric colour forms, based on male preferences for female retreat silk (Borges et al., 2007). Evidence for polymorphism in this species was found, with males demonstrating greatest preference for silk of their own colour morph.

In Peninsular Malaysia, attempts to study the relative degrees of *Myrmachne*-ant species associations confirmed that *Myrmarachne plataleoides* was invariably co-existing with *Oecophylla smaragdina* exclusively (Edmunds, 2006). In the Philippines, another species, *Myrmarachne assimilis* Banks is most closely associated with *Oecophylla smaragdina* (Nelson et al., 2005). The diversity of the genus *Myrmarachne* MacLeay, with an almost worldwide distribution, has already surpassed 210 species (Platnick, 2011), testimony to the benefits and success of its ant-mimicking body plan and lifestyle.
While exploring the back mangroves of Pasir Ris, attention was drawn towards an insect that also resembled a weaver ant, in terms of size, body shape, colour, and even behaviour. Upon closer inspection, it was determined to be a micropezid fly (Diptera: family Micropezidae). It was walking around with slender limbs in ant-like fashion on the leaves of a mangrove fern, *Acrostichum aureum* (family Pteridaceae), pausing occasionally to rest or preen itself (Fig. 20, ZRC.6.22176, body length: 9 mm, forewing: 5 mm). On the very same fern, weaver ants were observed to be patrolling the young fronds at its base (Fig. 21), and venturing up to the mature fronds above. Hence, there is a high likelihood that this micropezid fly is a mimic of the weaver ant, with further studies required to determine the underlying relationships. Amongst the Diptera, at least nine genera (in seven families) are known to be myrmecomorphs, including two micropezids, *Badisis* and *Metopochetus* (McIver & Stonedahl, 1993).

In Australia, a myrmecophilic species of jumping spider is also known to have an intimate association with weaver ants. However, this salticid, *Cosmophasis bitaeniata* (Keyserling) neither resembles the weaver ant in terms of morphology nor behaviour, but instead hides under a cloak of cuticular hydrocarbons that mimics the mono- and dimethylalkanes of the ants in order to infiltrate a colony and prey on their larvae, after removing them from the mandibles of minor workers (Allan & Elgar, 2001; Allan et al., 2002; Chadwick, 2011). Thus, chemical mimicry has become an effective strategy employed by this myrmecophile. In Singapore, it remains to be seen if any jumping spiders may be using similar techniques to exploit local colonies of weaver ants.
DISCUSSION

The fascinating topic of mimicry within the animal kingdom has intrigued many scientists for a long time, and continues to arouse interest as well as debate, with the adaptive significance of various forms of mimicry being proposed (Shelford, 1902; McIver & Stonedahl, 1993; Ruxton et al., 2004; Maderspacher & Stensmyr, 2011).

Among the three different mimics of weaver ants presented here, two candidates (moth caterpillar, Homodes bracteigutta, and jumping spider, Myrmarachne plataleoides) belong to the category of Batesian mimicry, whereby a palatable mimic derives a certain degree of immunity from potential predators that recognise and avoid feeding on a noxious/unpalatable model (McIver & Stonedahl, 1993; Ruxton et al., 2004).

The evolution of Batesian mimicry is driven and sustained by a combination of behavioural and ecological scenarios, including: (i) the model must be an unacceptable prey item; (ii) the mimic must be a potentially acceptable prey item; (iii) the model must be common, relative to the mimic; (iv) the model and mimic must share similar temporal and spatial distributions; (v) the mimic must have signal properties that deceive visually oriented predators within a community of alternative prey; and (vi) predator avoidance of the model/mimic must either be innate or learnt (McIver & Stonedahl, 1993).

For Batesian mimics, the relative accuracy of the mimic in copying the putative model also affects the graded ability to deceive ant-averse predators (Nelson, 2011). Experimental studies have demonstrated that praying mantids, key predators in the ecosystem, possess an innate aversion to ants, and even avoid accurate myrmecomorphic spider mimics in the laboratory (Nelson et al., 2006).
In the case of the crab spider, *Amyciaea lineatipes*, its masquerade as a weaver ant may be regarded as a form of aggressive, or Peckhamian mimicry, whereby the predator mimics its targeted prey to facilitate approach and close contact (McIver & Stonedahl, 1993; Cushing, 1997). This, and a number of other species of myrmecomorphic/myrmecophilic spiders that are obligate ant-eaters, have thus capitalized on the fact that ants are an abundant, widespread, and conspicuous source of protein for potential predators (McIver & Stonedahl, 1993). In Singapore, myrmecomorphic and myrmecophagic representatives from other spider families, such as Corinnidae and Zodariidae, are known to occur (Murphy & Murphy, 2000; T. M. Leong, pers. obs.) and further research would help to shed light on their actual identities, behavioural patterns, hunting strategies, as well as specific ant prey preferences.

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LITERATURE CITED


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