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A Guide to *Macaranga* (Euphorbiaceae) of Lambir Hills National Park, Sarawak, Malaysia

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ABSTRACT Lambir Hills National Park, Sarawak, Malaysia, in Borneo has an extremely species-rich flora. At least 17 species of the euphorbiaceous tree genus *Macaranga* are distributed to the park. We list the species together with a key to their identification, and provide brief notes on the vegetative morphology and ecology for each species.

KEY WORDS ant–plant mutualism / *Camponotus* / *Crematogaster* / identification key / myrmecophyte / pioneer species / Southeast Asian tropics

Introduction

Macaranga Thouars (Euphorbiaceae) is a palaeotropical genus with its greatest diversity in Southeast Asia, particularly in Borneo. Of the 308 species of *Macaranga*, at least 50 species classified in eight sections/informal species groups of the genus are distributed in Borneo (Whitmore 2008; POWO 2024). Most of the species are small to medium-sized trees and early successional species, which are common in forest gaps, on riverbanks, at edges of primary forests, or in secondary and disturbed vegetation. Most *Macaranga* species are easily recognizable by their large peltate leaves and long petioles. This genus is also notable for its symbiotic relationship with ants. More than 25 species are "myrmecophytes" or "ant-plants," which host ant colonies within the hollow stems of the plant (Davies 2001a; Davies et al. 2001). Myrmecophytic *Macaranga* species provide ants with nesting spaces and food resources, such as extrafloral nectar and food bodies, and, in return, the ants protect the host tree from herbivores, pathogens, and vines (Fiala et al. 1989). The mutualism presents a superb opportunity to study plant–ant interactions.

Situated in Sarawak, Malaysia, in northwestern Borneo, the lowland tropical rainforest in Lambir Hills National Park (LHNP) has long been known as an extremely floristically species-rich ecosystem. At least 17 species of *Macaranga* from five sections or groups are distributed within the park. This comprises almost half the number of known *Macaranga* species that grow in lowland areas throughout Sarawak and includes 12 myrmecophytic species. Since 1996, numerous ecological studies on *Macaranga* species have been conducted in LHNP (e.g., Davies 1998, 2001b; Davies and Ashton 1999; Davies et al. 1998; Itino et al. 2001; Itioka et al. 2000; Nomura et al. 2001). In addition, several articles on the systematics and ecology of *Macaranga* in Borneo have been published (e.g., Davies 2001a; Slik & van Welzen 2000; Whitmore 2008). However, it remains difficult for visitors to LHNP to identify *Macaranga* species in the field because of the lack of an identification guide highlighting the species that grow in the park. The guide presented here includes a species checklist, photographs of individual species, and a systematic key to distinguish each *Macaranga* species found in LHNP together with a brief introduction to their biological traits and ecological preferences. For more detailed information on each species, such as morphological characters and distribution areas, consult the additional references listed at the end of the guide.

Checklist of *Macaranga* species in Lambir Hills National Park

Conifera group

M. conifera (Rchb.f. & Zoll.) Müll.Arg.

M. recurvata Gage

Section Pachystemon

M. aëtheadenia Airy Shaw

M. bancana (Miq.) Müll.Arg.

M. beccariana Merr.

M. havilandii Airy Shaw

M. hullettii King ex Hook.f.

M. hypoleuca (Rchb.f. & Zoll.) Müll.Arg.

M. lamellata Whitmore

M. trachyphylla Airy Shaw

M. umbrosa S.J.Davies

Section Pruinosae

M. gigantea (Rchb.f. & Zoll.) Müll.Arg.

M. hosei King ex Hook.f.

M. rufescens S.J.Davies

Section Pseudrottlera

M. brevipetiolata Airy Shaw

M. praestans Airy Shaw

Section Winklerianae

M. winkleri Pax & K.Hoffm.

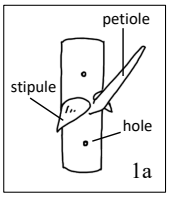
Note: Although *M. caladiifolia* Becc. (sect. *Pachystemon*) is reported to grow on the summit of Mt. Lambir (Davies 2001a), we did not include this species in the current guide because it has not been sighted or confirmed in LHNP for the past 15 years.

An identification key to *Macaranga* species in Lambir Hills National Park

(based on vegetative traits, not applicable for seedlings or heavily damaged trees)

1a. Stems and twigs hollow, inhabited by ants, entrance holes vertically aligned 2

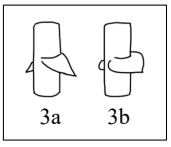
1b. Stems and twigs solid, not inhabited by ants, without entrance holes 13



2a. Stipules*[1] flat, not recurved 3

2b. Stipules strongly recurved 6

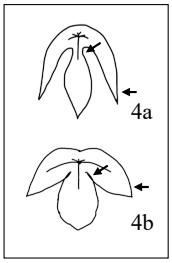
*[1] Appendages of the leaf, situated in pairs at the base of a leafstalk (petiole)



3a. Stipules triangular; food bodies*[2] produced only on the lower surface of young leaves 4

3b. Stipules broadly ovate, semi-circular; food bodies produced only on the upper surface of young stipules 5

*[2] White or yellow granules providing a nutrient-rich food source for ants



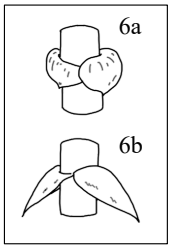
4a. Central lobe of leaf blade strongly constricted near the base; lateral lobes slightly curved downward; lateral veins on lower surface indistinct because of white wax ..... ***M. beccariana***

4b. Central and lateral lobes of leaf blade weakly constricted near the base; lateral lobes ±flat; lateral veins prominent on lower surface ..... ***M. hypoleuca***

5a. Petiole yellowish green; leaf blade sparsely hairy on upper surface and densely hairy on lower surface ..... ***M. hosei***

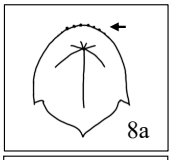
5b. Petiole crimson red; leaf blade densely hairy on both surfaces ..... ***M. rufescens***

6a. Stipules dome-shaped 7
6b. Stipules horn-like 11

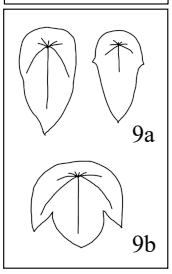


7a. Stems and twigs whitish, strongly glaucous (covered with wax) 8
7b. Stems and twigs greenish, not glaucous 9

8a. Leaves shallowly 3-lobed; nectary glands along the leaf margin prominent, particularly larger near the leaf base ..... ***M. aëtheadenia***
8b. Leaves distinctly 3-lobed, sometimes 5-lobed or subentire; nectary glands along the leaf margin not prominent, uniform in size ..... ***M. havilandii***



9a. Leaf blade subentire (not lobed), length more than 1.2 times the width ..... ***M. hullettii***
9b. Leaf blade mainly 3- (rarely 5-) lobed, length less than 1.2 times the width 10

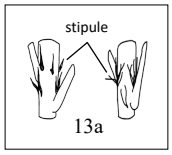


10a. Stems, twigs, and leaves very rough to touch with coarse hairs (i.e., scabrous) ..... ***M. trachyphylla***
10b. Stems, twigs, and leaves glabrous (lacking hairs) or covered with scattered minute hairs ..... ***M. bancana***

11a. Lower leaf surface, twigs, and stems strongly glaucous ..... ***M. lamellata***
11b. Leaves, twigs, and stems not glaucous 12

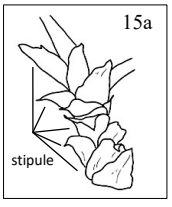
12a. Leaf blade dark shiny green on both surfaces, or dark purplish red on lower surface, margin entire, or sometimes with short lateral cusps; grows in shaded understory or semi-open areas ..... ***M. umbrosa***
12b. Leaf blade bright green on both surfaces, margin entire without cusps; grows in canopy openings ..... ***M. winkleri***

13a. Stipules needle-like or narrowly lanceolate; nectary glands 2, prominent at leaf base; grows in forest understory 14
13b. Stipules broader, shape not as described above; nectary glands many, along leaf margin, or if 2–4, not prominent at leaf base; grows in canopy openings 15

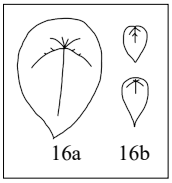


14a. Petioles longer than 5 cm, glabrous or with stiff hairs ca. 2 mm long ..... ***M. praestans***
14b. Petioles shorter than 3 cm, covered with soft, minute hairs ..... ***M. brevipetiolata***

15a. Leaves 3-lobed; stipules longer than 4 cm, upright, densely arranged in a cluster at the shoot apex ..... ***M. gigantea***
15b. Leaves not lobed; stipules shorter than 4 cm, not in a cluster 16



16a. Leaves longer than 20 cm, strongly peltate*[3] with petiole attached ca. 5 cm from margin ..... ***M. recurvata***
16b. Leaves shorter than 15 cm, shallowly peltate with petiole attached up to 1 cm from margin ..... ***M. conifera***



*[3] Petiole attached to the leaf blade away from the margin

Species accounts

Species are arranged in alphabetical order. Local names of each species is given in local languages: Berawan (Ber.), Iban (Ib.), Kayan (Kay.), Kedayan (Ked.), Kenyah (Ken.), Malay (Mal.), and Penan (Pen.). All photos were taken by T. Itioka or U. Shimizu-kaya in Lambir Hills National Park between 1994 and 2024.

1. ***Macaranga aëtheadenia*** Airy Shaw

Local name: Benuah (Mal.), Benuah semut (Mal.)

Observation: Tree to 20 m tall, growing on riversides and hillsides, rather rare. LEAVES 3-lobed with shallowly dissected lobes, conical nectar glands along leaf margin large at the leaf base, lower surface glaucous. STIPULES recurved, dome-shaped with shortly pointed apex, fleshy, crimson red, producing food bodies on lower surface. TWIGS not glaucous, glabrous, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage.

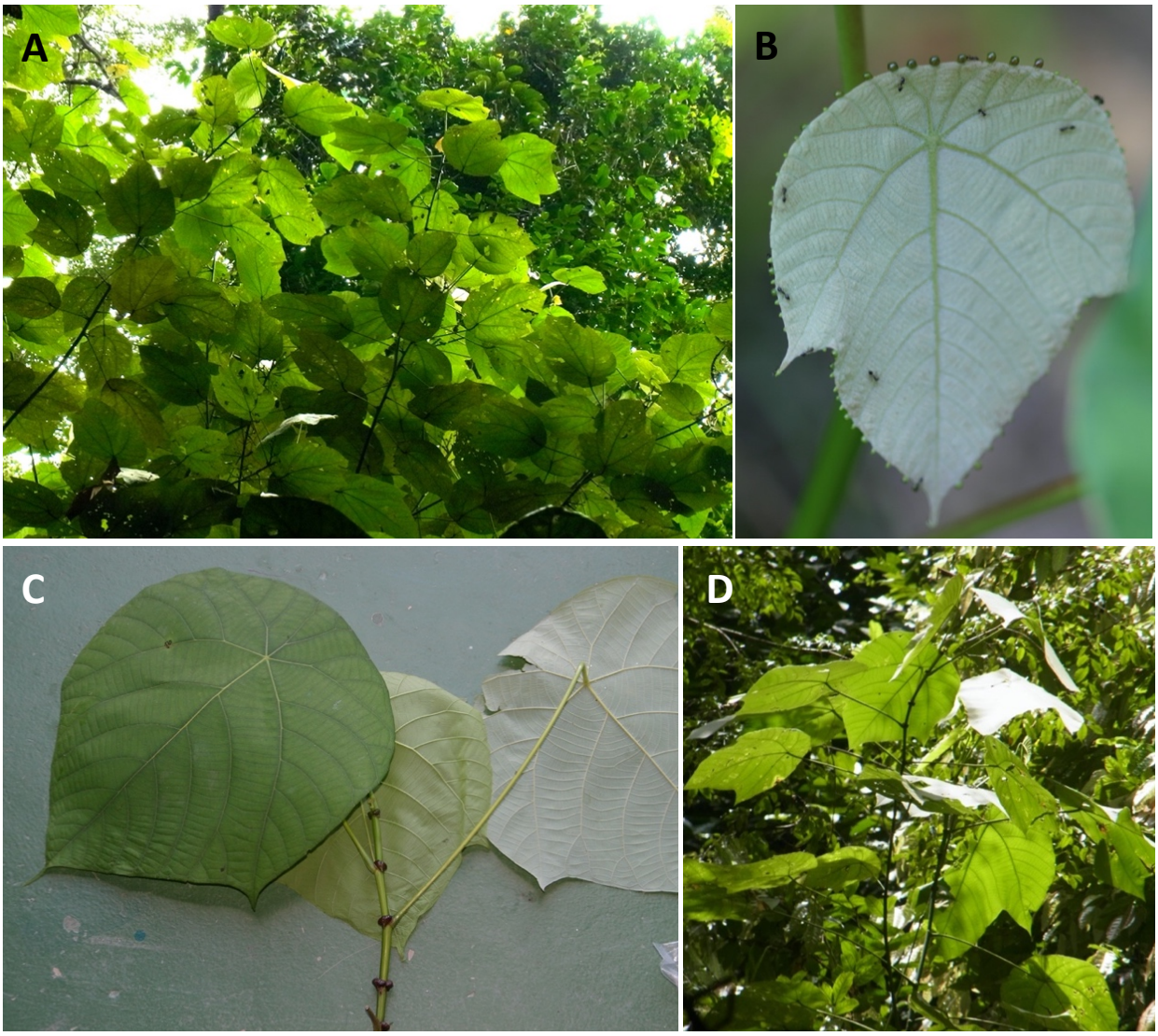


Fig. 1. ***Macaranga aëtheadenia***. **A** young branching tree, **B** young leaf with prominent nectar glands on the margin, **C** leafy twig, **D** branches in a forest gap.

2. ***Macaranga bancana*** (Miq.) Müll.Arg.

Local name: Benuah (Mal.)

Observation: Tree to 20 m tall, common in forest edges and gaps, waterside, and on hillsides. LEAVES 3-lobed, glabrous but with short hairs on veins. STIPULES recurved, dome-shaped with shortly pointed apex, fleshy, reddish, producing food bodies on lower surface. TWIGS glabrous, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.

Notes: *M. bancana* is similar to *M. aëtheadenia* and *M. trachyphylla*, but can be distinguished from those species by the uniform size of nectar glands along the leaf margin, and smooth leaves and petioles.

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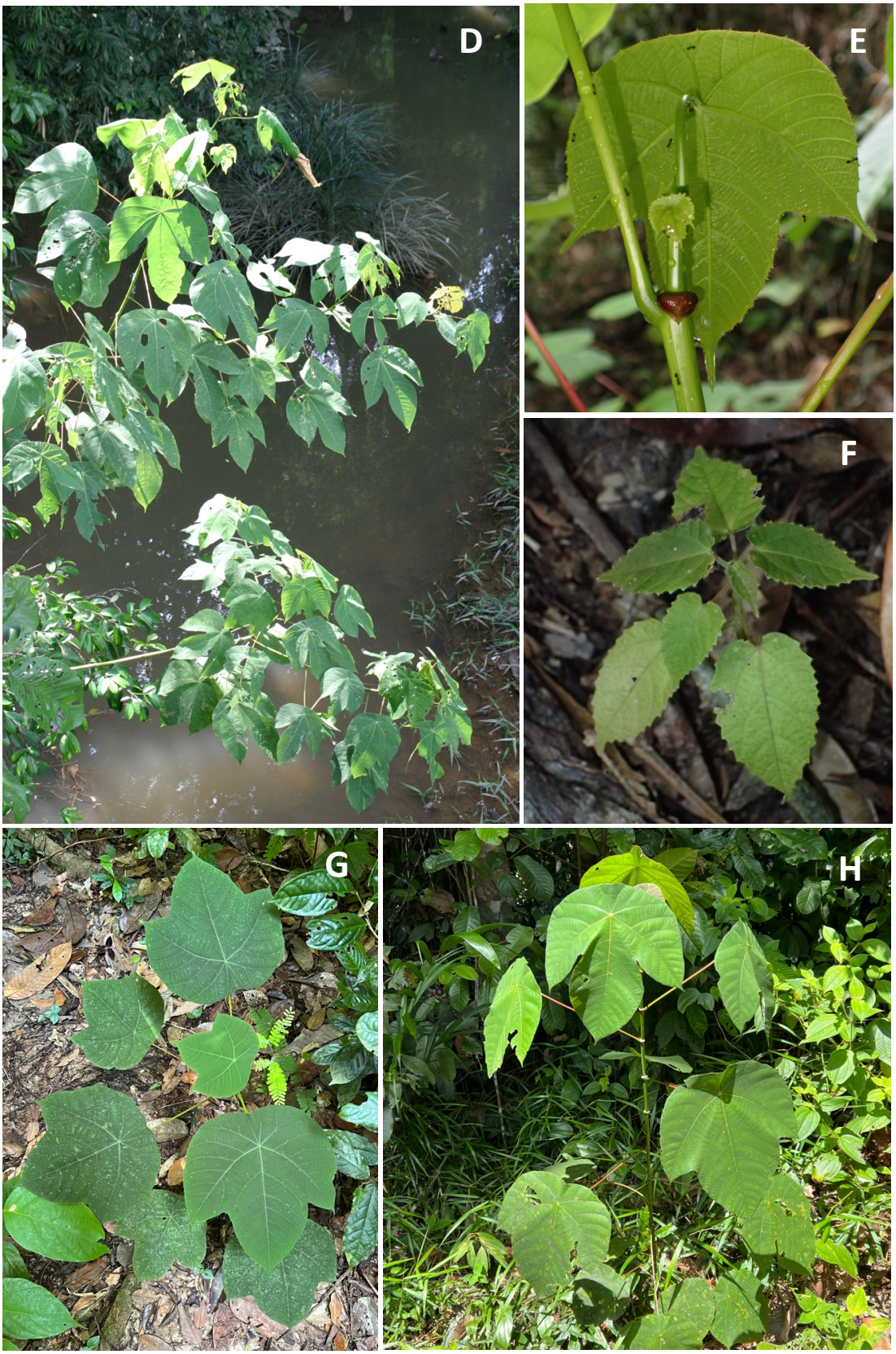

Fig. 2. ***Macaranga bancana***. **A** flowering male tree, **B** staminate inflorescence, **C** infructescence, **D** leafy branches, **E** young leaf attended by symbiotic ants and dark purple, recurved stipule, **F** seedling before ant colonization, **G** sapling on forest floor, **H** young tree at forest edge.

3. ***Macaranga beccariana*** Merr.

Local name: Purang ruman (Ib.), Benuah ruman (Ib./Mal.)

Observation: Tree to 20 m tall, common in forest edges and gaps, and waterside. LEAVES entire when young, soon deeply 3-lobed, lower leaf surface slightly glaucous, producing white food bodies when young. STIPULES spreading, erect, narrowly triangular. TWIGS glaucous, glabrous, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.

Notes: *M. beccariana* is similar to *M. hypoleuca*, but the leaves at a young stage are rather bullate in *M. beccariana* vs. smooth and slightly glossy in *M. hypoleuca*, and the lobes of deeply lobed leaves are usually oblong in *M. beccariana* vs. almost round or broader than long in *M. hypoleuca*.

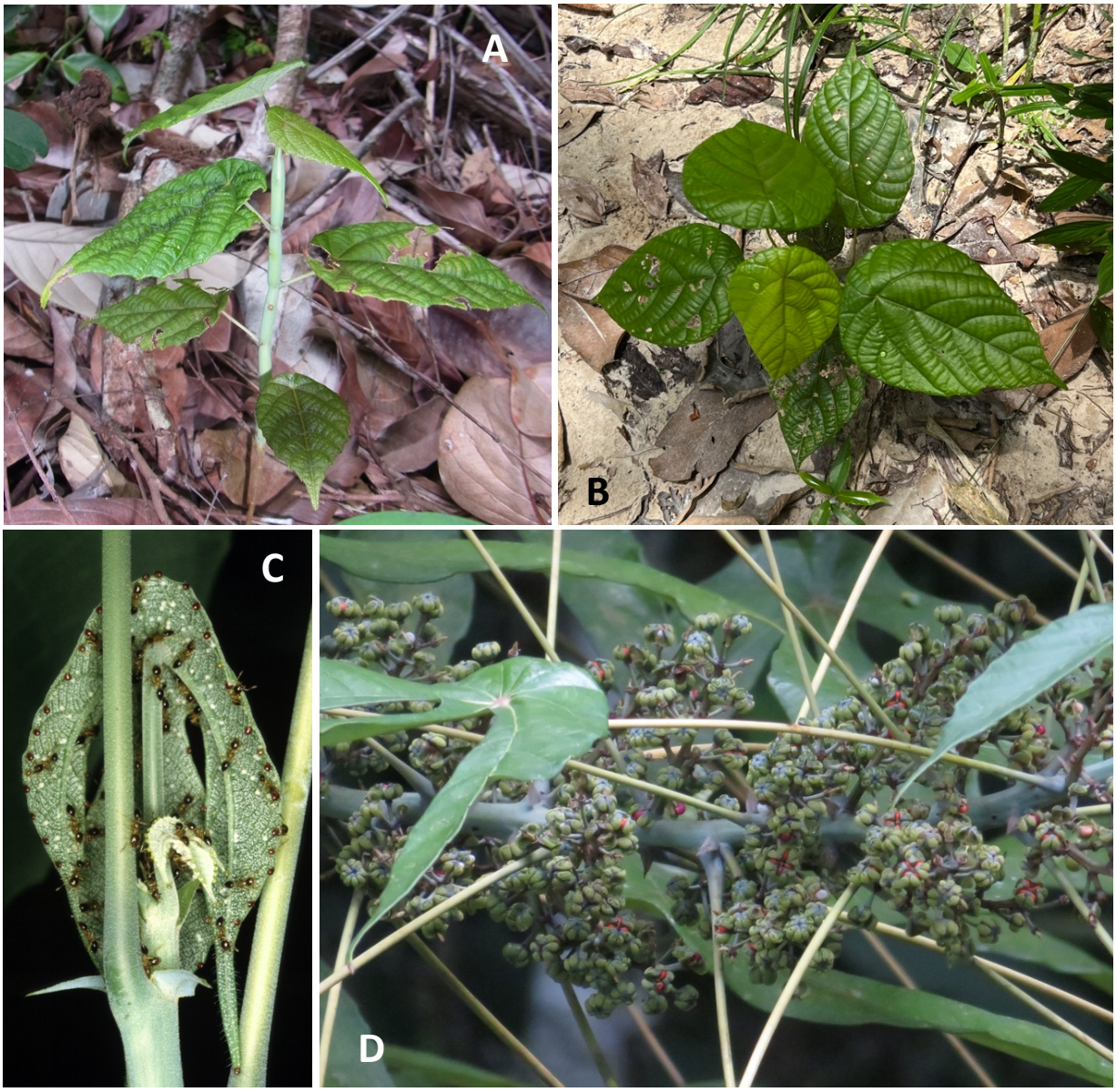

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Fig. 3. ***Macaranga beccariana***. **A** sapling just after start of ant colonization, **B** sapling on riverbank, **C** young leaf producing food bodies and attended by symbiotic ants, **D** infructescence, **E** adult tree, **F** leafy branch, **G** staminate inflorescence.

4. ***Macaranga brevipetiolata*** Airy Shaw

Local name: Entak-empulu (Ib.), Benuah entak-empulu (Ib./Mal.), Chaprie (Kay.)

Observation: Tree to 20 m tall, common on streambanks and in understory of primary forest. LEAVES elliptic to obovate, not lobed, base cordate, with two glands. STIPULES narrowly lanceolate, erect. TWIGS sparsely covered with short hairs, rough to touch, not hollow.

Interaction with ants: Not myrmecophytic, but attracts various ant species by producing extrafloral nectar on the disc-like nectar glands at the leaf base.

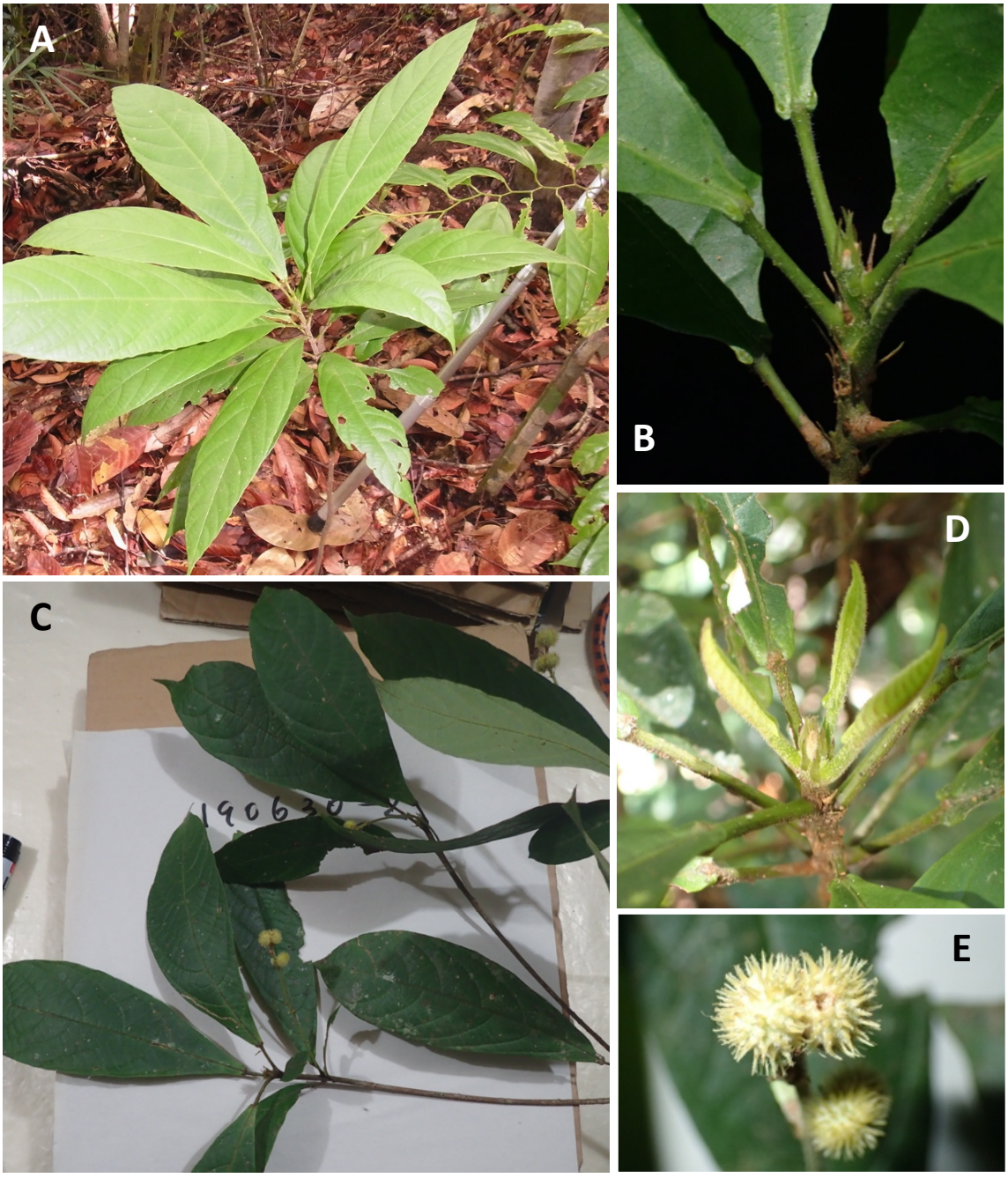

Fig. 4. ***Macaranga brevipetiolata***. **A** sapling on forest floor, **B** portion of shoot apex showing disc-like glands on cordate leaf base and lanceolate stipules, **C** fruiting branches, **D** flushing leaves, **E** fruits.

5. ***Macaranga conifera*** (Rchb.f. & Zoll.) Müll.Arg.

Local name: Engkalumai (Ib.), Benuah engkalumai (Ib./Mal.)

Observation: Tree to 30 m tall, common at edges of primary forest. LEAVES not lobed, lower leaf surface slightly glaucous, smallest among the *Macaranga* species in LHNP. STIPULES ovate, flat, thin, erect. TWIGS not hollow.

Interaction with ants: Not myrmecophytic, but attracts various ant species by producing extrafloral nectar on circular nectar glands near the base of young leaves.

Fig. 5. ***Macaranga conifera***. **A** adult tree at forest edge, **B** young leaf with circular nectar glands near the base, **C** sapling, **D** portion of shoot apex, showing stipules and glaucous lower leaf surface.

6. ***Macaranga gigantea*** (Rchb.f. & Zoll.) Müll.Arg.

Local name: Merkubong (Ib.), Benuah merkubong (Ib./Mal.), Benuah kubong (Ken.), Gela guvong (Kay.), Selbong (Ber.), Kayo gugong (Pen.), Mekubong (Ked.)

Observation: Tree to 30 m tall, common in secondary forest, and at riversides and edges of primary forest. LEAVES up to 60 cm in length, largest among the *Macaranga* species in LHNP, 3-lobed. STIPULES broadly ovate to oblong, erect, envelop stem, persistent in cluster. TWIGS not hollow, hairy when young.

Interaction with ants: Not myrmecophytic, but attracts various ant species by producing extrafloral nectar on bowl-like nectar glands along young leaf margin.

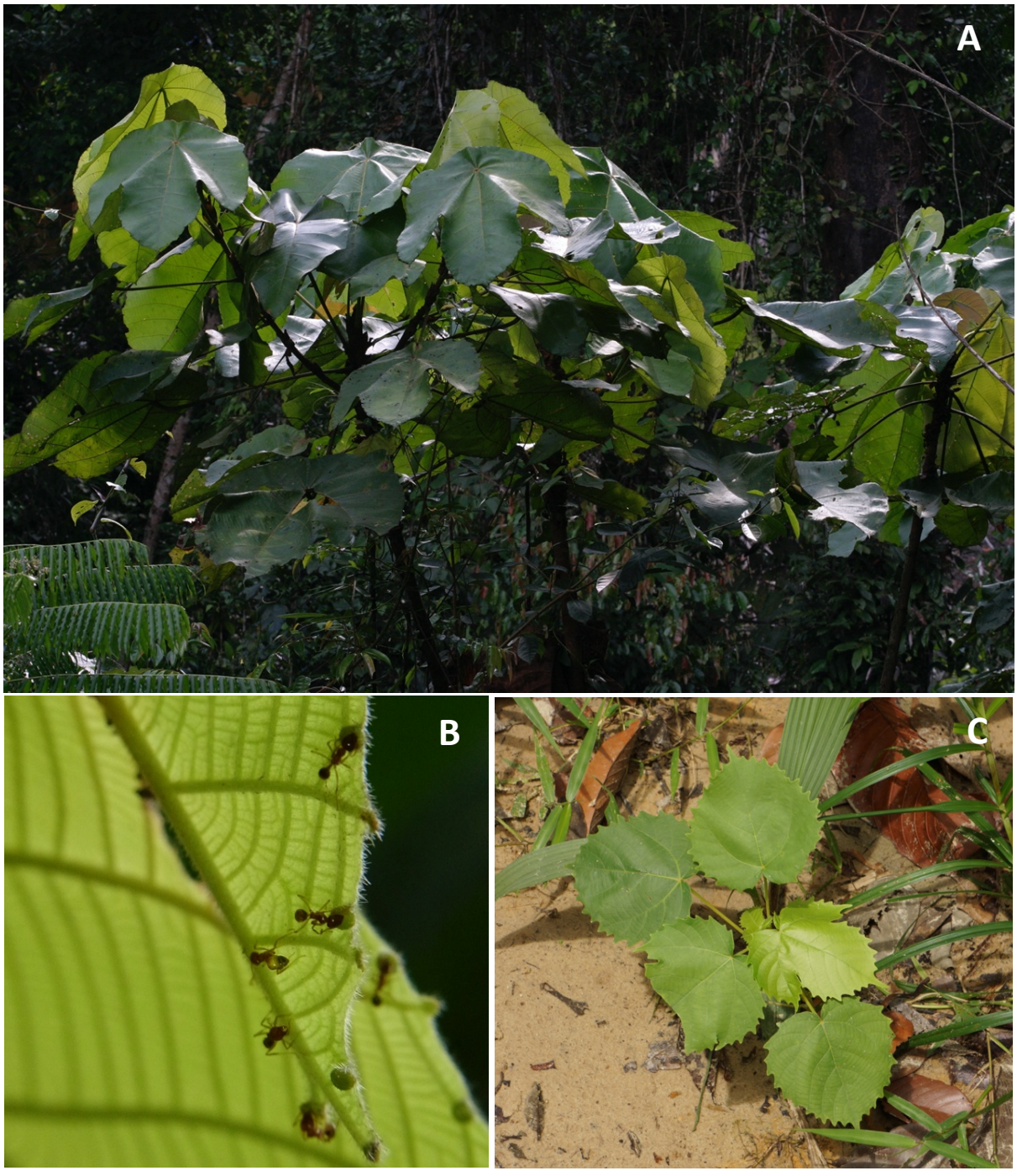

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Fig. 6. ***Macaranga gigantea***. **A** adult tree in forest gap, **B** nectar glands along young leaf margin, attended by ants, **C** seedling on riverbank, **D** staminate inflorescence, **E** stem covered with stipules, **F** young tree at forest edge.

7. ***Macaranga havilandii*** Airy Shaw

Local name: Benuah semut (Mal.), Purang semut (Ib.)

Observation: Small tree to 6 m tall, common at waterside in primary forest, flowering and fruiting starts at 2 m tall. LEAVES not lobed at young stage, usually 3-lobed, rarely 5-lobed, lower surface glaucous, velvety. STIPULES recurved, dome-shaped, fleshy, pale green to reddish, producing food bodies on lower surface. PETIOLES green or reddish, TWIGS glaucous, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.

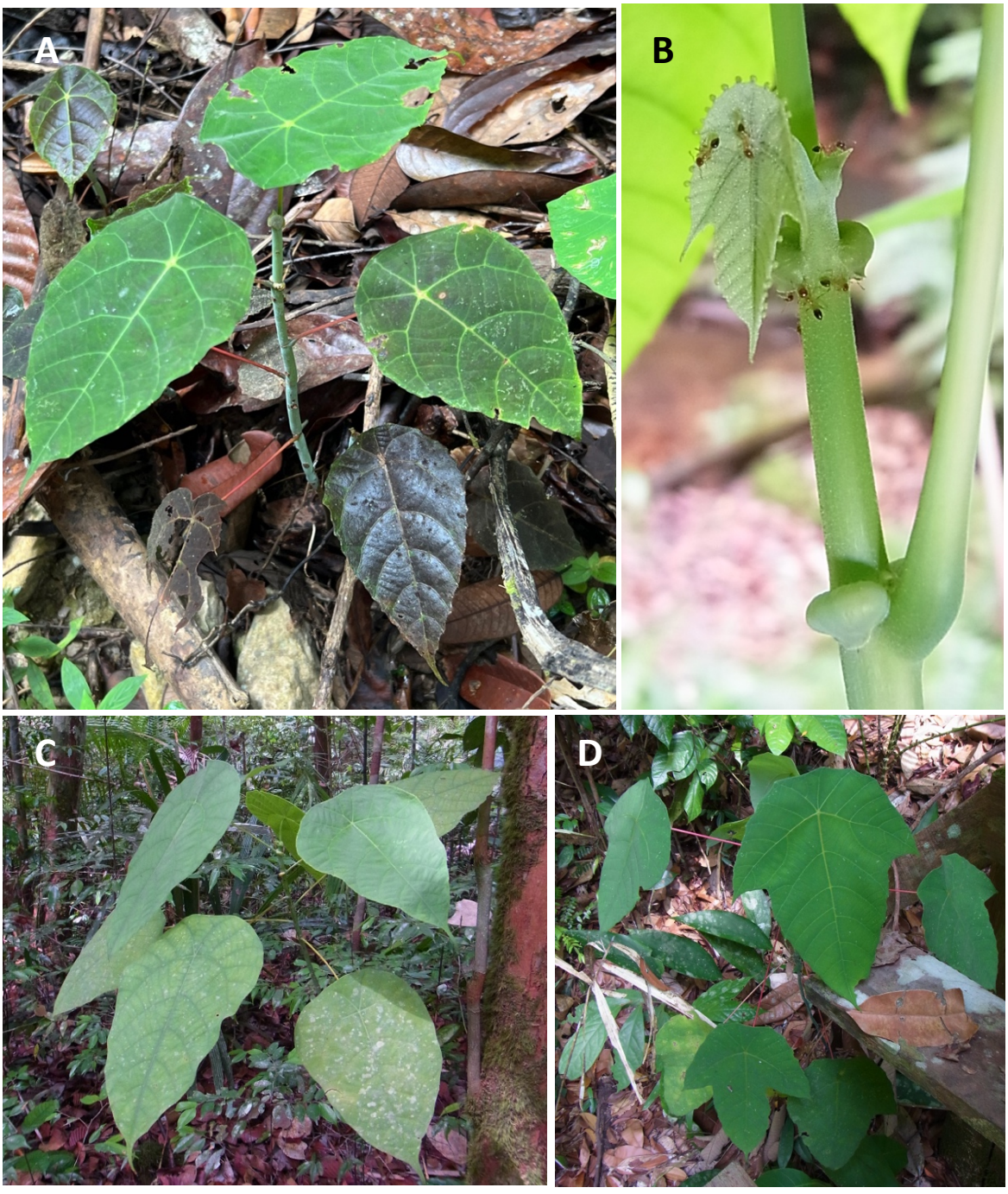

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Fig. 7. ***Macaranga havilandii***. **A** small sapling just after start of ant colonization, **B** nectar glands along margin of young leaf blade, attended by ants, and pale green stipules, **C** sapling with entire leaves, **D** sapling with incised leaves and reddish petioles, **E** fruiting tree, **F** fruits, **G** young tree with 5-lobed and 3-lobed leaves, in a forest gap, **H** trees with shallowly 3-lobed leaves at riverside (lower tree with deeply 3-lobed leaves is *M. beccariana*).

8. ***Macaranga hosei*** King ex Hook.f.

Local name: Benuah (Mal.), Purang lingkau (Ib.)

Observation: Tree to 30 m tall, grows in forest edges and gaps, and waterside in primary forest. LEAVES 3-lobed, hairy when young. STIPULES spreading, rounded, producing food bodies on upper surface. TWIGS smooth, sometimes glaucous, hollow from a tree height of ca. 70 cm.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, >70 cm tall.

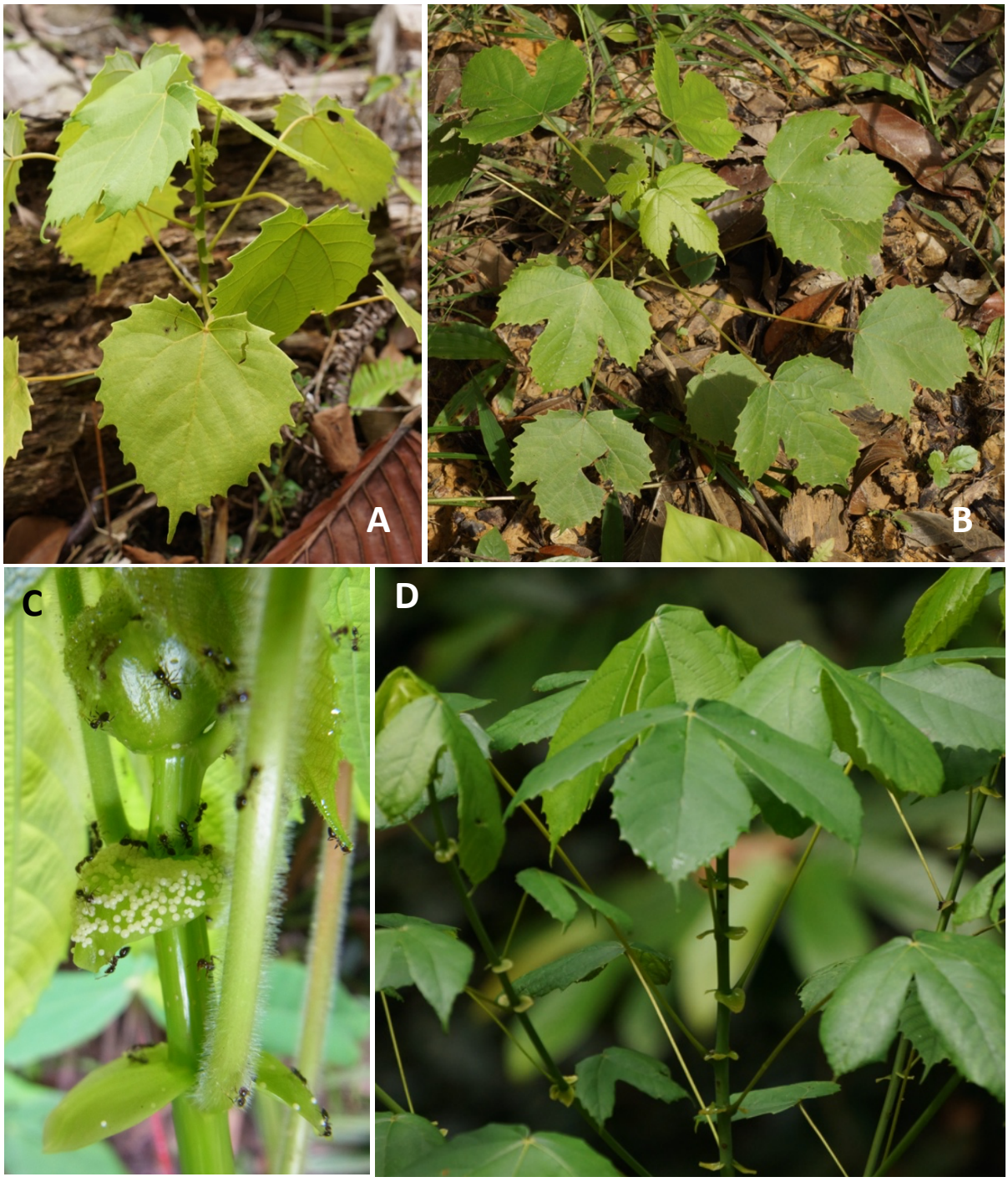

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Fig. 8. ***Macaranga hosei***. **A** small sapling with leaves that are yet to be lobed, **B** sapling with 3-lobed leaves, **C** stipules producing food bodies, attended by ants, **D** leafy twigs of young tree, **E** young tree on riverbank, **F** glaucous stem and rounded stipules, **G** staminate inflorescences.

9. ***Macaranga hullettii*** King ex Hook.f.

Local name: Benuah cincin hijau (Mal.), Nyakubong (Kay.), Benua poran (Kel.)

Observation: Tree to 20 m tall, scattered in forest gaps and waterside in primary forest. LEAVES not lobed, rarely 3-lobed with short cusps. STIPULES broad ovate, apex pointed, recurved, greenish, producing food bodies on lower surface. TWIGS smooth or covered with short hairs, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.

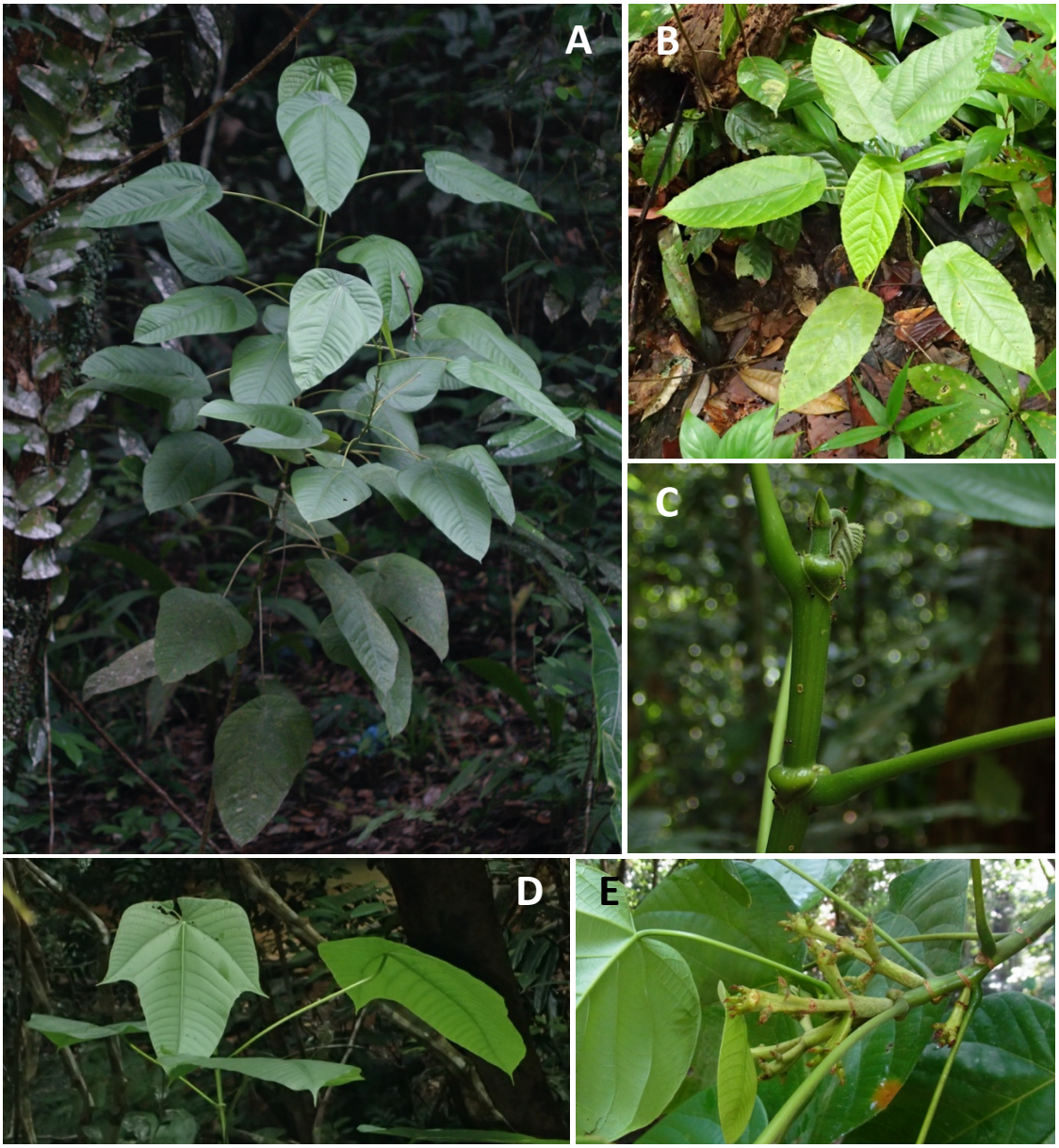

Fig. 9. ***Macaranga hullettii***. **A** young tree, **B** sapling, **C** shoot apex showing stipules and symbiotic ants, **D** shallowly lobed leaves, **E** pistillate inflorescence.

10. ***Macaranga hypoleuca*** (Rchb.f. & Zoll.) Müll.Arg.

Local name: Benuah daun putih (Mal.)

Observation: Tree to 40 m tall, common in forest edges and gaps, and waterside in primary forest. LEAVES 3-lobed, rarely 5-lobed, nectar glands along young leaf margin dark red, lower leaf surface glaucous, producing food bodies when young. STIPULES spreading, erect, oblong-triangular. TWIGS glaucous, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.

Fig. 10. ***Macaranga hypoleuca***. **A** young tree on riverbank, **B** adult tree at forest edge, **C** shoot apex attended by ants, **C** (inset) food bodies on the back of new leaf and red nectar glands along the leaf margin, **D** upper surface of 3-lobed leaf, **E** lower surface of 5-lobed leaf, **F** sapling with shallowly 3-lobed leaves.

11. ***Macaranga lamellata*** Whitmore

Local name: Purang seluwah taji (Ib.), Purang hantu (Ib.), Benuah seluwah (Ib./Mal.)

Observation: Small tree to 15 m tall, grows in forest gaps and understory of primary forest because of its shade tolerance, relatively uncommon. LEAVES not lobed, or rarely shallowly 3-lobed with very short cusps, lower surface mostly glabrous, glaucous, upper surface scattered with silvery hairs. STIPULES horn-like, recurved, producing food bodies on lower surface. TWIGS glaucous, hollow.

Interaction with ants: Hosts ant colony of *Crematogaster* spp. or *Colobopsis macarangae* inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.

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Fig. 11. ***Macaranga lamellata***. **A** sapling before colonization by ants, **B** sapling after colonization by ants inside the stem, **C** shoot apex and young leaf attended by workers of *Colobopsis macarangae*, **D** stipules with workers of *C. macarangae*, **E** food bodies (white granules) produced on the lower surface of the stipule, **F** young tree on forest floor, **G** fruit, top view, **H** fruit, side view, **I** portion of lower leaf surface, showing cordate leaf base; trees at juvenile stage.

12. ***Macaranga praestans*** Airy Shaw

Local name: Entak-empulu (Ib.), Benuah entak-empulu (Ib./Mal.)

Observation: Small tree to 10 m tall, common in understory of primary forest. LEAVES oblong, not lobed, two nectar glands on the base of young leaf. STIPULES needle-like, in bunch. TWIGS not hollow.

Interaction with ants: not myrmecophytic, but attracts various ant species by producing extrafloral nectar on red circular nectar glands at the base of young leaf.

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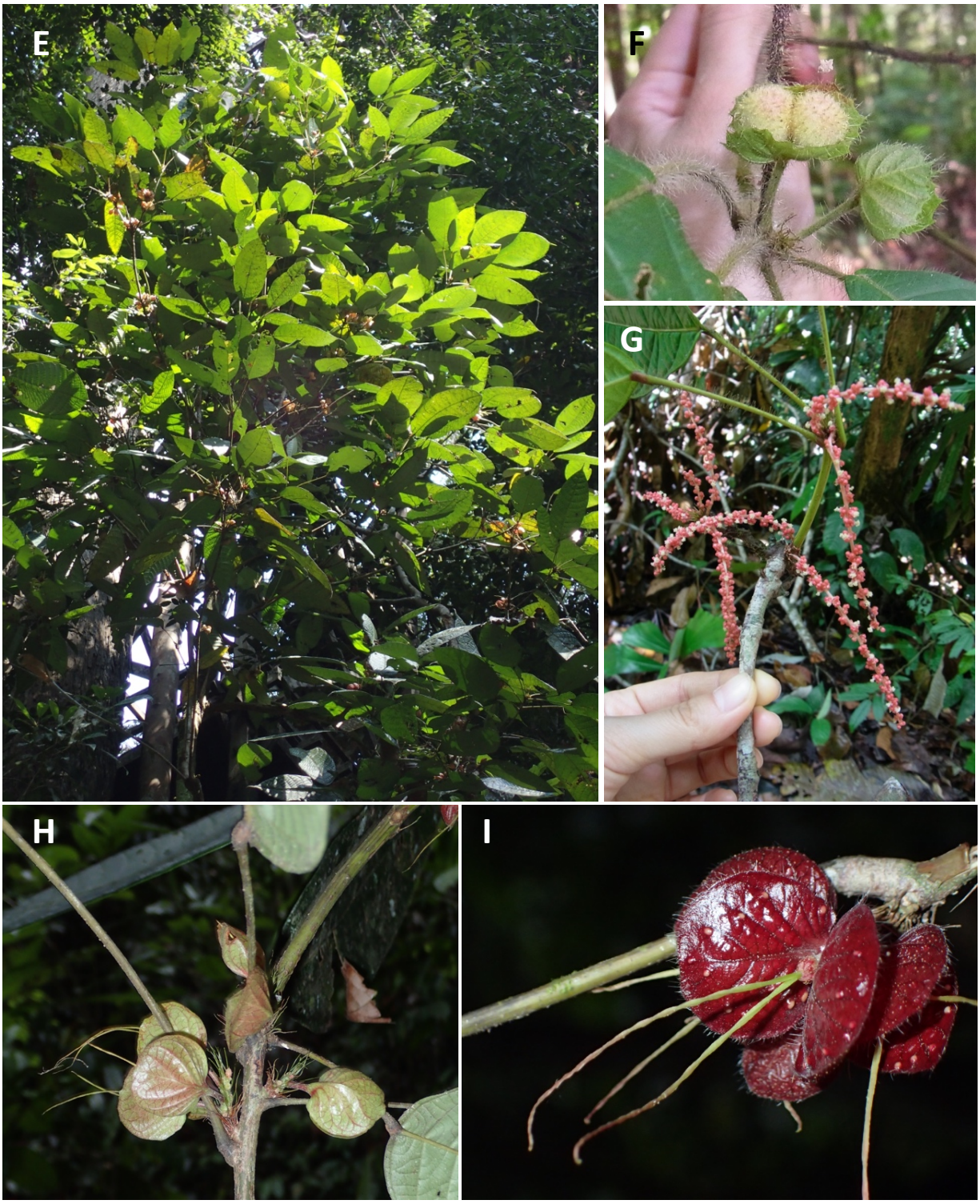


Fig. 12. ***Macaranga praestans***. **A** newly sprouting leaves, with *Crematogaster* ants on nectar glands, **B** new leaves with prominent nectar glands and needle-like stipules, **C** sapling, **D** young leaves, **E** flowering female tree, **F** young fruits, **G** staminate inflorescence, **H**, **I** pistillate inflorescences.

13. ***Macaranga recurvata*** Gage

Local name: Benuah (Mal.)

Observation: Tree to 30 m tall, common in secondary forest and at edges of primary forest. LEAVES ovate, not lobed, deeply peltate, lower surface slightly glaucous. STIPULES ovate to oblong, ascending, lateral margin loosely curved inward. TWIGS smooth, not hollow.

Interaction with ants: not myrmecophytic, but attracts various ant species by producing extrafloral nectar on the nectar glands along young leaf margin.

Notes: *M. recurvata* is similar to *M. lamellata* in having large ovate leaf blades with a glaucous lower surface, but is distinguished by its stipules incurved upwards (vs. recurved downwards in *M. lamellata*), and stems and twigs greenish and solid (vs. glaucous and hollow, with symbiotic ants).

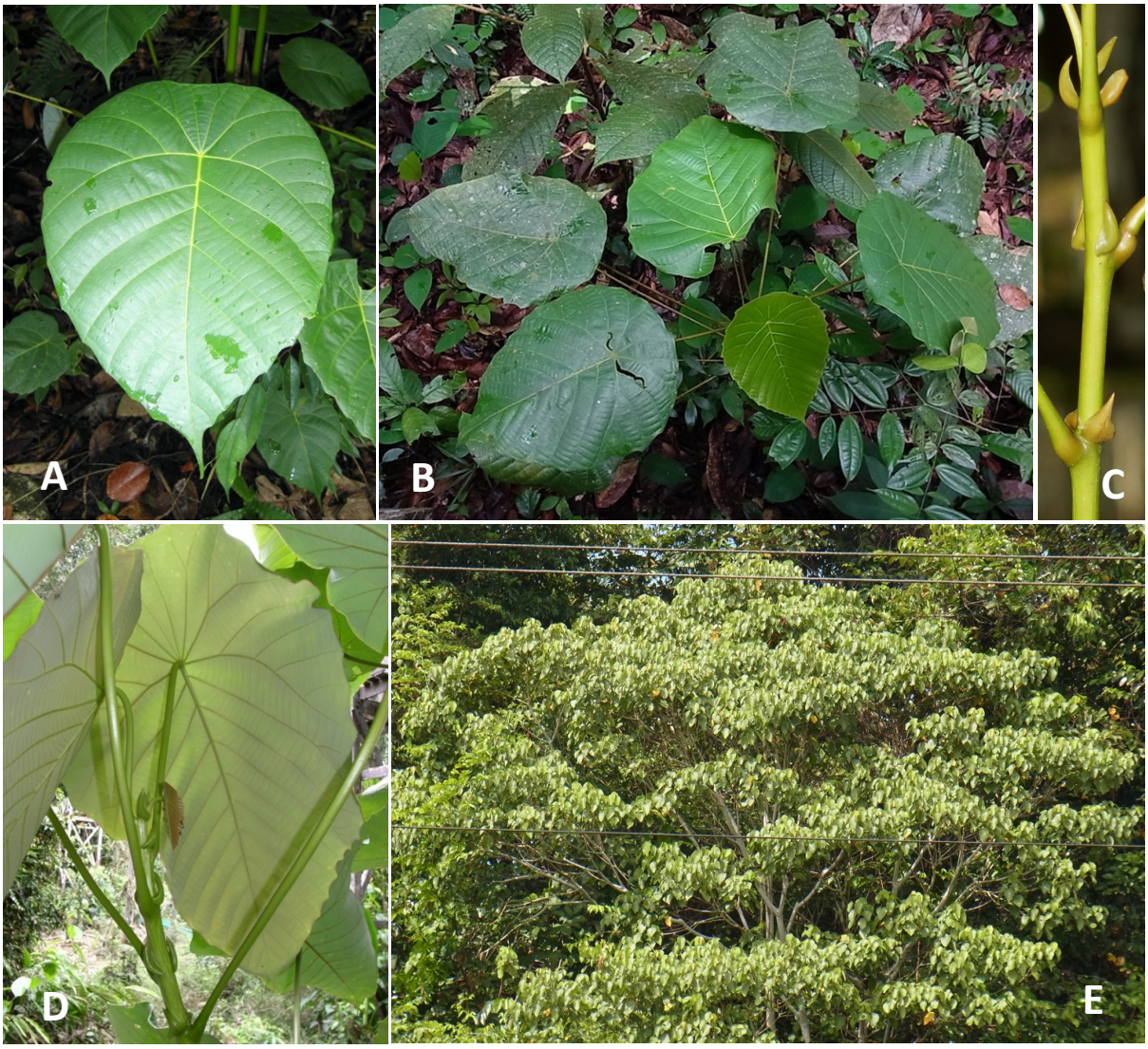


Fig. 13. ***Macaranga recurvata***. **A** upper leaf surface of sapling, **B** sapling on forest floor, **C** stipules, **D** shoot apex showing glaucous lower leaf surface and stipules, **E** mature tree at forest edge (roadside).

14. ***Macaranga rufescens*** S.J.Davies

Local name: Benuah (Mal.)

Observation: Tree to 35 m tall, grows in forest edges and gaps, and waterside in primary forest, relatively uncommon. LEAVES 3-lobed, petioles reddish, hairy when young. STIPULES spreading, rounded, producing food bodies on upper surface. TWIGS covered with minute hairs at young stage, hollow from ca. 70 cm tall.

Interaction with ants: Hosts *Crematogaster* ant colony inside hollow stems and twigs. The symbiosis begins from the sapling stage, >70 cm tall.

Notes: *M. rufescens* is easily confused with *M. hosei* owing to the similar shape of the stipules and leaves, but the species differ in petiole color and the stems of *M. rufescens* are not glaucous.

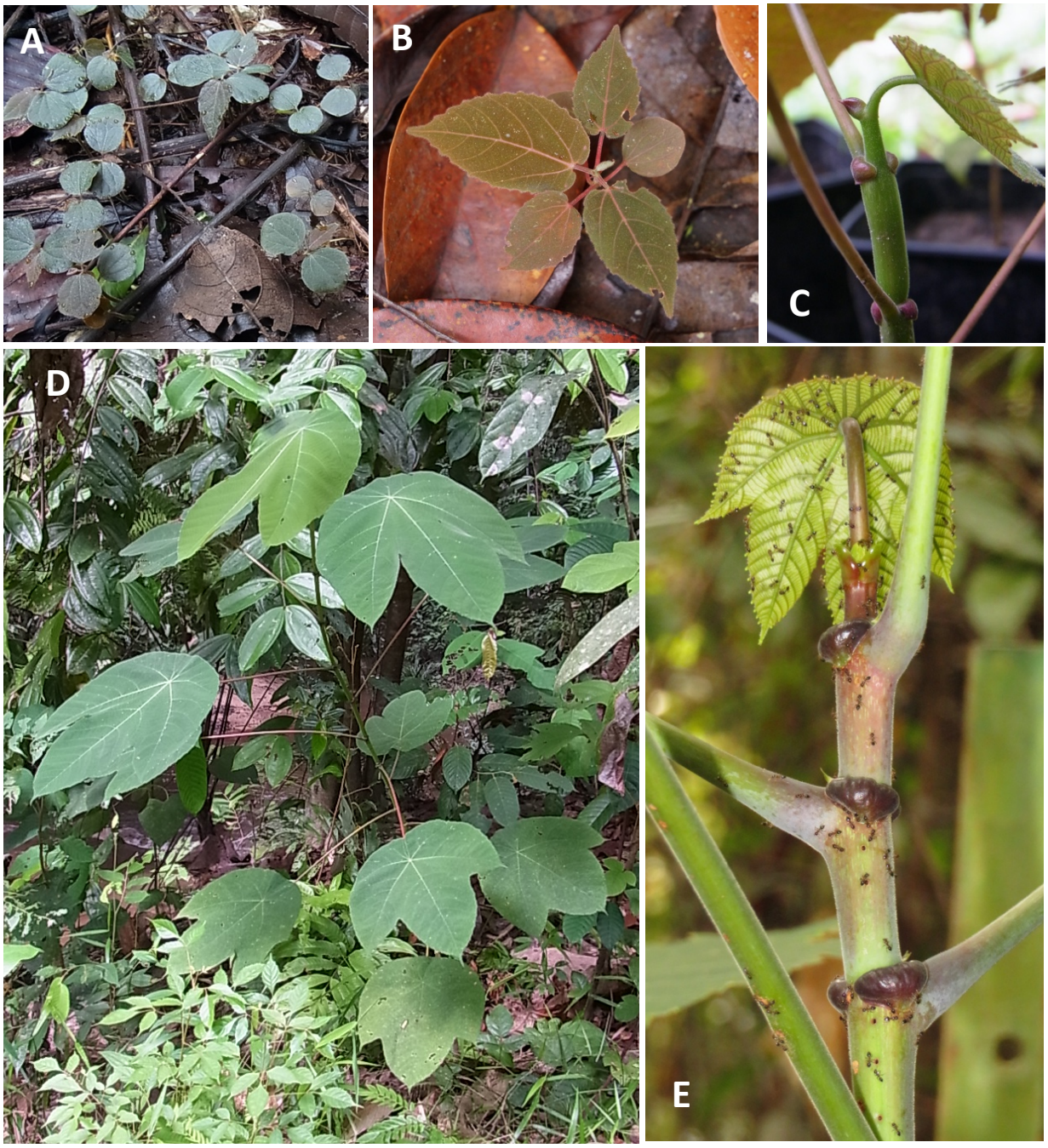
Fig. 14. ***Macaranga rufescens***. **A** adult tree in forest gap, **B** shoot apex of sapling, **C** food bodies and ants on young stipule, **D** sapling, **E** stipules of adult tree, **F** fruiting branches.

15. ***Macaranga trachyphylla*** Airy Shaw

Local name: Benuah cicin merah (Mal.), Benuah taji daun merah (Mal.), Sedaman merah (Ked.)

Observation: Tree to 20 m tall, common in gaps and waterside in primary forest. LEAVES 3-lobed, rarely 5-lobed, both surfaces covered with short hairs, rough to touch. STIPULES recurved, dome-shaped with shortly pointed apex, fleshy, dark red, producing food bodies on lower surface. TWIGS covered with short hairs, rough to touch, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.



(*to be continued*)

Fig. 15. ***Macaranga trachyphylla***. **A, B** seedlings, **C** shoot apex of sapling, **D** young tree, **E** shoot apex of young tree attended by ants, **F** adult tree, **G** staminate inflorescence, **H** infructescence.

16. ***Macaranga umbrosa*** S.J.Davies

Local name: Purang seluwah (Ib.), Purang hantu (Ib.), Benuah seluwah (Ib./Mal.)

Observation: Small tree up to 15 m tall, grows at waterside or in understory of primary forest, relatively uncommon. LEAVES ovate, often margin shallowly crenate with short cusps, not glaucous, deeply peltate, dark purplish red on both surfaces when young, soon dark shiny green but lower surface often remains dark red. STIPULES horn-like, recurved, producing food bodies on lower surface. TWIGS not glaucous, glabrous, hollow, housing ants.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall.

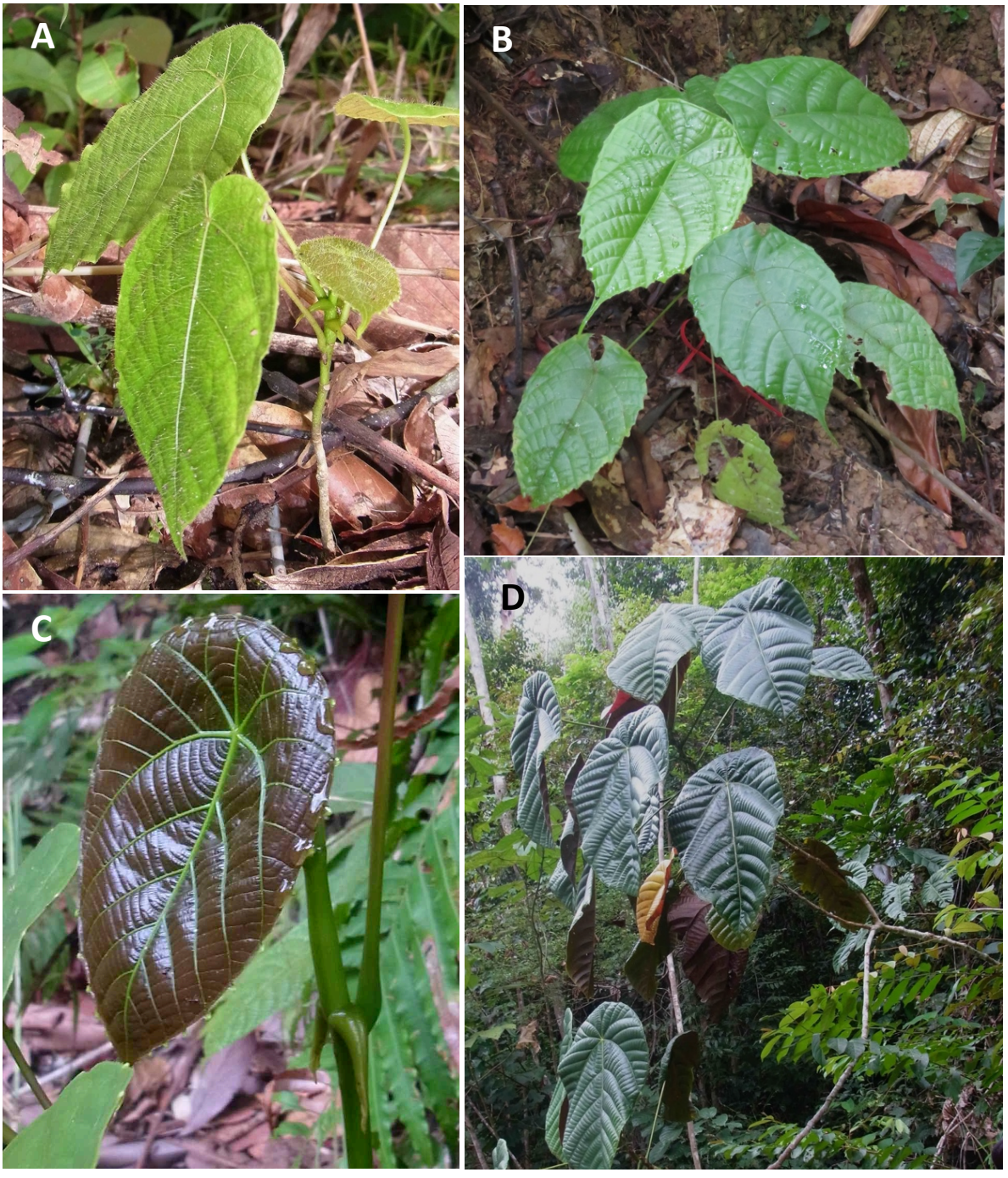


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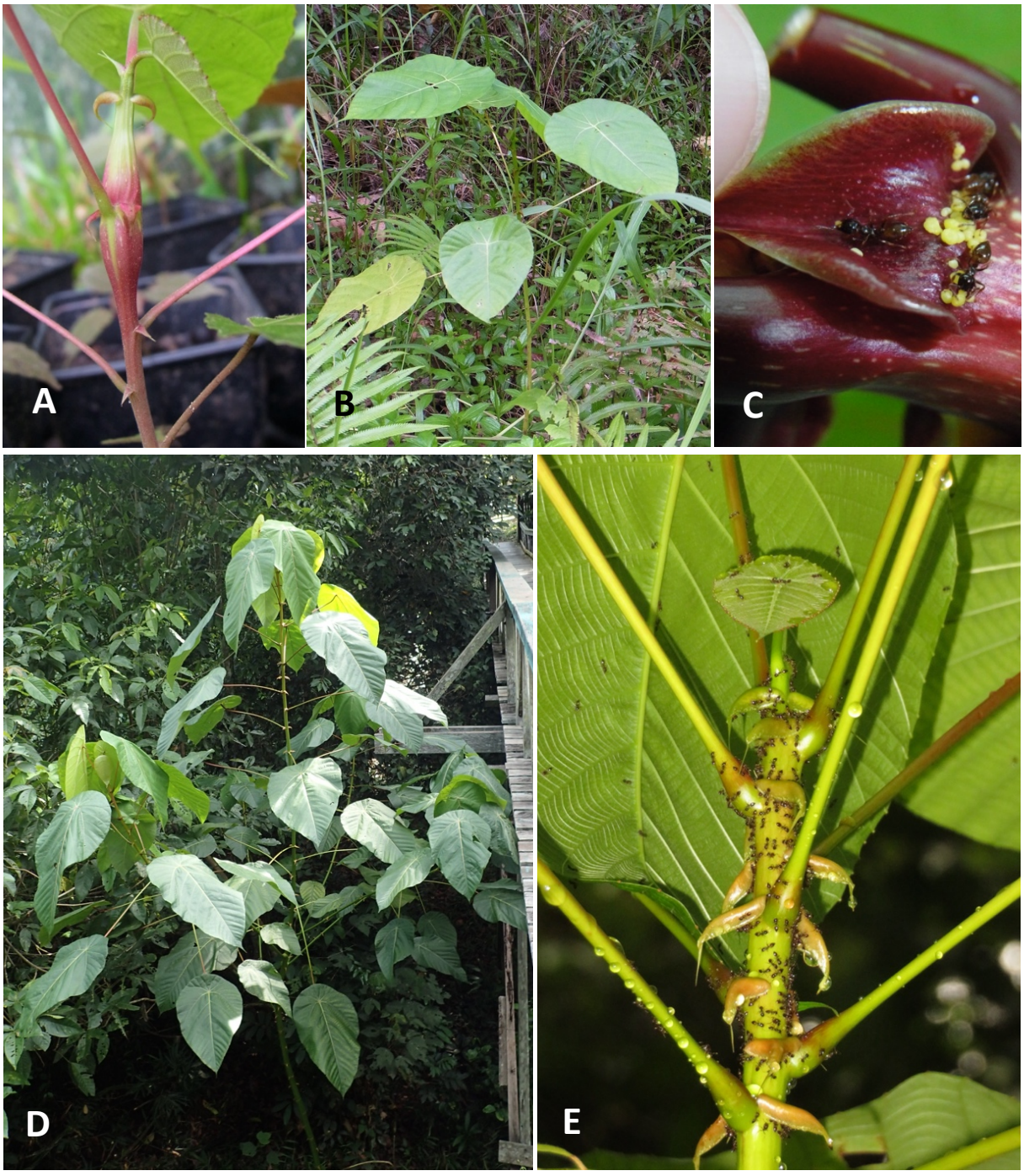
Fig. 16. ***Macaranga umbrosa.*** **A** small sapling before ant colonization, leaves covered with hairs on both surfaces, **B** sapling, **C** young leaf and horn-like stipules, **D** adult tree, **E** fruiting branch, **F** pistillate inflorescences, **G** mature tree, **H** fruiting branch, with dark red lower leaf surface.

17. ***Macaranga winkleri*** Pax & K. Hoffm.

Local name: Purang ruman (Ib.), Purang taji (Ib.), Benuah taji (Mal.)

Observation: Small slender tree to 20 m tall, common at forest edges, riverside, and on hill slopes in primary forest. LEAVES ovate, thin, soft. STIPULES horn-like, recurved, producing yellow food bodies on lower surface. TWIGS green to red, hollow.

Interaction with ants: Hosts *Crematogaster* ant colony inside the hollow stems and twigs. The symbiosis begins from the sapling stage, ca. 10–30 cm tall. The abundance per tree and aggressiveness of the symbiotic ants are exceptional among the myrmecophytic *Macaranga* species distributed in LHNP.



(*to be continued*)

Fig. 17. ***Macaranga winkleri.*** **A** swollen stem nodes of sapling before ant colonization, **B** sapling, **C** food bodies attended by symbiotic *Crematogaster* ants on lower surface of stipule, **D** young tree, **E** stem and stipules attended by the ants, **F** adult tree, **G** red stem, stipules, and petioles, **H** flowering tree at forest edge, **I** staminate inflorescences.

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