

Biological notes on herbivorous insects feeding on myrmecophytic *Macaranga* trees in the Lambir Hills National Park, Borneo

Usun SHIMIZU-KAYA, Keiko KISHIMOTO-YAMADA, Takao ITIOKA

ABSTRACT Myrmecophytes are plants that harbor ant colonies in domatia, which are hollows in the plant body. Most ant species that colonize myrmecophytes aggressively attack and regulate the abundances of herbivorous insects that would otherwise feed on the leaves of host trees. Although previous studies have described the interactions between myrmecophytes and herbivorous insects, a large proportion of herbivores that are able to feed on these trees are still unrecorded and details of their feeding habits are largely unexplored. Here, we compile biological notes on some of the herbivorous insects that feed on several species of *Macaranga* (Euphorbiaceae) growing in the Malayan archipelago, including those that are myrmecophytic. The information assembled here is based on our field observations, sampling, and rearing of insects, which we have conducted since 1994 in the tropical lowland forest of the Lambir Hills National Park, Sarawak, in Malaysian Borneo. We also summarize existing published information. For the convenience of future studies of herbivores that feed on *Macaranga*, we have included a large selection of images to show the morphologies and ecological traits of herbivores, including their structures at different growth stages and the marks made by their activities, such as leaf-chewing, leaf-mining, and gall formation. Among the herbivorous insects that feed on *Macaranga* species, we focus on butterflies, phasmids, gall midges, and myrmecophilous bugs.

KEY WORDS ant-plant interactions / *Arhopala* lycaenids / gall midges / insect fauna / myrmecophilous bugs / *Orthomeria* phasmids / tropical rainforests

Introduction

Myrmecophytes are plants that host ant colonies within hollows known as domatia. Most myrmecophytic species are distributed in Neotropical and Paleotropical rainforests (Davidson & McKey 1993). Many ant species that colonize myrmecophytes have adaptive traits for symbioses with their hosts. Most of the ant species in these symbiotic relationships attack herbivorous insects that feed on host plants and/or patrol plant shoot surfaces to exclude herbivores. Through these

activities, the ants regulate the abundances of the herbivores (Izzo & Vasconcelos 2005) and hence the level of herbivory pressure (Itioka et al. 2000; Rico-Gray & Oliveira 2007). Thus, mutualistic relationships have been formed between myrmecophytes and their symbiont ants (Davidson & McKey 1993; Rico-Gray & Oliveira 2007).

Herbivores that feed on myrmecophytes must first overcome the anti-herbivore defenses of symbiont ants, and indeed adaptive specializations to ant defenses are to be found among species that eat the plant hosts. Information on the taxonomic identities of herbivores that feed on myrmecophytes and the mechanisms they use to overcome ant defenses contributes significantly to interpreting three-way coevolutionary relationships between plants, their herbivores, and their ant defenders. Although there have been many studies on the interactions between myrmecophytes and herbivorous insects (Janzen 1972; Rehr et al. 1973; Fiala et al. 1989; Seufert & Fiedler 1996a, b; Gaume et al. 1997; Letourneau & Barbosa 1999; Itioka et al. 2000; Fincher et al. 2008; Moraes & Vasconcelos 2009; Pringle et al. 2012), an enlargement of the database of available information on herbivores that feed on myrmecophytes will certainly improve our understanding of the evolutionary biology of the species interactions.

The tree genus *Macaranga* Thouars (Euphorbiaceae) is widely distributed from Africa to the Pacific Islands (Whitmore 1969, 2008); 26 of the congeners are myrmecophytic species found in the Malayan archipelago (Davies 2001; Davies et al. 2001). These species are defended against herbivores through the guarding behavior of symbiotic ants (ant defense) and by their own innate physical and chemical anti-herbivore defenses, which occur in most other plant species (non-ant defense). The effectiveness of ant defenses (Itioka et al. 2000) and non-ant defenses (Nomura et al. 2000, 2011; Eck et al. 2001) varies widely among *Macaranga* species, and this variability is expected to affect host plant use and the feeding behaviors of herbivores that feed on *Macaranga*. Although insects feeding on *Macaranga* have been studied (Maschwitz et al. 1984; Itino & Itioka 2001; Okubo et al. 2009; Shimizu-kaya et al. 2013a, b, 2014; Shimizu-kaya & Itioka 2015), a large proportion of the herbivores have not been identified and details of their feeding habits are largely unexplored.

Here, we compile biological notes on some of the herbivorous insects that

feed on *Macaranga* species. These notes are based on our field observations, sampling, and rearing programs conducted since 1994 in the tropical lowland forests of the Lambir Hills National Park, Sarawak, Malaysian Borneo. We provide a summary of the known ecological characteristics of *Macaranga* plants and a compilation of previously published information. For the convenience of future studies on *Macaranga*-feeding herbivores, we have included as many images as possible to illustrate the morphological and ecological traits of the herbivores. The images show morphologies at different growth stages, and the effects of herbivore feeding activities, such as leaf-chewing, leaf-mining, and gall formation on the host plants. Among the herbivores that feed on *Macaranga*, we focus especially on butterflies, phasmids, gall midges and myrmecophilous bugs.

Study site

This study was conducted from 1994 to 2014 in the Lambir Hills National Park, Sarawak, Malaysia (4°20'N, 113°50'E). Most of the park is vegetated with primary lowland mixed dipterocarp forest. The study site was described in detail in Roubik et al. (2005), and the basic features of the climate were described by Kumagai et al. (2009). At least 17 *Macaranga* species occur in the forest (Davies 2001; Lee et al. 2002; Fig. 1). We have conducted routine censuses on ca. 100–200 trees belonging to the 17 *Macaranga* species at least three times a year since 1997 (we performed similar censuses once a year from 1994 to 1996).

Summary of ecological characteristics of *Macaranga* species

Approximately 260 species of *Macaranga* have been described; many are conspicuous large-leaved pioneers of disturbed habitats (Whitmore 2008). Of the 17 species found at our study site, *M. trachyphylla* Airy Shaw, *M. bancana* (Miq.) Müll. Arg. and *M. hullettii* King ex Hook.f., *M. beccariana* Merr. and *M. hypoleuca* (Rchb.f. & Zoll.) Müll. Arg., *M. lamellata* Whitmore and *M. umbrosa* S. J. Davies, and *M. hosei* King ex Hook.f. and *M. rufescens* S. J. Davies have close pairwise taxonomic relationships (Davies 2001; Fig. 1).

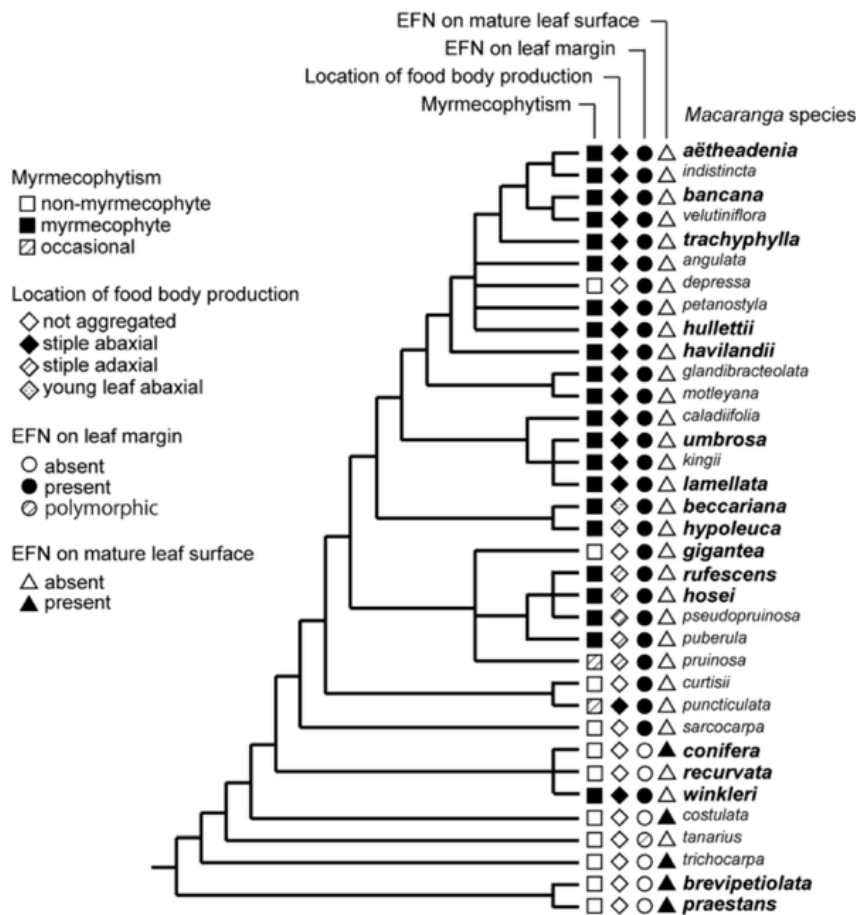


Figure 1. Phylogenetic relationships of 35 *Macaranga* species in Borneo displayed in one of six most parsimonious trees emerging from a combined analysis of morphological and molecular characters (after Davies 2001 and Davies et al. 2001). Myrmecophytism and three morphological characters (location of aggregated food body production, presence or absence of extrafloral nectaries [EFN] on leaf margins and mature leaf surfaces) are indicated by squares, diamonds, circles, and triangles, respectively. Species found in Lambir Hills National Park are indicated in boldface.

Habitat

The spatial distribution patterns of individual trees vary among *Macaranga* species with respect to light, soil, and water conditions (Davies et al. 1998; Itioka 2005), but at our study site distributions of the congeners were not obviously distinctive, and partially or largely overlapped in some cases. *Macaranga winkleri* Pax & K. Hoffm., *M. trachyphylla*, *M. bancana*, *M. hullettii*, *M. beccariana*, *M.*

hypoleuca, *M. havilandii* Airy Shaw, *M. hosei*, *M. rufescens* and *M. conifera* (Rchb.f. & Zoll.) Müll. Arg. occurred primarily in gaps, along the edges of primary forest, and along riversides. Some of the species were often found together in a single microhabitat. *Macaranga gigantea* (Rchb.f. & Zoll.) Müll. Arg. commonly grows in secondary forests; it has a stronger preference for disturbed microhabitats, compared with the other *Macaranga* species at the study site. *Macaranga gigantea* also grows along forest edges and riversides within the primary forest (Davies et al. 1998; Davies 2001; Itioka 2005). In contrast, *M. lamellata*, *M. umbrosa*, *M. praestans* Airy Shaw, *M. brevipetiolata* Airy Shaw and *M. aëtheadenia* Airy Shaw are more shade-tolerant and occur in dimly lit area of the forest floor (Maschwitz et al. 1996; Davies et al. 1998; Davies 2001; Itioka 2005; *authors' unpublished data*).

Symbiotic ants (plant-ants)

Most of the ants associated with myrmecophytic species are members of the genus *Crematogaster* (Baker 1934; Fiala et al. 1999), or in some cases with the genus *Camponotus* (Maschwitz et al. 1996, 2004; Federle et al. 1998; Itino et al. 2001a). The partnerships between myrmecophytic *Macaranga* trees and their symbiont ants are highly species-specific (Fiala et al. 1999; Itino et al. 2001a; Quek et al. 2004, 2007).

Myrmecophytes provide nutrient-rich food bodies (Rickson 1980; Hatada et al. 2002) and hollow stems that are used as domatia by the symbiont ants (plant-ants) (Ridley 1910; Fiala & Maschwitz 1992b). Plant-ants often harvest honeydew from scale insects (Coccidae) that reside inside the domatia (Ridley 1910; Heckroth et al. 1998; Ueda et al. 2008). Although all *Macaranga* myrmecophytes form stem domatia and food bodies, the development of these features, and thus the associations with plant-ants, vary among the different *Macaranga* species (Ridley 1910; Rickson 1980; Fiala et al. 1989, 1994; Fiala & Maschwitz 1990, 1992a,b).

Of the 17 *Macaranga* species at our study site, 12 (*M. winkleri*, *M. trachyphylla*, *M. bancana*, *M. hullettii*, *M. beccariana*, *M. hypoleuca*, *M. havilandii*, *M. lamellata*, *M. umbrosa*, *M. hosei*, *M. rufescens* and *M. aëtheadenia*) are myrmecophytic, and most of their symbiont ant species have mutualistic interactions

with one or a few closely related *Macaranga* species (Fiala et al. 1999; Itino et al. 2001a; Feldhaar et al. 2003; S. Ueda *personal communication*; Fig. 1).

Among 10 of the myrmecophytic species at the study site (excluding *M. hosei* or *M. rufescens*), their symbiosis with plant-ants begins when the seedlings are ca. 10–30 cm tall (Fiala & Maschwitz 1992b; Maschwitz et al. 1996; Davies 2001; *authors' unpublished data*). As seedlings of these 10 species grow, the stems begin to swell and the piths degrade, forming hollows in which the ant queens can settle. Ant symbioses with *M. hosei* and *M. rufescens* begin when seedlings are > 70 cm tall (Davies 2001; Eck et al. 2001; Itioka 2005). Ant queens settled within the stem hollows begin to feed their initial workers with regurgitated food. The initial ant workers emerge from the hollow stems and start to defend the host plant (Fiala & Maschwitz 1990) ca. 1 month after the queen has settled, and at about this time, the plants begin to produce food bodies inside domatia-shaped stipules or on the leaf surfaces; the food bodies are collected by the ant workers (Fiala & Maschwitz 1990, 1992a).

Anti-herbivore defenses by plant-ants (ant defense)

Plant-ants on *Macaranga* myrmecophytes attack intruders, including insect herbivores, thereby preventing grazing on their hosts (Baker 1934; Tho 1978; Fiala et al. 1989). The plant-ant workers are so aggressive that most intruders leave immediately following the first encounter (Fiala & Maschwitz 1990). Plant-ant workers capture small insects, such as small caterpillars, with their mandibles and drop them onto the ground below. When an intruder remains on the plant, ant workers aggregate and attack from all sides, using defensive secretions and biting with their mandibles. Ant aggregations are also induced by leaf damage to host plants (Inui & Itioka 2007). Workers preferentially defend younger leaves and shoot parts (Fiala & Maschwitz 1990; Itioka et al. 2000; Heil et al. 2004).

The non-myrmecophytic species *M. gigantea*, *M. conifera*, *M. recurvata* Gage, *M. praestans*, and *M. brevipetiolata* were also present at our study site. These plants do not have domatia within the stems (the stems are not hollow) and do not harbor any specific plant-ant species, but extra-floral nectaries (EFNs) on young leaf

surfaces and margins attract a range of non-specific ant species (Fiala & Maschwitz 1991; Fig. 1).

Although ants attracted by EFNs on non-myrmecophytic *Macaranga* plants do patrol the leaf surfaces, their densities are lower and their offensive behaviors against herbivores are weaker than those of ants that are symbiotic with myrmecophytic *Macaranga* species (Fiala & Maschwitz 1991; Heil et al. 2001).

Innate physical and chemical mechanisms used by plants in anti-herbivore defenses (non-ant defense)

In addition to protection provided by their ants, *Macaranga* plants have non-ant defenses, such as tough leaves and deterrent chemicals. Janzen (1966) suggested that strategic allocation of limited resources likely reduces myrmecophyte investment in non-ant defense mechanisms. Indeed, there is a trade-off between the two defense mechanisms in *Macaranga*. The intensity of ant defense estimated by the level of herbivory in ant-exclusion experiments, the aggressiveness of plant-ants, and the ratio of ant biomass to plant biomass vary among *Macaranga* species (Itioka et al. 2000; Itino et al. 2001b). Similarly, the intensity of non-ant defense estimated by the fecundity response and the survival rate of polyphagous cutworm larvae reared on *Macaranga* leaves, leaf toughness, and total phenol content vary among *Macaranga* species (Nomura et al. 2000, 2011). The *Macaranga* species with the strongest ant defenses have the weakest non-ant defenses (Nomura et al. 2000, 2011; Eck et al. 2001).

Among the *Macaranga* species at our study site, *M. winkleri* has the strongest ant defense and weakest non-ant defenses (Itioka et al. 2000; Nomura et al. 2011). Non-ant defenses are strongest in non-myrmecophytic *M. praestans* (Nomura et al. 2000, 2011). Allocations to the two defense mechanisms shift gradually between the two species (Itioka et al. 2000; Nomura et al. 2000, 2011).

Inactivation of plant-ants on myrmecophytes

Although almost all *Macaranga* myrmecophyte trees at the study site maintained symbioses with particular plant-ant colonies from colony foundation by a

solitary queen through tree maturation, plant-ant activities and abundances were sometimes drastically reduced by a range of disturbances experienced by the host trees, such as flooding, toppling, severe drought, and grazing by mammals. We sometimes observed considerable physical damage inflicted by such disturbances and associated reductions in the production of food bodies, which affected the activity and fecundity of plant-ants. It is reasonable to surmise that reduced food body production will cause decreases in plant-ant activities and abundances.

In addition to disturbance damage to host plants, direct predation on plant-ant colonies sometimes decreases their activities and abundances. Previous observations have indicated that a few species of vertebrates, such as woodpeckers and reptiles, prey on plant-ants (Maschwitz et al. 1994; Itioka 2005). We observed the maroon woodpecker *Blythipicus rubiginosus* opening up stem sections of *M. winkleri*, *M. trachyphylla* and *M. bancana* to feed on the ant colonies inside the hollow stems; we also observed a reptile (*Draco* sp., Fig. 2a) preying on plant-ant workers moving on the stem surfaces of a *M. trachyphylla* sapling. We often found species of spiders preying on plant-ant workers living on several myrmecophytic species (Fig. 2b–d).

Table 1. Host plant used by five species of *Arhopala* (Lycaenidae) in the Lambir Hills National Park, Sarawak, Malaysia in Borneo.

<i>Arhopala</i> species	<i>Macaranga</i> species (Host plant)
<i>A. zyl da</i>	<i>M. beccariana</i> , <i>M. hypoleuca</i>
<i>A. dajagaka</i>	<i>M. rufescens</i>
<i>A. amphimuta</i>	<i>M. bancana</i> , <i>M. trachyphylla</i> <i>M. havilandii</i> , <i>M. hullettii</i>
<i>A. major</i>	<i>M. gigantea</i>
<i>A. kinabala</i>	<i>M. winkleri</i> *, <i>M. bancana</i> *

*Only ant-inactive saplings were used as host plants (i.e., those with considerably reduced plant-ant defenses).

Here, we define “ant-inactive (plant or myrmecophyte) individuals” as myrmecophytes with considerably reduced plant-ant defenses (as a result of physical disturbance and/or predation on the ants). Although the proportion of ant-inactive individuals of each myrmecophytic species appeared not to exceed 10% (*authors’*

unpublished data), we always found ant-inactive trees while patrolling our census routes over a 20-year period. Leaf area losses to insect leaf chewers were markedly larger among ant-inactive individuals than among trees with active ant colonies (Fig. 3).

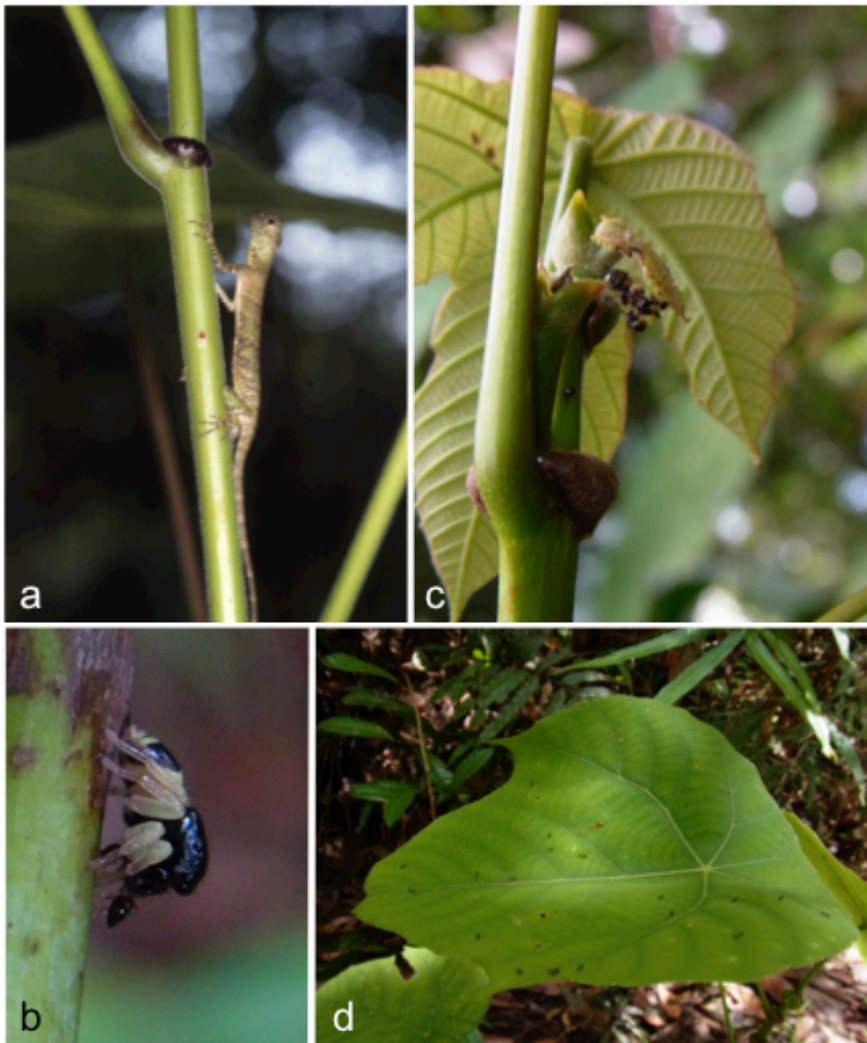


Figure 2. Predation on plant-ants located on *Macaranga* myrmecophytes at the study site: (a) the flying lizard, *Draco* sp. (? *Draco quinquefasciatus* Hardwicke & Gray), foraging on plant-ants near an exit hole from an ant colony inside the stem of a *M. trachyphylla* sapling (1997, August), (b) a jumping spider (Salticidae sp.) preying on plant-ants located on *M. hosei* (2014, April), (c) a snaring spider trapping plant-ants in its web near the apex of a *M. bancana* sapling (2014, April), (d) a snaring spider making a web on a leaf of *M. bancana*; patrolling plant-ants are visible (2014, April).



Figure 3. Major leaf losses due to the chewing of polyphagous herbivores on “ant-inactive” *Macaranga* myrmecophytes at the study site: (a) heavy chewing damage on *M. trachyphylla* caused by a moth larva (presumed to be polyphagous, based on our previous observations) (2009, July), (b) damage to *M. winkleri* (2008, August), (c) damage to *M. bancana* caused by diverse herbivorous species (2006, September), (d) damage to *M. umbrosa* caused by larvae of an unknown moth species (2013, March), (e) damage to *M. lamellata* caused by unknown herbivores (2013, March).

Herbivores

(1) Butterflies

Six lycaenid species and at least one nymphalid species fed on several *Macaranga* species at our study site (Table 1). Of the six lycaenid species, five belonged to the genus *Arhopala* (Lycaenidae, Lepidoptera).

Among the *Arhopala* species, three feed on *Macaranga* myrmecophytes: *A. amphimuta* (C. & R. Felder, 1980), *A. dajagaka* Bethune-Baker and *A. zylda* Corbet (Okubo et al. 2009; Shimizu-kaya et al. 2013a; Figs. 4–6). As Megens et al. (2005)

indicated, the host ranges of these *Arhopala* species are narrow (which is also the case for plant-ants), especially in *A. dajagaka* and *A. zylde* (Shimizu-kaya et al. 2013a).

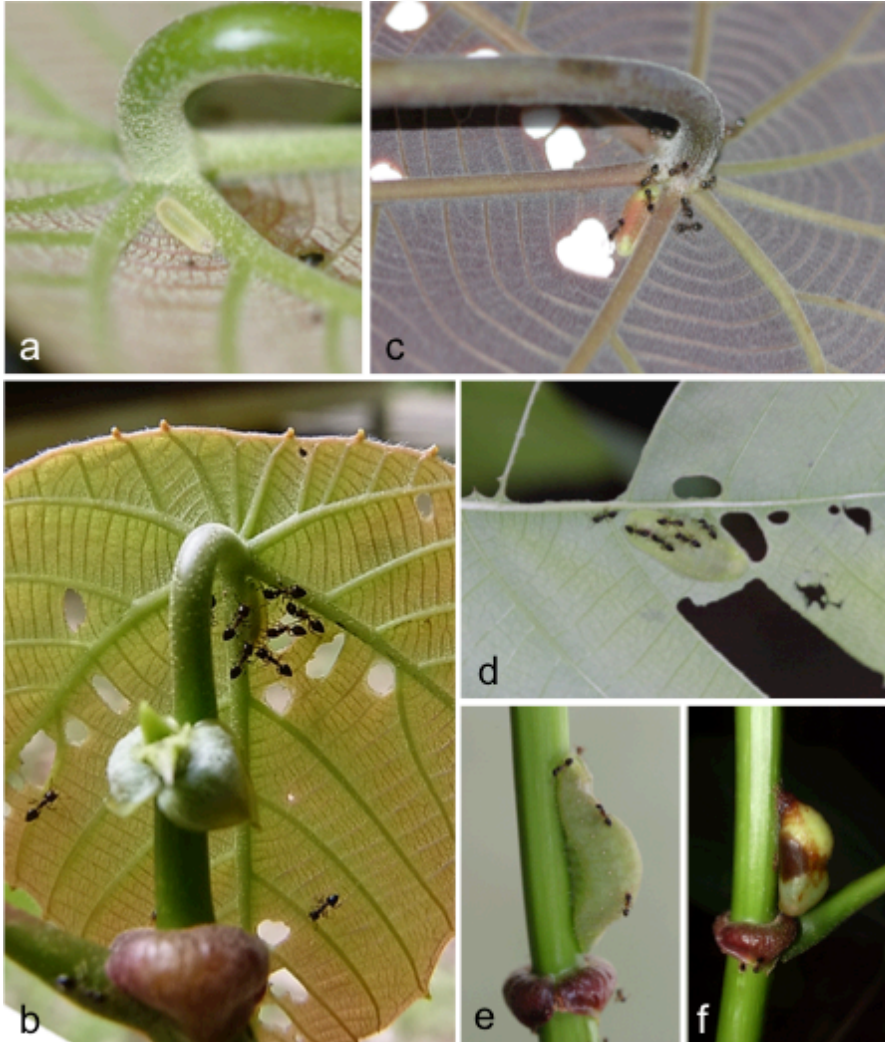


Figure 4. Immature stages of *Arhopala amphimuta* (Lycaenidae) at the study site: (a) a young-instar larva on the abaxial side of a young leaf of a host plant (*Macaranga trachyphylla*) (2011, June), (b) a young-instar larva (elder than the specimen in [a]) attended by plant-ants (*Crematogaster borneensis*) on the youngest leaf of a *M. trachyphylla* plant (2012, May), (c) a middle-instar larva on *M. trachyphylla* attended by plant-ants (2009, August), (d) a pre-final instar larva on *M. bancana* attended by plant-ants (2006, September), (e) a final instar larva resting on a stem near the apical leaf of a sapling (*M. bancana*) (2006, September), (f) a pupa on the stem of a *M. bancana* sapling (2007, May).
(to be continued)

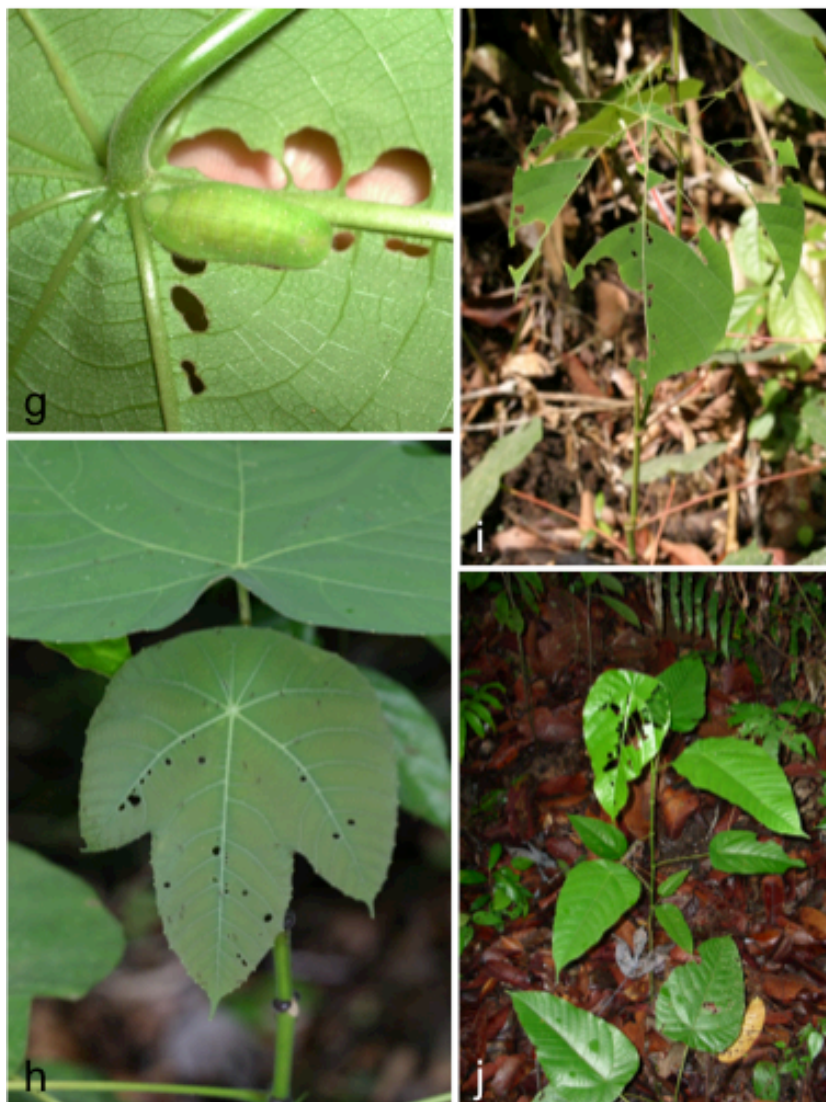


Figure 4. (continued) Immature stages of *Arhopala amphimuta* (Lycaenidae) at the study site: (g) a final instar larva resting on the abaxial side of a *M. hullettii* leaf (2008, May), (h) leaf-chewing marks made by a young instar larva on a sapling of *M. trachyphylla* (2006, October), (i) leaf-chewing marks made by a caterpillar (through the entire span of its larval life) on the apical leaf of a sapling (*M. bancana*) (2006, September), (j) leaf-chewing marks made by a final-instar larva on the apical leaf of a sapling (*M. hullettii*) (2008, August).

Larvae of *A. major* were commonly found to feed on young leaves of *M. gigantea* at the study site (Fig. 7). Non-feeding larvae often gathered in spaces shielded by stipules on the surfaces of host plant stem close to the shoot apices (Fig. 7c,d). Adult females often flew in the vicinity of *M. gigantea* shoot apices and leaf-chewing marks that were likely inflicted by the larvae were common at the study site; thus, the species has a narrow range of food plants and most likely prefers *M. gigantea* at least at the study site. Although Okubo et al. (2009) suggested that *A. major* feeds on non-myrmecophytic *Macaranga* species other than *M. gigantea*, the width of the *A. major* host range is still unresolved.

Okubo et al. (2009) described basic ecological characteristics of four *Arhopala* species specialized for feeding on *Macaranga* trees. Shimizu-kaya et al. (2013a) subsequently examined the potential ranges of host plants used by these four species. Shimizu-kaya et al. (2013b) described myrmecoxeny in *A. zylda* and Shimizu-kaya et al. (2014) described food-body feeding by *A. zylda* larvae particularly in the growth stages preceding the final instar.

Arhopala kinabala H. H. Druce was sometimes found to feed on a few *Macaranga* myrmecophytic species at the study site (Table 1, Fig. 8). However, feeding was likely restricted to ant-inactive saplings. *Arhopala kinabala* uses host species belonging to a selection families (Fig. 8c,d). Across all host plant species, all of > 20 larvae of this species that we found at the study site were attended by many workers of *Myrmicaria* sp. A (Fig. 8b,d; *authors' unpublished data*).

Maschwitz et al. (1984) reported that *A. moolaiana* Corbet feeds on *M. hullettii*, but we did not obtain any clear corroborative evidence at the study site, where this tree species is common; we never found a larva of *A. moolaiana* on a *aranga* plant, but we did collect an adult specimen.

We found four larvae of *Rapala dieneces* (Hewitson) (Lycaenidae, Lepidoptera) feeding on ant-inactive *M. winkleri* individuals at the study site (Fig. 9); the insects were able to reach the adult stage when fed only the leaves of this tree. On July 10 and 15, 2014, we observed these four larvae attended by unidentified ants (which were not plant-ant species of *M. winkleri*) on young leaves of a toppled, live *M. winkleri* seedling ca. 5 m tall. We raised the larvae in the laboratory; they pupated in the period July 16–28, 2014, and emerged from the pupae in the period July 27–

August 7, 2014. We have not seen other larvae of this species feeding on *Macaranga* plants at the study site. We do not know whether this lycaenid species regularly or exceptionally use *Macaranga* plants as food.

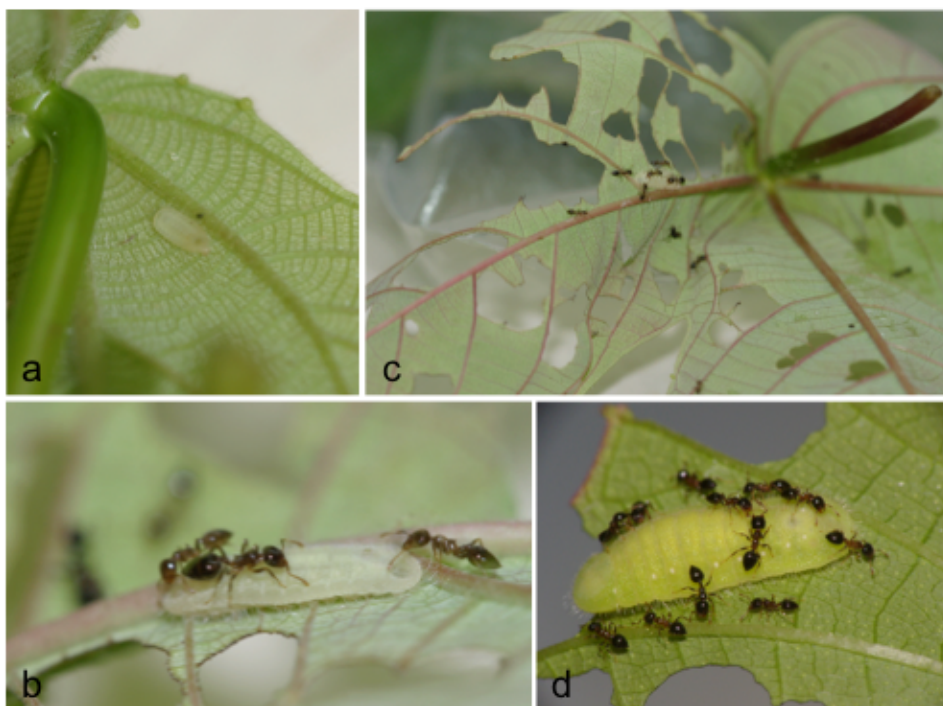


Figure 5. Immature stages of *Arhopala dajagaka* (Lycaenidae) on *Macaranga rufescens* at the study site: (a) a young instar larva on the abaxial side of a young leaf (2012, May), (b) a middle instar larva attended by plant-ants (*Crematogaster* sp.) on a young leaf (2012, May), (c) a middle instar larva in a laboratory setting attended by plant-ants (*Crematogaster* sp.); image shows damage to a young leaf caused by chewing of this larva (2012, May), (d) a final instar larva attended by plant-ants (image by T. Okubo).

Larvae of Nymphalidae spp. were sometimes found to feed on young leaves of ant-inactive *Macaranga* myrmecophytes or on old leaves located far from the plant apices (Fig. 10). Nymphalid larvae were not attended by ants, unlike those of lycaenid species. Because the strong similarity in adult morphology among these closely related taxa makes species identification difficult, we did not determine the number of nymphalid species that feed on *Macaranga* plants at the study site.



Figure 6. Immature stages of *Arhopala zylde* (Lycaenidae) on host plants (*Macaranga beccariana* and *M. hypoleuca*) at the study site: (a) a young or middle instar larva located on a new apical leaf of a sapling, (b) a middle or final instar larva reared on a sapling of *M. hypoleuca*, (c) a final instar larva on *M. beccariana* (2006, September), (d) a final instar larva on *M. beccariana* (2008, November), (e) a prepupa on a leaf of *M. beccariana* in a laboratory setting (2007, May), (f) a leaf of *M. beccariana* damaged by a final instar larva, (g) a pupa on the petiole of a new apical leaf (2009, March) (images (a), (b) and (f) were published previously by Shimizu-kaya et al. (2014), who described details of the feeding-habits of *A. zylde* larvae).

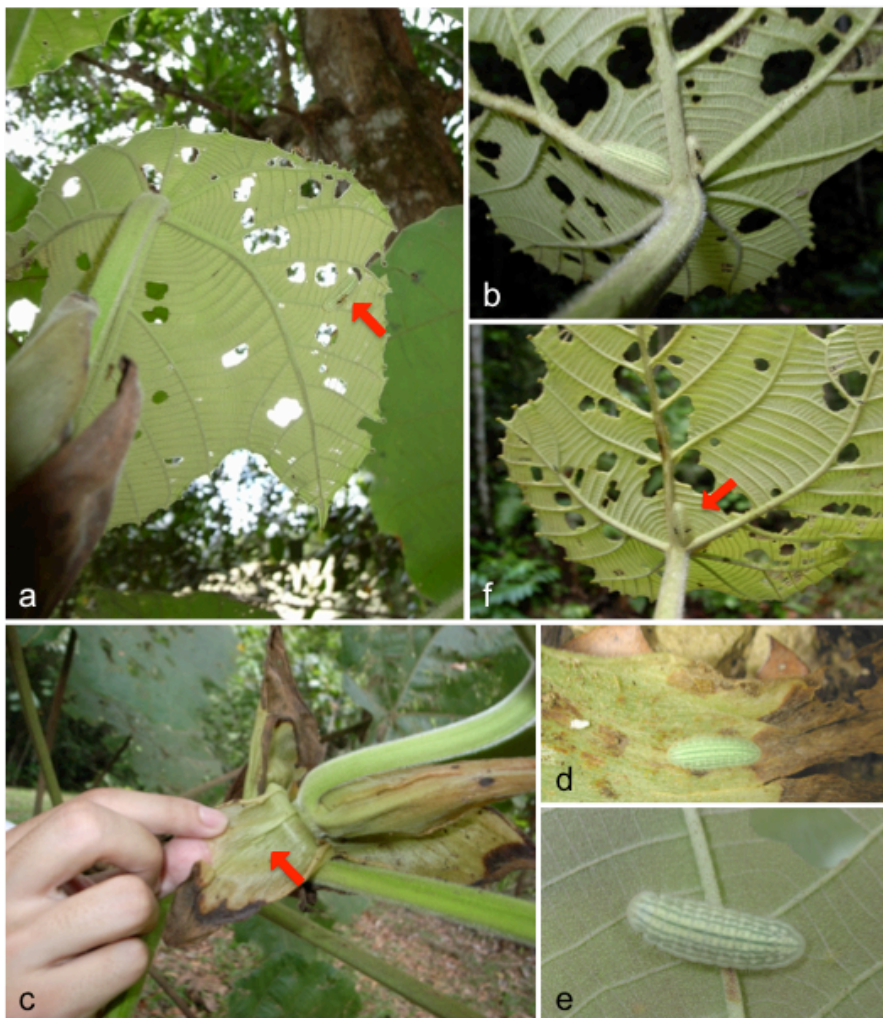


Figure 7. Immature stages of *Arhopala major* (Lycaenidae) on host plants (*Macaranga gigantea*) at the study site: (a) a final instar larva attended by an ant worker (*Anoplolepis gracilipes*) on an apical leaf of a sapling; leaf-chewing marks are visible on the leaf (2009, March), (b) final instar and middle instar larvae attended by ant workers (*Technomyrmex* sp.) (2009, January), (c) a middle instar larva located on the adaxial side of an apical stipule (2009, March), (d) a final instar larva located on the adaxial side of a stipule, (e) a final instar larva on a leaf of *M. gigantea* in a laboratory setting (2006, September), (f) leaf-chewing marks on the apical leaf of a sapling made by larvae at diverse developmental stages (2009, January).

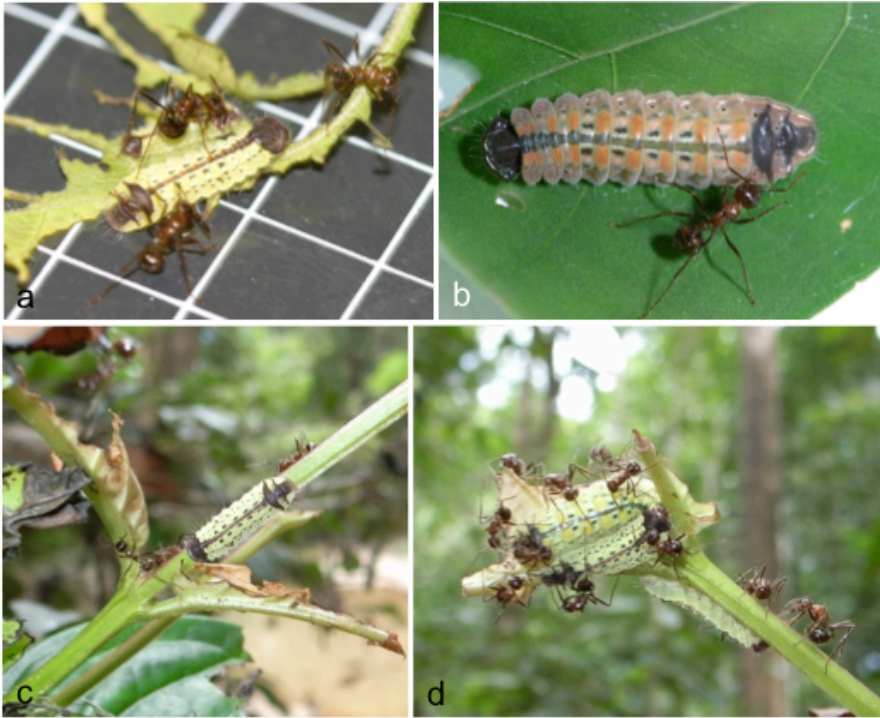


Figure 8. Immature stages of *Arhopala kinabala* (Lycaenidae) on diverse host plants at the study site: (a) laboratory-raised larva found on the leaf of an ant-inactive sapling (*Macaranga winkleri*) with attendant ants (*Myrmicaria* sp. A), (b) a final instar larva and attendant ant (*Myrmicaria* sp. A) (2006, September), (c) a pre-final instar larva on a plant (not *Macaranga*) (2009, March), (d) three mature larvae attended by several ant workers (*Myrmicaria* sp. A) on a plant (not *Macaranga*) (2009, March).

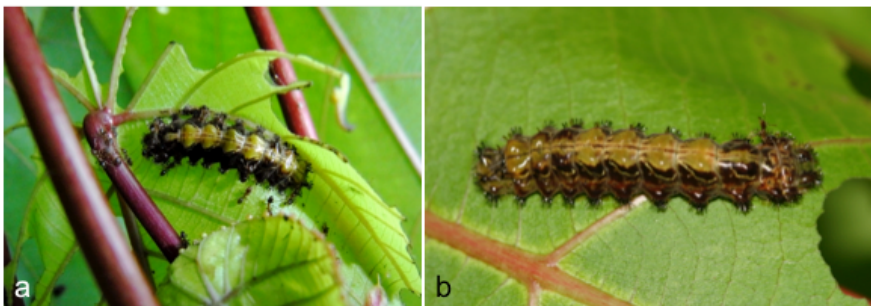


Figure 9. A final instar larva of *Rapala dieneces* (Lycaenidae) on a leaf of an ant-inactive sapling (*Macaranga winkleri*) with attendance by ant workers of non plant-ant species at the study site (2014, July) (a), and under rearing conditions for larvae in the laboratory (2014, July) (b).

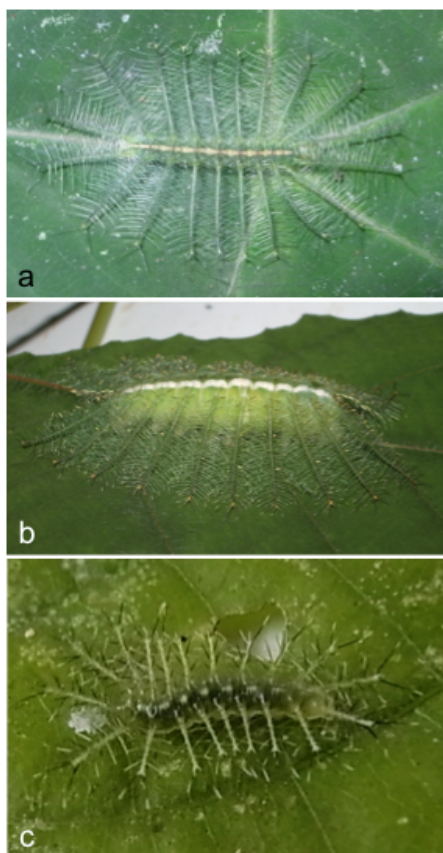


Figure 10. Mature larvae of nymphalid butterflies (Adoliadini spp.) at the study site feeding on *M. bancana* (a) (2010, September), *M. trachyphylla* (b) (2008, March), and *M. beccariana* (c) (2012, March). All larvae were on old leaves far below the apices of ant-intact saplings or on young apical leaves of ant-inactive.

(2) *Phasmids*

Two phasmid species, [*Orthomeria alexis* (Westwood) and *O. cuprinus* Bragg (Aschiphasmataidae, Phasmatodea)], at the study site have commonly been found to feed on several *Macaranga* myrmecophytes (Shimizu-kaya & Itioka 2015).

Although these two phasmids have similar morphologies (Fig. 11, 12), their feeding habits and host plant uses are clearly different (Shimizu-kaya & Itioka 2015). Thus, *O. alexis* uses *M. bancana* and *M. trachyphylla* (Fig. 11) as major hosts and sometimes feeds on *M. havilandii*, *M. hullettii* and *M. lamellata*. Only *M. beccariana* and *M. hypoleuca* are used as hosts by *O. cuprinus* (Fig. 12). *Orthomeria alexis* was usually found feeding on older leaves located in lower sections of the plants far from the apices; *O. cuprinus* was generally found on younger leaves located near the apices.

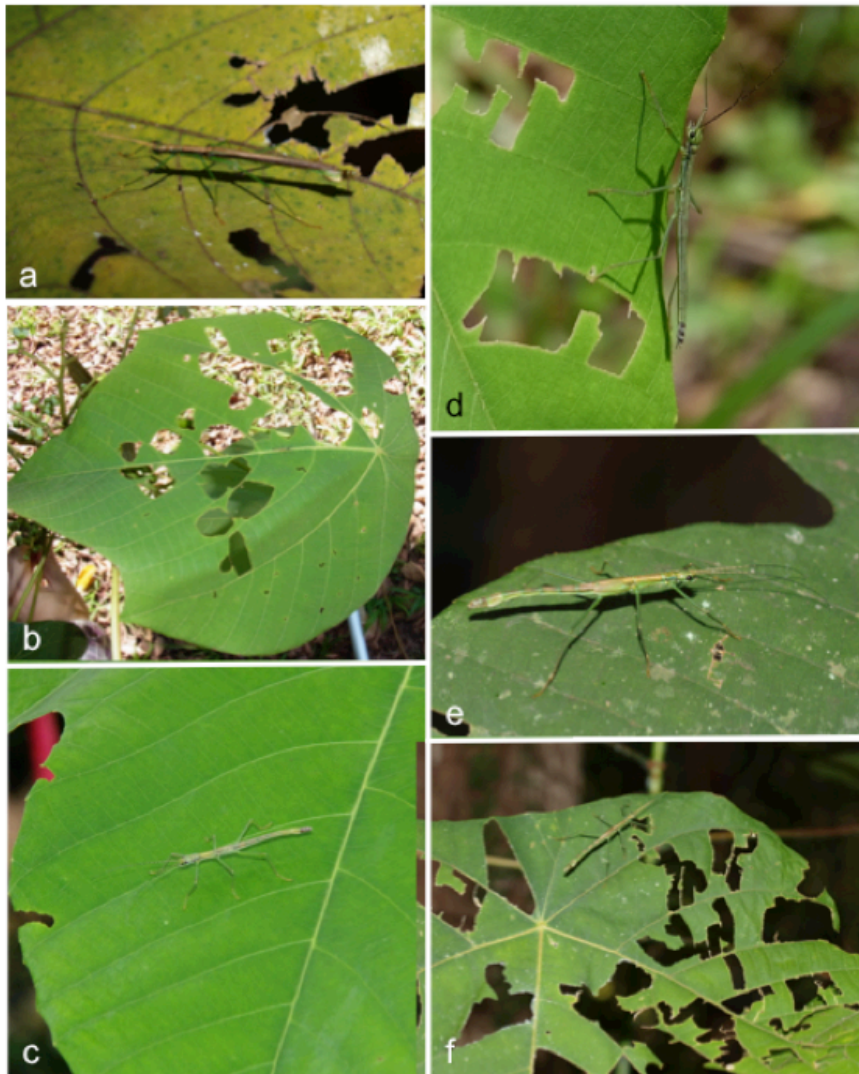


Figure 11. *Orthomeria alexis* (Aschiphasmataidae, Phasmatodea), a phasmid species likely specialized for feeding on several *Macaranga* myrmecophytes, at the study site: (a) an adult female on *M. trachyphylla* (2009, May), (b) a young instar nymph on a *M. bancana* leaf with chewing marks likely made by conspecifics of the previous generation (2014, September), (c) and (d) middle stage nymphs on *M. bancana* [(c): 2011, November; (d): 2012, November], (e) a final instar nymph on *M. bancana* (2009, May), (f) a final instar nymph on *M. bancana*; leaf chewing marks likely made by the nymph (2009, May).
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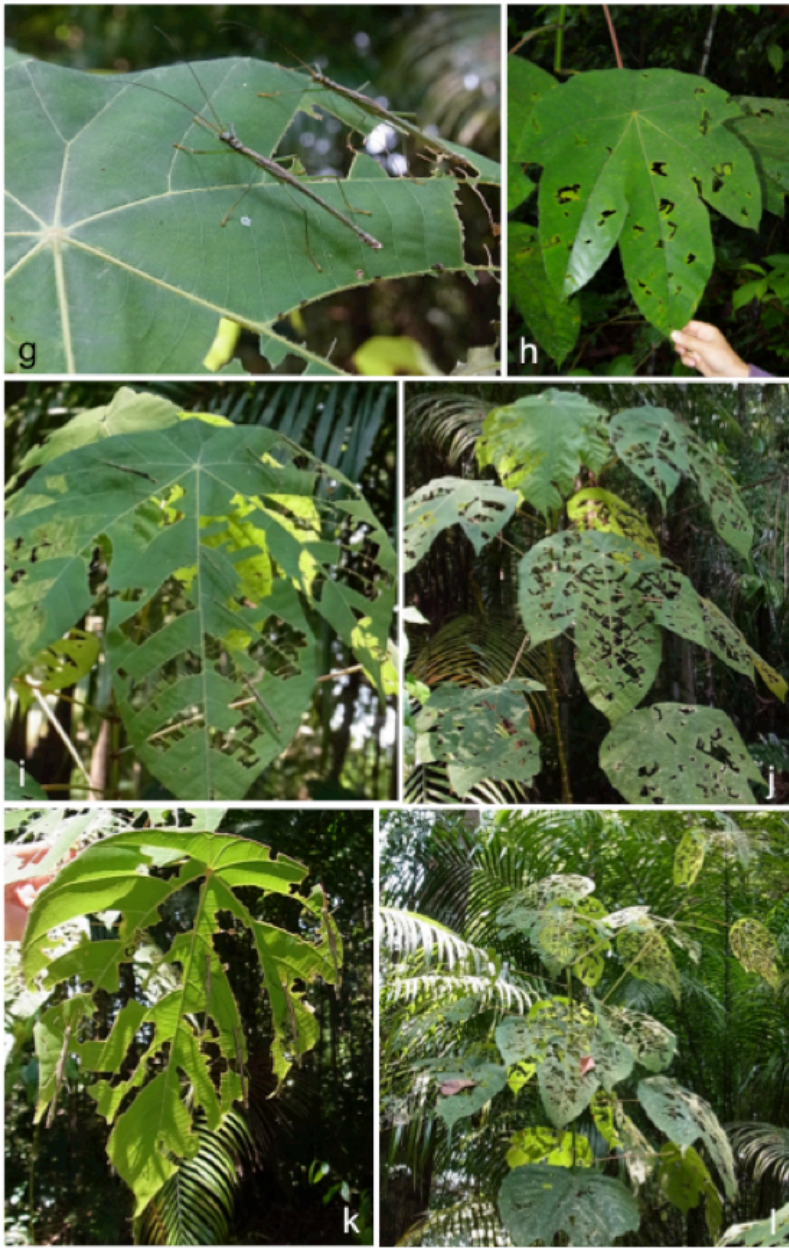


Figure 11. (continued) *Orthomeria alexis* (Aschiphasmatidae, Phasmatodea), a phasmid species likely specialized for feeding on several *Macaranga* myrmecophytes, at the study site: (g) two final instar nymphs on *M. bancana* (2013, June), (h) leaf-chewing marks on *M. bancana* made by young instar nymphs (2012, December), (i) a *M. bancana* leaf heavily grazed by several later nymphal stage individuals or by adults (2013, June), (j) selection of leaf-chewing marks on *M. bancana* made by aggregated middle or final instar nymphs (2013, June), (k) gregarious individuals in the final instar nymphal stage and in the adult stage on *M. bancana* (2013, June), (l) *M. bancana* sapling with heavy grazing damage caused by gregarious nymphs and adults (2013, June).

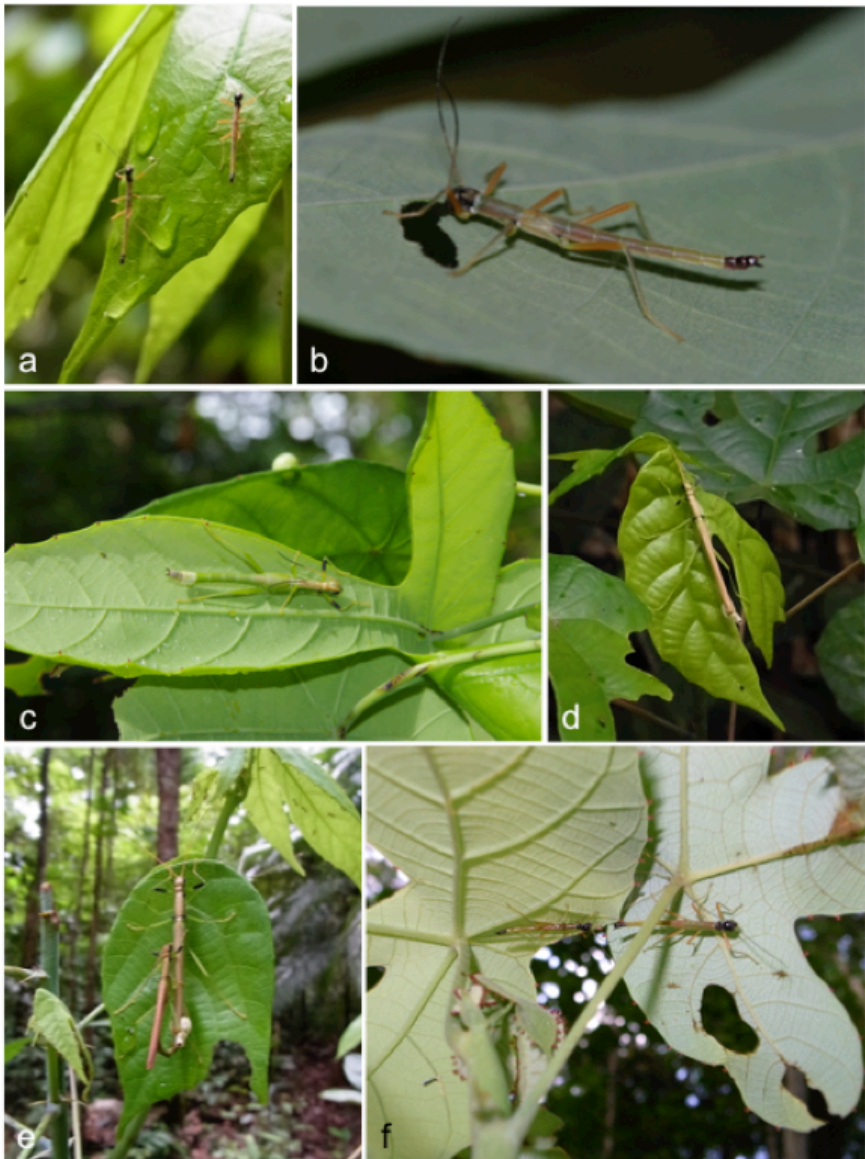


Figure 12. *Orthomeria cuprinus* (Aschiphasmataidae, Phasmatodea), a phasmid species likely specialized for feeding on *Macaranga beccariana* and *M. hypoleuca*, at the study site: (a) two individuals at the young instar nymphal stage on *M. beccariana* (2012, December), (b) a middle instar nymph feeding on a leaf of *M. hypoleuca* (2014, April), (c) a pre-final or final instar nymph on a sapling of *M. beccariana* (2011, November), (d) an adult female on a young apical leaf of a *M. beccariana* sapling (2014, July), (e) a copulating pair on a young apical leaf of a *M. beccariana* sapling (2012, January).

Several individuals at various growth stages often aggregated in spaces surrounded by a few young leaves, or on the abaxial sides of apical leaves borne by saplings: (f) two middle instar nymphs on *M. hypoleuca*,
(to be continued)

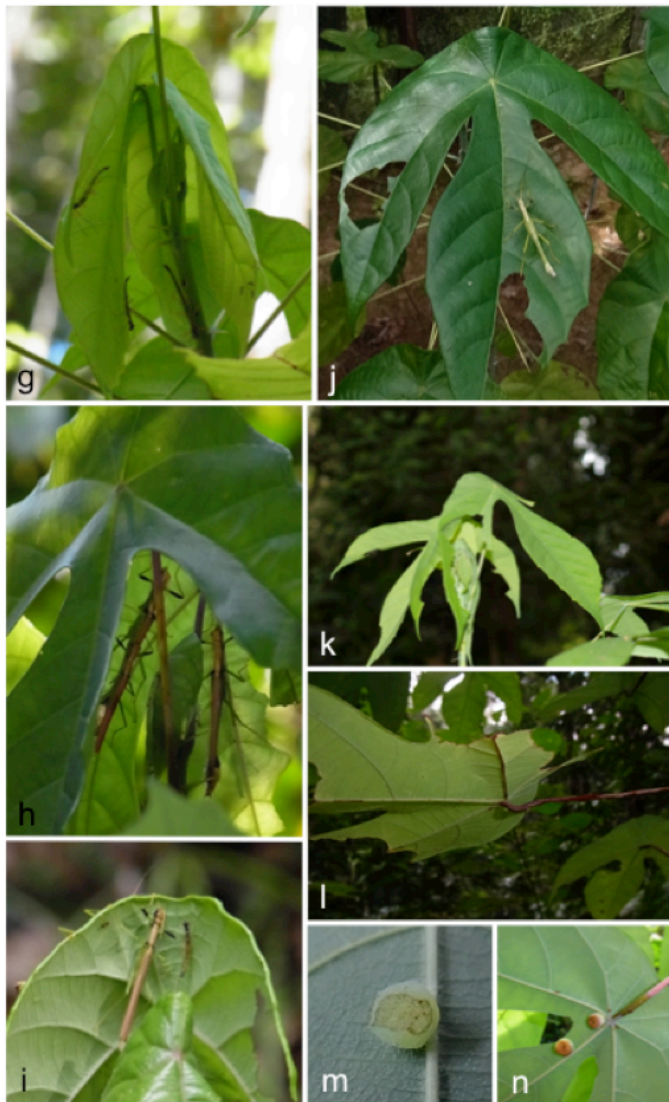


Figure 12. (continued) (g) middle and pre-final (or middle and final) instar nymphs on *M. beccariana* (2014, April), (h) a copulating pair and an adult female on *M. beccariana* (2012, November), (i) an adult male and a nymph at an early stage (2012, December) Leaf-chewing marks caused by *O. cuprinus* at various growth stages, (j) leaf-chewing by a final instar nymph on *M. beccariana* (2012, November), (k) leaf-chewing by an adult female on *M. beccariana* (2009, May), (l) chewing on the abaxial side of a petiole of *M. beccariana*, presumably by an adult female (2013, Mar), (m) phasmids grazing galls formed by a cecidomyiid species on a *M. beccariana* leaf (2014, September), (n) gall-grazing and chewing of the abaxial side of a petiole on a *M. beccariana* leaf presumably made by an adult female (2014, July).

Both species of *Orthomeria* frequently copulated on the host plants (Fig. 12e), and two or more individuals often shared a host plant individual (Fig. 11g,i,k; Fig. 12f–i). Larvae of *O. alexis* preferentially fed on leaves of *M. winkleri* and complete the growth cycle ($n = 4$, authors' unpublished data) when we removed defending ants in the laboratory, but we never saw larvae of this species feeding on *M. winkleri* in the field.

We often saw chewing marks on the abaxial side of a petiole that were likely made by the female adults of *O. cuprinus* (Fig. 12l,n). Both nymphs and adults of this species were frequently found feeding on galls formed by gall midges (Fig. 12m,n). Young and middle instar nymphs, in particular, seem to preferentially feed on galls; they were frequently seen feeding on galls in the field and in the laboratory rearing.

We obtained no clear evidence of feeding by any other phasmid species on ant-intact individuals of *Macaranga* myrmecophytes at the study sites. Only one phasmid species, *Asceles margaritatus* Redtenbacher (Heteronemiidae, Phasmatodea), which is somewhat polyphagous (Bragg 2001), was found feeding on ant-inactive saplings of *Macaranga* myrmecophytes (*M. bancana* and *M. hypoleuca*) (Fig. 13). There was no clear evidence that phasmid species feed on *Macaranga* non-myrmecophytes at the study site.



Figure 13. An adult female of *Asceles margaritatus* (Heteronemiidae, Phasmatodea) on a leaf of an ant-inactive sapling of *M. bancana* at the study site (2010, January).

(3) *Gall midges*

Thus far, we have found at least 13 species of gall midges (Cecidomyiidae, Diptera) that formed galls on *Macaranga* plants at the study site (Table 2, Fig. 14). The relationship between gall midges and *Macaranga* species was highly species-specific: a single plant species was used as a host plant by one or a few species of gall midge; one cecidomyiid species used a single species of *Macaranga* or a group of closely related *Macaranga* species. We have a taxonomic study of these gall midges underway.

The density of galls per leaf was considerably higher on ant-inactive saplings than on ant-intact saplings of *M. beccariana* (Fig. 15, Itioka et al. 2000).

Some species of parasitoid wasps inoculate eggs into the larvae of these gall midges residing inside the galls (Fig. 16); however, details of this process are not yet available.

Table 2. Host plant use by 13 species of *gall midge* (Cecidomyiidae) in the Lambir Hills National Park, Sarawak, Malaysian Borneo.

Gall midge taxon*	<i>Macaranga</i> species (Host plant)
Schizomyiina sp. 1	<i>M. beccariana</i> , <i>M. hypoleuca</i>
Schizomyiina sp. 2	<i>M. beccariana</i> , <i>M. hypoleuca</i>
Cecidomyiidae sp. 1**	<i>M. hypoleuca</i>
Cecidomyiidae sp. 2	<i>M. bancana</i> (petiole)
Cecidomyiidae sp. 3**	<i>M. bancana</i> (leaf)
Cecidomyiidae sp. 4	<i>M. lamellata</i>
Cecidomyiidae sp. 5	<i>M. trachyphylla</i>
Cecidomyiidae sp. 6	<i>M. gigantea</i>
Cecidomyiidae sp. 7	<i>M. hosei</i>
Cecidomyiidae sp. 8	<i>M. rufescens</i>
Cecidomyiidae sp. 9**	<i>M. hosei</i>
Cecidomyiidae sp. 10	<i>M. lamellata</i>
Cecidomyiidae sp. 11	<i>M. hypoleuca</i>

* J. Yukawa and M. Tokuda are working on the taxonomy of these midges.

** Very rare species; the galls were found only once or twice.



Figure 14. Galls and gall midges on *Macaranga* plants at the study site: (a) galls of *Schizomyiina* sp. 1 (Cecidomyiidae, Diptera) on *M. beccariana* (2009, July), (b) mature galls of *Schizomyiina* sp. 2 (Cecidomyiidae, Diptera) on *M. beccariana* (2012, November), (c) two empty galls from which adult gall midges had previously emerged (*left and middle*) and a mature individual (*right lower*) of *Schizomyiina* sp. 2 (2010, September), (d) a pupa inside a gall (2012, March), (e) and (f) galls of *Cecidomyiidae* sp. 11 on *M. hypoleuca* (gall size is markedly larger than those of *Schizomyiina* spp. on *M. beccariana* and *M. hypoleuca*) (2014, September, and 2013, September), (g) galls of *Cecidomyiidae* sp. 2 on a petiole of *M. bancana* (2013, June), (h) an ovipositing female on the petiole of newly developing leaf of *M. bancana* (2014, April), (i) a gall of *Cecidomyiidae* sp. 4 on the abaxial side of a *M. lamellata* leaf (2014, September), (j) an immature gall of *Cecidomyiidae* sp. 5 on the abaxial side of a *M. trachyphylla* leaf (2012, November).

(to be continued)

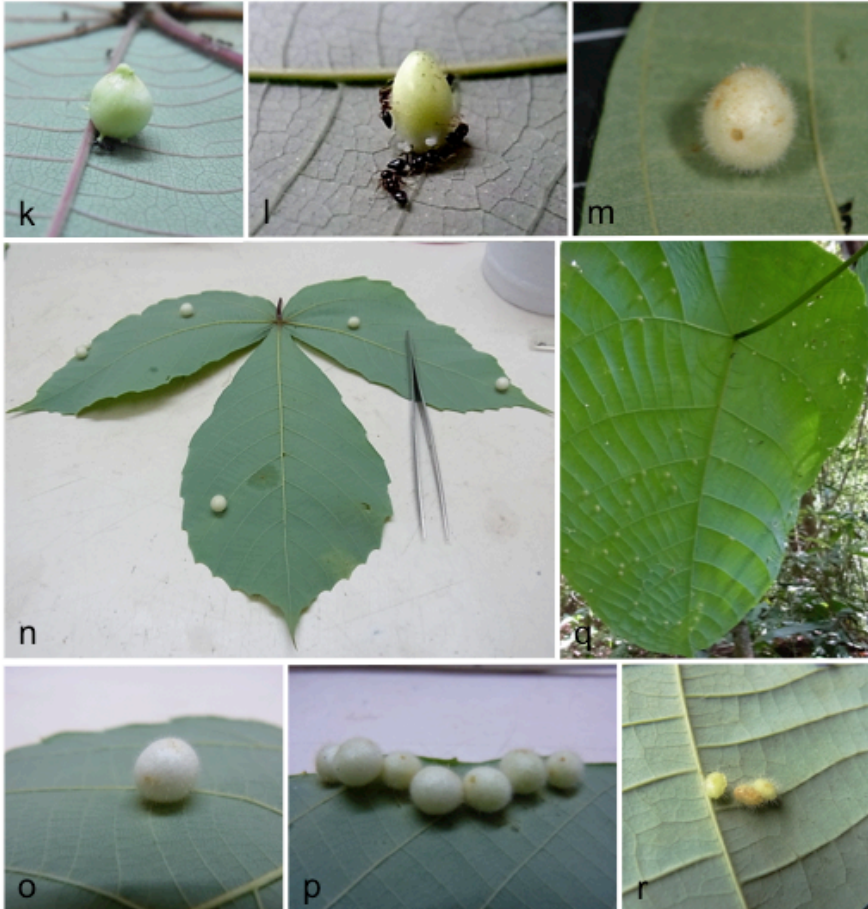


Figure 14. (continued) Galls and gall midges on *Macaranga* plants at the study site: (k) a mature gall of Cecidomyiidae sp. 5 on the abaxial side of a *M. trachyphylla* leaf (2012, November), (l) plant-ants aggregating around an immature gall of Cecidomyiidae sp. 5 on *M. trachyphylla*; the ants are touching the gall with their antennae (2014, September), (m) galls of Cecidomyiidae sp. 7 on the abaxial side of *M. hosei* leaf (2014 Apr), (n)–(p) galls of Cecidomyiidae sp. 8 on the abaxial side of a *M. rufescens* leaf (2012, May), (q) and (r) galls of Cecidomyiidae sp. 10 on the abaxial side of a *M. lamellata* leaf (2012, November and 2014, September).

(to be continued)

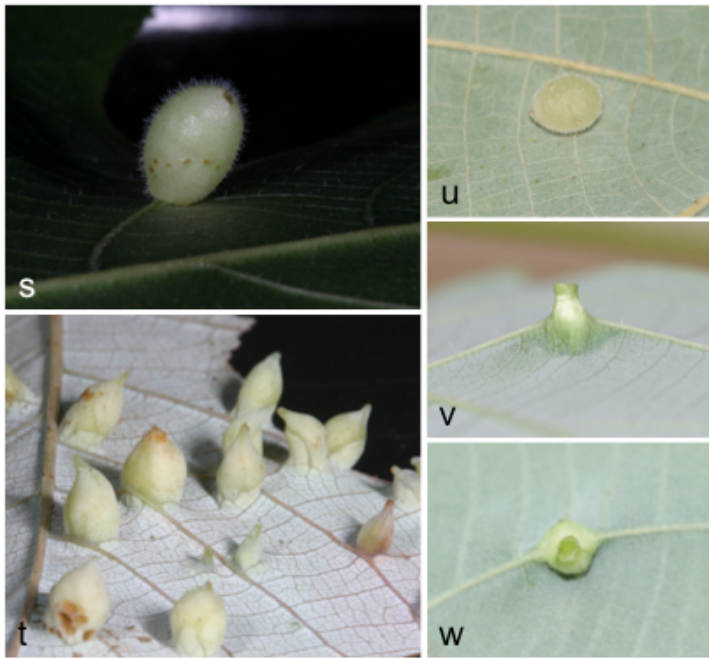


Figure 14. (continued) Galls and gall midges on *Macaranga* plants at the study site: (s) a gall of Cecidomyiidae sp. 3 on the abaxial side of a *M. bancana* leaf (2010, August), (t) galls of Cecidomyiidae sp. 1 on the abaxial side of a *M. hypoleuca* leaf (2010, August), (u) a gall of Cecidomyiidae sp. 6 on the abaxial side of a *M. gigantea* leaf (2010, January), (v) and (w) gall of Cecidomyiidae sp. 9 on the abaxial side of a *M. hosei* leaf (v: lateral view, w: topside view; 2010, February).

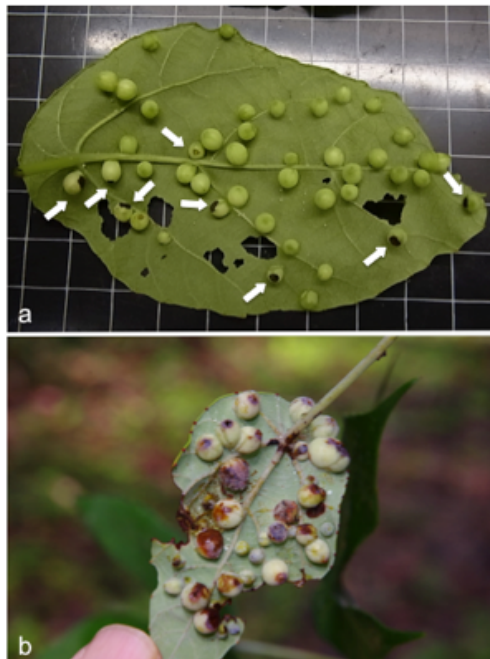


Figure 15. Galls of Schizomyiina sp. 2 on ant-inactive saplings of *Macaranga beccariana* at the study site: (a) mature galls and those damaged by the phasmid *Orthomeria cuprinus* (arrows) on a young leaf (2013, March), (b) empty galls from which parasitoid wasps had previously emerged; these wasps parasitized the gall formers (2011, November).

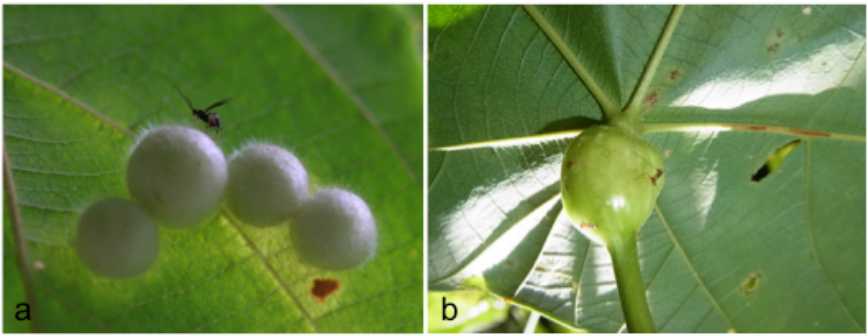


Figure 16. Parasitoid wasps that parasitize immature gall midges occupying galls at the study site: (a) an ovipositing female on a gall formed by Cecidomyiidae sp. 8 on *Macaranga rufescens* (2014, September), (b) an ovipositing female on a gall formed by Cecidomyiidae sp. 2 on *M. bancana* (2013, June).

Table 3. Host plant use by heteropteran species in the Lambir Hills National Park, Sarawak, Malaysian Borneo.

Heteropteran species	<i>Macaranga</i> species (Host plant)
Miridae, Phylinae	
<i>Pilophorus</i> *	
<i>P. unifasciatus</i> Nakatani & Komatsu	<i>M. beccariana</i>
<i>P. aurifasciatus</i> Nakatani & Komatsu	<i>M. beccariana</i>
<i>P. gracilipennis</i> Nakatani & Komatsu	<i>M. beccariana</i>
<i>P. lambirensis</i> Nakatani & Komatsu	<i>M. rufescens</i> , <i>M. hosei</i>
<i>Pilophorus</i> sp. 1	<i>M. winkleri</i>
<i>Pilophorus</i> sp. 2	<i>M. bancana</i>
<i>Pilophorus</i> sp. 3	<i>M. bancana</i>
<i>Pilophorus</i> sp. 4	<i>M. havilandii</i>
Unidentified genus	
Phylinae sp. 1	<i>M. beccariana</i>
Nabidae	
<i>Arbela</i> sp. 1	<i>M. beccariana</i>

* Y. Nakatani is working on the taxonomy of these insects.

(4) *Myrmecophilous bugs*

We found diverse myrmecophilous bugs with body shapes and colorations resembling those of plant-ants living on several *Macaranga* myrmecophytes at the study site. These bugs inhabited the apical portions of host plant saplings where plant-ant workers were abundant (Fig. 17–19). The bugs belong to the family Miridae or Nabidae (Hemiptera) (Table 3).

Nakatani et al. (2013) described four *Pilophorus* species associated with *Macaranga* trees at the study site. Host plant species-specificity was relatively high for most *Pilophorus* species. Adults and nymphs were usually located on stems or leaves around the apical parts, sometimes walking with patrolling plant-ant workers. Some of the mirid species and *Arbela* sp. 1 often fed on food bodies when we removed ants in laboratory experiments (Fig. 17b,c,e; Fig. 18b).

We often found *Phylinae* sp. 1 and *Arbela* sp. 1 sharing a host tree at the study site. When the two bug species shared a tree, the plant sectors they occupied were differentiated with a little overlap: *Phylinae* sp. 1 tended to inhabit stem sections close to the apical part and young leaves, while *Arbela* sp. 1 tended to inhabit lower stem sections distant from the apex and separate from the microhabitat of *Phylinae* sp. 1. Full details of habitat differentiation are as yet unavailable. The taxonomy and ecology of myrmecophilous bugs inhabiting *Macaranga* myrmecophytes require further investigation.

(5) *Others*

Thus far, we are able to confirm that at least 79 insect species belonging to 34 families and six orders fed on *Macaranga* plants at our study site. Other than the four insect groups listed above, we found leaf chewers, such as diverse polyphagous lepidopteran species, a few species of Orthoptera (including a species of Grylloidea, and two or more species of Acridoidea) (Figs. 20, 21), leaf miners (mainly Gracillariidae) (Fig. 22), and sap-feeders such as planthoppers, leafhoppers and scale insects (Hemiptera). Except for leaf miners, most of these insects occurred more frequently on ant-inactive individuals of myrmecophytic species than on intact (or ant-active) individuals of myrmecophytic species or non-myrmecophytic species

(*authors' unpublished data*). We do not have species identities for most of these other herbivores and simply present images of typical feeding marks on leaves that were made by a small fraction of the species.

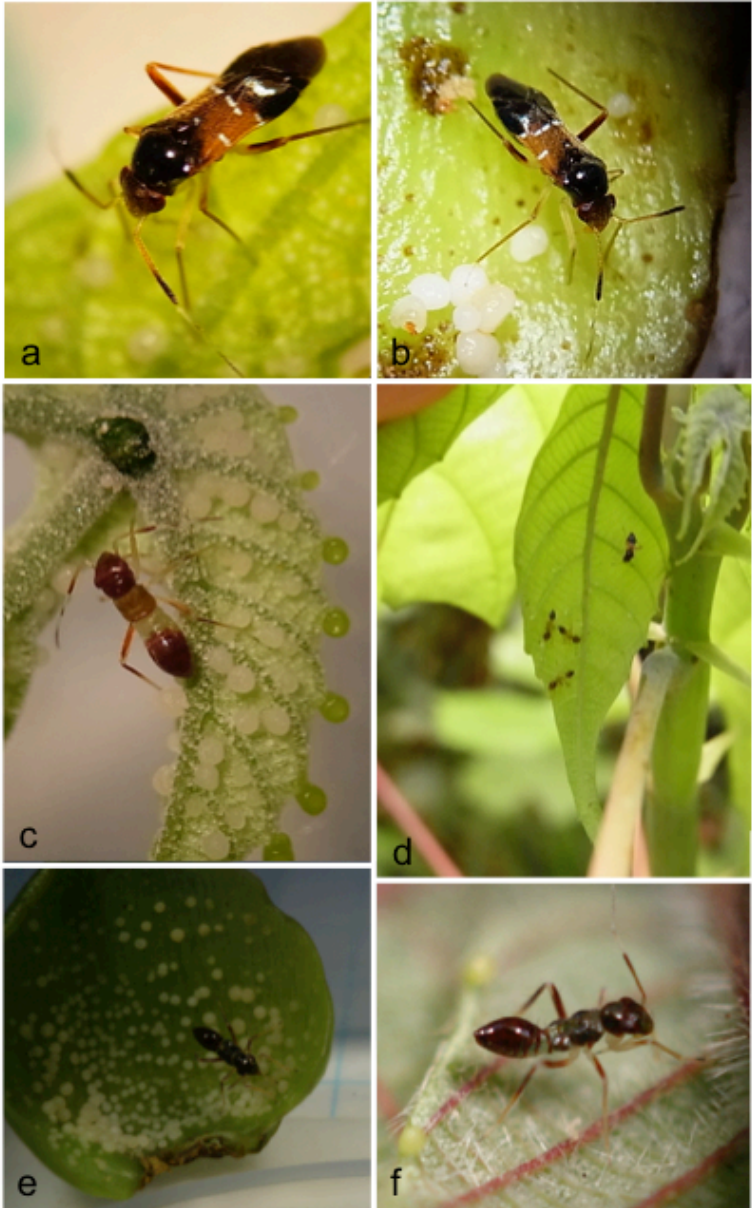


Figure 17. (*to be continued*)



Figure 17. Ant-mimicking mirid bugs of the genus *Pilophorus* (Phylinae, Miridae, Hemiptera) on *Macaranga* myrmecophytes at the study site: (a) an adult of *P. unifasciatus* on an apical leaf of *M. beccariana* (2012, June), (b) an adult of *P. unifasciatus* (collected from *M. beccariana*) raised in the laboratory on food bodies of *M. rufescens* (2012, June), (c) a nymph of *Pilophorus* sp. on an apical leaf bearing many food bodies (2012, April), (d) an adult of *P. unifasciatus* and a few specimens of plant-ant workers located on a sapling of *M. beccariana* (2012, November), (e) a mature nymph of *P. lambirensis* feeding on a food body of *M. rufescens* (2011, June), (f) a middle-instar nymph of *P. lambirensis* on a young leaf of *M. rufescens* (2011, June), (g) nymphs of *P. lambirensis* at various growth stages with large numbers of plant-ant workers located around the apex of a sapling (*M. hosei*) (2013, June), (h) an ovipositing female of *Pilophorus* sp. 1 and a plant-ant worker on a young leaf of *M. winkleri* (2014, August), (i) an adult of *Pilophorus* sp. 2 on a stem close to the apex of *M. bancana* (2013, June), (j) an adult of *Pilophorus* sp. 4 on a stem close to the apex of *M. havilandii* (2013, July), (k) a nymph of *Pilophorus* sp. 4 on a stem close to the apex of *M. havilandii* (2013, July), (l) a nymph of *Pilophorus* sp. on the apical leaf bud of *M. beccariana* (2011, July; image by T. Komatsu).

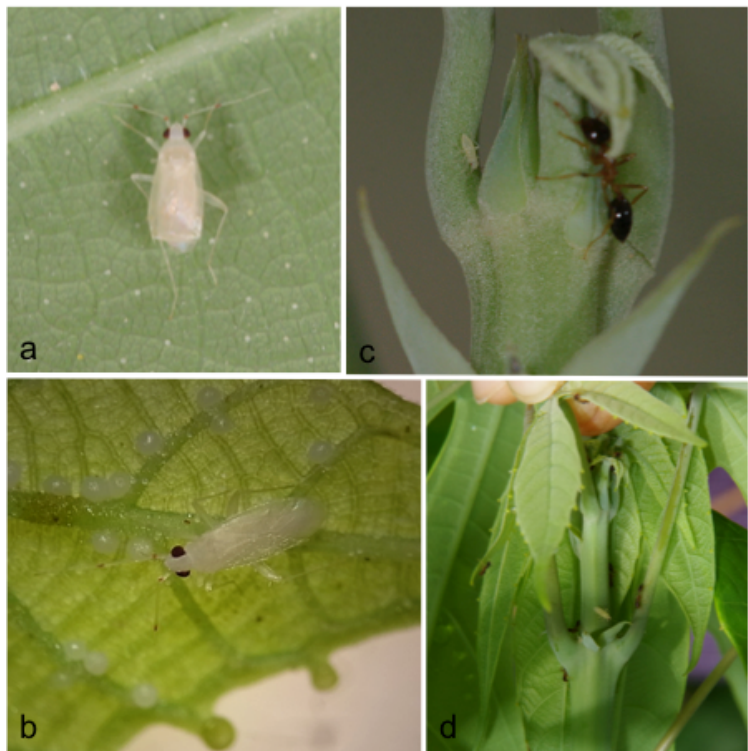


Figure 18. *Phylinae* sp. 1, an unidentified mirid bug species (*Phylinae*, *Miridae*, *Hemiptera*) often found feeding on *Macaranga beccariana* saplings at the study site: (a) an adult on a leaf (2013, July), (b) an adult feeding on a food body (2012, June), (c) a young instar nymph close to a plant-ant worker near the apex of a sapling (2013, July), (d) an adult moving near an ant aggregation at the apex of a sapling (2013, July).



Figure 19. An ant-mimicking bug species of the genus *Arbela* (*Nabidae*, *Hemiptera*) at the study site: (a) a nymph on a leaf of *Macaranga beccariana* (2011, July; image by T. Komatsu), (b) a nymph on a leaf of *M. beccariana* preying on a plant-ant worker (2012, June).

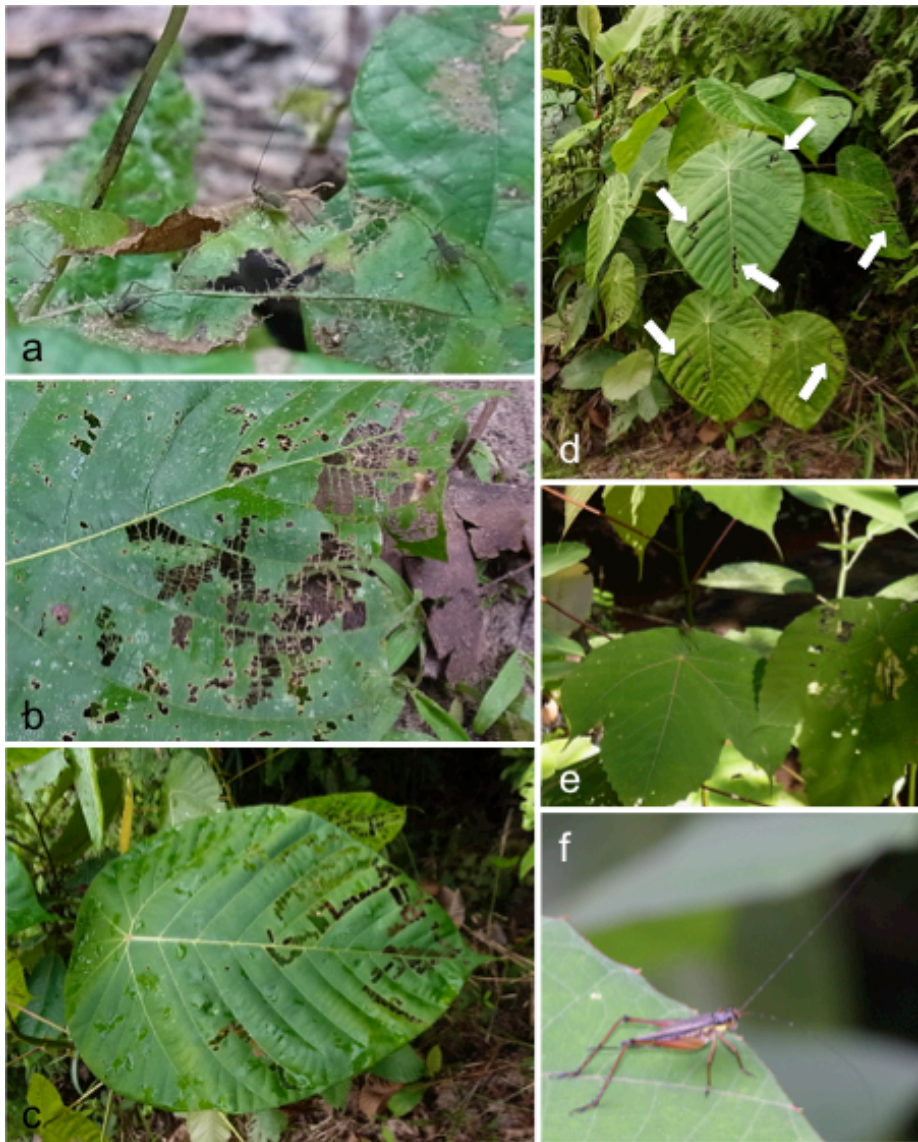


Figure 20. Cricket species feeding on ant-inactive seedlings of *Macaranga* myrmecophytes (Gryllidae sp. A) at the study site: (a) nymphs on an ant-inactive sapling of *M. beccariana* (2013, March), (b)–(d) leaf-chewing marks made by this cricket on *M. winkleri* (2013, March), (e) leaf-chewing marks on *M. bancana*; an adult of this cricket species is visible (2012, January), (f) leaf-chewing marks on *M. trachyphylla*, (g) an adult female; leaf veins frequently remained visible at sites of grazing damage inflicted by this cricket species (2013, February).

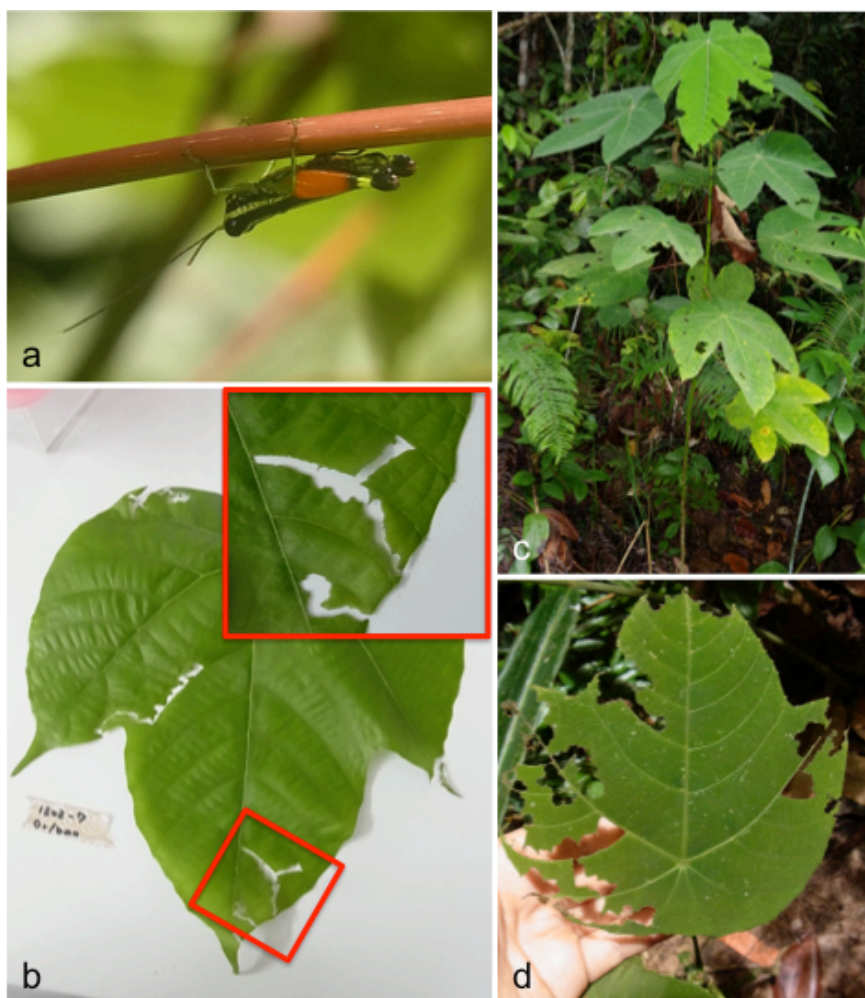


Figure 21. Feeding of Orthoptera (Acridoidea spp.) on ant-inactive seedlings of *Macaranga* myrmecophytes at the study site: (a) a grasshopper species (found to feed on ant-inactive saplings of selected *Macaranga* myrmecophytic species at the study site) on a leaf petiole of *M. bancana* (2012, October), (b) chewing marks on a *M. bancana* leaf most likely inflicted by a grasshopper species (2013, March), (c) leaf-chewing marks on a *M. bancana* sapling (2011, November), (d) leaf-chewing marks on a *M. trachyphylla* leaf (2011, November).



Figure 22. Leaf mines on *Macaranga* myrmecophytes at the study site: (a) a leaf mine excavated by Gracillariidae sp. A in *M. beccariana* leaf tissue (2013, September), (b) leaf mines of unknown insects excavated into an ant-inactive sapling of *M. winkleri* (2006, September).

Closing remarks

We provided information on the biological characteristics of herbivorous insects found on *Macaranga* in Lambir Hills National Park, where the diversity of *Macaranga* is very high, and presented a brief summary of relevant published studies along with our images showing life history and ecological traits. All of these data are based on our 20-year observation period and the field experiments that we performed. This information improves our understanding of the evolutionary and ecological relationships of herbivorous insects feeding on *Macaranga* plants. Nevertheless, obvious knowledge gaps demonstrate the need for further study, which we will pursue with particular focus on the herbivores listed here as “others.”

Acknowledgements

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