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The earth figs (*Ficus*, Moraceae) of Kapit, Sarawak, with five taxa new to science

E.M. Gardner[1,2,3], Y.Y. Ho[1,2], K.K. Pham[1] & Aida Shafreena Ahmad Puad[4]

[1]Case Western Reserve University, Department of Biology, Cleveland, Ohio, USA
elliot.gardner@case.edu
[2]Singapore Botanic Gardens, National Parks Board,
1 Cluny Road, Singapore 259569, Singapore
[3]International Centre for Tropical Botany at The Kampong,
Florida International University, Miami, Florida, USA
[4]i-CATS University College, Kuching, Sarawak, Malaysia

ABSTRACT. Recent collections from Kapit, Sarawak (Borneo), have revealed several new species of stoloniflorous figs (earth figs). These plants bear their figs on ground-level or subterranean stolons rather than on aerial stems and have therefore been under-collected, appearing sterile to those who do not know to look at the ground. This study presents four newly described species (*Ficus aureopilosa* E.M.Gardner, *F. pulchrifolia* E.M.Gardner, *F. rubrostellata* E.M.Gardner, and *F. salangii* E.M.Gardner), one new variety (*F. subterranea* Corner var. *pubescens* E.M.Gardner), and one new name for a variety elevated to species level (*Ficus pseudobeccarii* E.M.Gardner = *F. beccarii* King var. *latifolia* Corner). We also provide a revised key and taxonomic notes for the earth figs of Kapit.

Keywords. Borneo, geocarpy, new species

Introduction

Among the splendid diversity of Malesian figs (*Ficus*, Moraceae) is a group of perhaps a dozen stoloniflorous species within sect. *Sycocarpus* (Berg & Chantarasuwan, 2007). These "earth figs" are mostly endemic to Borneo and produce their figs on rooting stolons up to 10 m long. Many can be found growing along small rivers at any elevation or along forest edges in montane areas such as Mount Kinabalu. The trunks of these treelets usually grow at an oblique angle (the taller straight *Ficus stolonifera* King is an exception), and from their bases arise a few to many branching stolons bearing figs. The figs may be on the ground or buried within it, and therefore these plants are often mistaken as sterile by collectors not familiar with their habit. The result has been under-collection of these fascinating figs (Corner, 1978).

The hill forests of Kapit, Sarawak, are rich in earth figs, especially along rivers. Fieldwork was conducted in 2020, 2022, and 2023, and near Kuching in 2020 and 2022. All specimens collected by the authors have been deposited at SING. We expect a complete set of duplicates to be deposited at SAR (reflected in our specimen citations below) and a partial set to be deposited at the herbarium of the Botanical Research Centre at Semenggoh Arboretum. However, processing and accessioning of

the duplicates remaining in Sarawak remained in progress as this article went to press. During fieldwork, we noted numerous plants that did not match any currently recognised species. This phenomenon was confirmed by review of specimens, revealing morphologically coherent groups with very few ambiguous specimens. Specimens were examined at MO, SING, SAN and SAR. Types and protologues of all Bornean stoloniflorous species were reviewed; in cases where types were not present in the herbaria visited, images were reviewed online (https://plants.jstor.org, https://bioportal.naturalis.nl, and https://idigbio.org). The species boundaries proposed here are also supported by phylogenetic work to be presented in a companion paper (Gardner et al., in prep.).

We present four species new to science, one new variety, and one new name for a variety elevated to species level, along with a revised key and taxonomic notes on the 15 stoloniflorous fig species present in Kapit.

Key to the stoloniflorous figs for Kapit, Sarawak

1a. Twigs hairy; leaf base minutely auriculate ..... 4. *Ficus geocharis*
1b. Twigs hairy or glabrous; leaf base otherwise 2

2a. Upper surface of the leaf (sub)glabrous and smooth, leaf base symmetrical or asymmetrical 3
2b. Upper surface of the leaf hairy, leaf base asymmetrical 7

3a. Cut twig oxidizing purple; figs with only one or two lateral bracts .... 14. *Ficus treubii*
3b. Cut twig not oxidizing purple; figs with numerous lateral bracts 4

4a. Twigs glabrous to minutely whitish puberulous; lamina slightly asymmetrical, apex acuminate; figs pale, glabrous to puberulous, with thickened, poorly defined bracts 5
4b. Twigs stigillose; lamina symmetrical, apex acuminate to caudate; figs red, hairy, with thin appressed triangular bracts 6

5a. Leaves with a bluish cast, not shiny, secondary veins 10–16, base obtuse to cuneate; figs glabrous ..... 12.1 *Ficus subterranea* var. *subterranea*
5b. Leaves green and shiny, secondary veins 17–20, base cordate, sometimes minutely auriculate on the broad side; figs puberulous ..... 8. *Ficus pulchrifolia*

6a. Stipules persistent for 10 nodes or more, indumentum whitish to yellowish; leaves not bullate, generally less than 9 cm wide ..... 2. *Ficus beccarii*
6b. Stipules cauducous, indumentum yellowish to reddish; leaves bullate, generally at least 9 cm wide ..... 7. *Ficus pseudobeccarii*

7a. Broad side of the leaf base generally not overlapping the petiole and twig 8
7b. Broad side of the leaf base auriculate and usually overlapping the petiole and twig 11

8a. Broad side of the leaf base obtuse to cordate (to inconsistently auriculate), hairs on petiole with echinate swollen bases 9
8b. Broad side of the leaf base obtuse to auriculate, hairs on petiole (if present) without echinate swollen bases 10

9a. New leaves deep red on lower surface, the broad side of the leaf base sometimes shallowly auriculate; figs bright red, minutely puberulous, with sparsely scattered minute thin appressed triangular bracts ..... 10. *Ficus salangii*
9b. New leaves green, the broad side of the leaf base never auriculate; figs pink to red, puberulous, with sparsely scattered lumpy thickened bracts ... 11. *Ficus stolonifera*

10a. Leaves with entire margin, secondary veins 10–14 .... 12.2 *Ficus subterranea* var. *pubescens*
10b. Leaves with serrulate margin, secondary veins 5–7 ..... 9. *Ficus rubrostellata*

11a. Leaf base narrowly cuneate on the narrow side; figs pale, (sub)glabrous, with inflexed to subappressed bracts ..... 3. *Ficus bukitrayaensis*
11b. Leaf base acute to cordate on the narrow side; figs red to green, hairy, with patent to appressed bracts 12

12a. Secondary veins 7 or fewer; figs with stiff, patent, curved lateral bracts .... 13. *Ficus uncinata*
12b. Secondary veins 10 or more; figs with flattened or recurved bracts 13

13a. Twigs with shining yellow-gold appressed hairs ..... 1. *Ficus aureopilosa*
13b. Twigs strigose or hirtellous 14

14a. Vegetative parts strigose; indumentum on twigs and petioles all the same length .. .. 5. *Ficus malayana*
14b. Vegetative parts hirtellous; indumentum on twigs and petioles with a secondary underlayer of minute whitish hairs ..... 6. *Ficus megaleia*

Taxonomic treatment

Prefatory note: the species here all belong to a subseries established by Corner (1960) within *Ficus* subgen. *Ficus* sect. *Sycocarpus* Miq. In the more recently and widely-cited *Flora Malesiana* treatment (Berg & Corner, 2005), that section is treated as part of subgen. *Sycomorus* (Gasp.) Miq., but without any combinations involving the series and subseries. Given the need for a comprehensive reassessment of the infrageneric

classification of *Ficus*, we decline to make any piecemeal infrageneric changes here, and we therefore follow the approach of Clement et al. (2020) and provisionally use an informal clade name for the treated group.

"Geocarpicae" clade, based on *Ficus* L. [subgen. *Ficus*] sect. *Sycocarpus* Miq. subsect. *Sycocarpus* Miq. ser. *Tuberculafasciculatae* Sata **subser. *Geocarpicae*** Corner, Gard. Bull. Singapore 18: 41 (1960); Berg & Chantarasuwan, Blumea 52(2): 313 (2007). – TYPE: *Ficus geocarpa* Miq.

Ficus subgen. *Sycomorus* (Gasp.) Miq. sect. *Sycocarpus* Miq. subsect. *Sycocarpus* (Miq.) C.C.Berg, "Group B, Flagelliflorae" p.p., Berg & Corner, Fl. Males., ser. I, 17 (2): 393 (2005).

Shrubs to trees. ***Leaves*** distichous, mostly asymmetrical, often with glands in the axils of one or more secondary veins. ***Figs*** geocarpic on branched rooting stolons arising from the base of the plant, with a few to many lateral bracts; internal hairs absent. ***Pistillate flowers:*** perianth absent or very reduced. ***Staminate flowers*** surrounding the ostiole, with one stamen per flower.

Distribution. A clade of 15 species in Borneo, Sumatra, Peninsular Malaysia, Thailand, and Sulawesi.

Notes. Corner (1960) established this subseries with eight species united by distichous leaves and stoloniferous stems bearing figs (usually) with conspicuous lateral bracts and lacking internal hairs (*Ficus treubii* King, with internal hairs, being the exception). In revising Corner's work for the *Flora Malesiana* (Berg & Corner, 2005), Berg recognised informal groupings within subsect. *Sycocarpus* instead of series and subseries. The species of Corner's subser. *Geocarpicae*, excluding *Ficus treubii*, were treated in Group B, "Flagelliflorae", mostly in subgroup B1, the "*Ficus stolonifera*-group". *Ficus treubii*, with internal hairs, was left unplaced at the end of the subsection. Berg & Chantarasuwan (2007), in preparation for the *Flora of Thailand* (Berg et al., 2011), revised some of these species, most notably breaking up the heterogeneous *Ficus uncinata* (King) Becc., resulting in two new species, the Borneo endemic *F. bukitrayaensis* C.C.Berg and the widespread and heterogeneous *F. malayana* C.C.Berg & Chantaras. Recent phylogenetic work by Gardner et al. (2023) recovered a clade consisting of all sampled Bornean stoloniflorous figs (six species) excluding *Ficus treubii*. Following the clade-naming convention of Clement et al. (2020), we can refer to this as the "Geocarpicae" clade.

1. *Ficus aureopilosa* E.M.Gardner, **sp. nov.**
Differs from *Ficus megaleia* Corner in the golden long appressed indumentum on the stipule and young twig and the entire margin of the leaf. – TYPE: Malaysia, Sarawak, Kapit Division, Kapit District, Sungai Balang, 12 July 2023, *E. Gardner et al. 1264* (holotype SING [SING0397914]; isotype SAR). (Figs 1, 2)

Fig. 1. *Ficus aureopilosa* E.M.Gardner. **A.** Trunk and bark slash. **B.** Leaf habit. **C.** Twig and stipule, showing golden indumentum. **D.** Leaf upper surface. **E.** Leaf lower surface. **F.** Young fig. **G, H.** Mature figs. (Photos: E.M. Gardner)

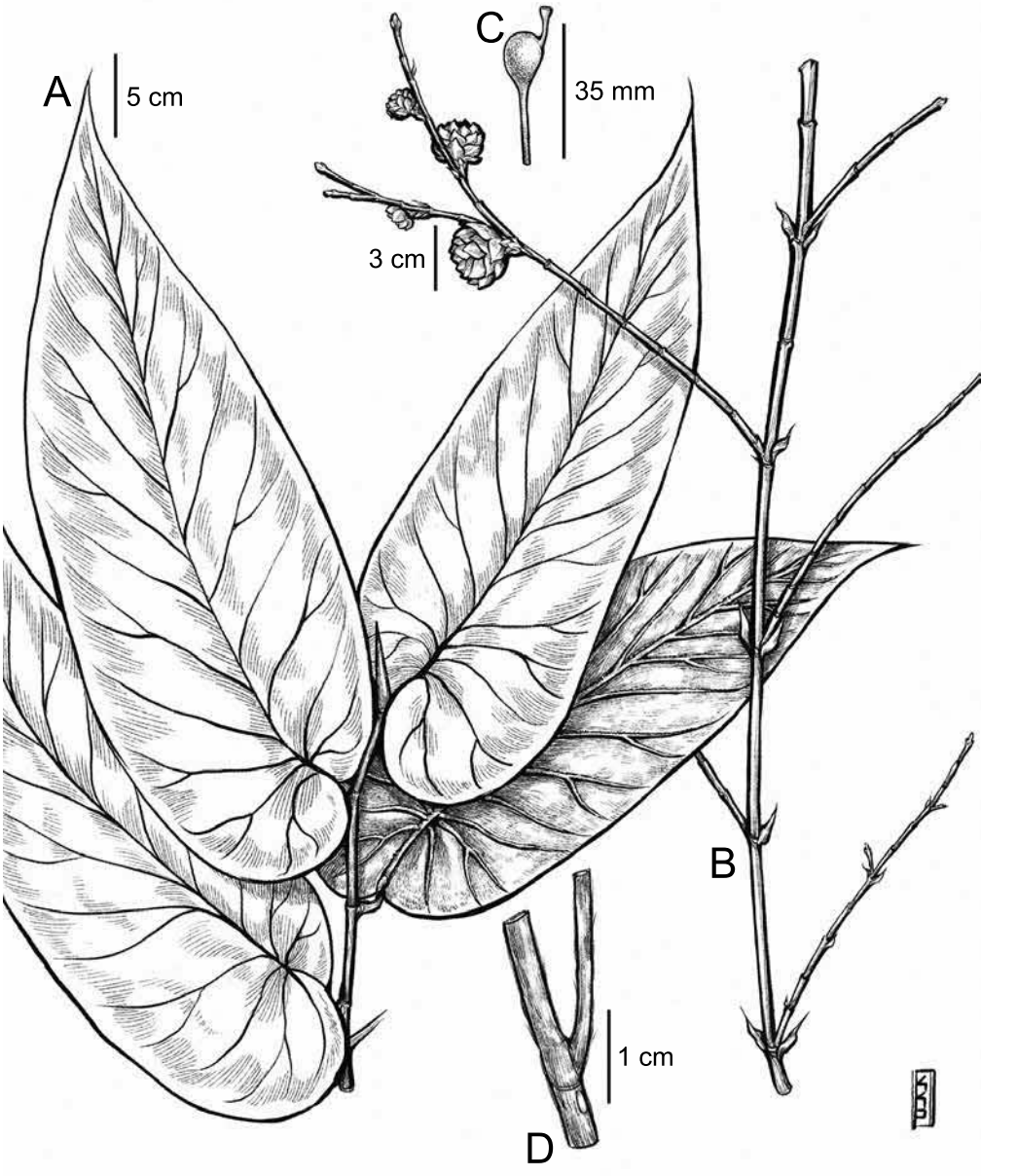

Fig. 2. *Ficus aureopilosa* E.M.Gardner. **A.** Leafy shoot. **B.** Stolon with young figs. **C.** Short-styled flower. **D.** Node with axillary bud. Drawn by K. Pham.

Trees to at least 7 m tall; bark pale brown, with small scattered lenticels; latex white. ***Leafy twigs*** 3.5–5 mm wide, densely yellow-gold appressed pubescent, subappressed to subpatent pubescent at the nodes; a single waxy gland usually present just below the node (but sometimes obscured by the indumentum on specimens); internodes solid. ***Stipules*** amplexicaul, 4–7 cm long, caducous, densely yellow-gold (sub)appressed pubescent, with a notable golden sheen when fresh, caducous. ***Leaves*** distichous, lamina elliptical-oblong and slightly inequilateral, 28–52 × 11–21 cm, asymmetric, apex acuminate to subcaudate, acumen up to 5 cm long, base strongly inequilateral, the narrow side rounded to cordate, the broad side cordate to auriculate, often overlapping the petiole and the narrow side, margin entire; upper surface minutely and rather densely whitish subappressed hispidulous and also thinly yellowish subappressed hirtellous, scabrid to the touch (in one direction), densely yellow-gold subappressed pubescent on the midrib and secondary veins; lower surface rather densely (to sparsely) pale yellow-gold hirtellous, the hairs denser and (sub)appressed on the midrib and secondary veins; secondary veins 15–18 pairs, rather strongly ascending in the upper half, many of them furcate before reaching the margin, especially on the broad side, with waxy glands present in the furcations; petiole 1–2 cm long, densely yellow-gold pubescent (sometimes also with whitish or brownish hairs), the hairs subappressed to more or less patent, soft to the touch; young leaves bronze with a notable golden sheen when very small. ***Figs*** on branched rooting stolons up to at least 8 m long arising from the base of the tree, internodes up to at least 6 cm long, shorter on the lateral branches; stipules c. 7 mm long, persistent; peduncle 1–2 mm long, yellow-gold pubescent; basal bracts at least 3; receptacle subglobose and somewhat compressed, c. 3 cm wide at maturity when dry, densely rusty-coloured (sub)appressed pubescent; lateral bracts numerous, triangular, to 5 mm long, rather thin and more or less covering the surface of the receptacle indumentum as on the receptacle, apex flattened; ostiole sunken to flat, covered by overlapping apical bracts. ***Long-styled flowers*** not seen. ***Short-styled flowers*** without perianth; styles glabrous, stigmas distinctly funnel-shaped.

Distribution and habitat. Borneo (Sarawak) in wet secondary forest along rivers from 100 m up to at least 450 m in elevation.

Etymology. The epithet refers to the golden indumentum on the twigs and stipules.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit Division, Sungai Balang, 12 Jul. 2023, *Gardner et al. 1259* (SAR, SING [SING0397873]), *1281* (SAR, SING [SING0397876]); Kapit Division, Bukit Patong, Sungai Talong, 19 Jul. 2023, *Gardner et al. 1399* (SAR, SING [SING0397875]), *1406* (SAR, SING [SING0397874]); Kapit Division, Sungai Senantang, 18 Jul. 2023, *Gardner et al. 1368* (SAR, SING [SING0397872]).

Notes. The indumentum is thick and velvety on the lower surface of the leaf in all specimens examined except one, *Gardner et al. 1259*, in which it is scabridulous.

2. *Ficus beccarii* King, Ann. Roy. Bot. Gard. (Calcutta) 1: 102, t. 130 (1888); Merrill, Bibliogr. Enum. Born. Pl.: 221 (1921); Corner, J. Malayan Branch Roy. Asiat. Soc. 11: 20 (1933); Corner, Wayside Trees Malaya, ed. 1, 1: 280 (1940); Corner, Gard. Bull. Singapore 18: 59 (1960); Corner, Gard. Bull. Singapore 21: 92 (1965); Kochummen, Tree Fl. Malaya 3: 141 (1978); Kochummen, Tree Fl. Sabah & Sarawak 3: 261 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 398 (2005); Berg & Chantarasuwan, Blumea 52(2): 314 (2007). – TYPE: Malaysia, Sarawak, Kuching Division, Mount Matang, December 1866, *Beccari P.B. 2900* (lectotype FI [FI013357 – a single specimen over two sheets], designated by Kochummen, Tree Fl. Sabah & Sarawak 3: 261 (2000); isolectotype P [P06879591]). (Fig. 3)

Shrub or treelet up to 5(–7) m tall. ***Leafy twigs*** 1.5–3 mm thick, yellowish strigose, with nodal waxy glands, internodes hollow, periderm persistent. ***Stipules*** 2–5 cm long, caudate and margin often inflexed, yellowish strigose to subsericeous, persistent for ten nodes or more. ***Leaves*** distichous; lamina lanceolate to oblong, (7–)15–35(–40) × (1.5–)3–9 cm, nearly symmetrical, chartaceous, apex caudate (the apex of the acumen often filiform), base obtuse to nearly rounded, margin entire; upper surface glabrous (also the midrib), smooth, not bullate; lower surface yellowish strigose to strigillose on the veins, smooth, cystoliths only beneath; lateral veins 5–13 pairs (in the lower part more closely together than more upwards), none of them branched or furcate away from the margin, tertiary venation scalariform, in the upper part of the lamina running perpendicular to the midrib; waxy glands in the axils of the upper lateral veins; petiole 0.5–1.2 cm long, yellowish strig(ill)ose, the epidermis persistent. ***Figs*** flagelliflorous on up to at least 6 m long slender branching stolons with up to 10 cm long internodes; subsessile or with a peduncle up to 0.5 cm long; basal bracts 3 and verticillate or up to 6 and subverticillate, 3–4 mm long; receptacle subglobose, 1–2 cm diam. when dry, brown hirtellous, with thin ± appressed lateral bracts (inflexed but not appressed when immature), reddish at maturity, apex convex to flat; ostiole 3–4 mm diam., surrounded by a rosette of apical bracts. ***Short- and long-styled flowers*** without perianth; styles glabrous.

Distribution and habitat. Thailand, Malay Peninsula, and Borneo, in primary and disturbed forest from sea level up to 1,300(–2,000) m in elevation.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit Division, Sungai Balang, 9 Aug. 2022, *Gardner et al. 1140* (SAR, SING [SING0397930]); ibidem, 12 Jul. 2023, *Gardner et al. 1280* (SAR, SING [SING0397750]); Kapit Division, Sg. Pinih, 14 Jul. 2023, *Gardner et al. 1308* (SAR, SING [SING0397747]); Kapit Division, Ulu Sg. Bena, 16 Jul. 2023, *Gardner et al. 1331* (SAR, SING [SING0397749]); Kapit Division, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1353* (SAR, SING [SING0397748]), *1360* (SAR, SING [SING0397751]); Kapit Division, Sg. Senantang, 18 Jul. 2023, *Gardner et al. 1383* (SAR, SING [SING0397746]); Kuching Division, Matang, Indian Temple Trail, 17 Feb. 2020, *Gardner et al. 889* (SAR, SING [SING0401874]).

Fig 3. *Ficus beccarii* King. **A.** Habit and riverside habitat. **B.** Leaf upper surface. **C.** Leaf lower surface. **D.** Trunk and bark slash. **E.** Persistent stipules. **F.** Stolon, with trunk several metres away. **G.** Young fig. **H.** Young and mature figs. (Photos: E.M. Gardner)

Notes. A closer examination of morphology as well as phylogenetic evidence (Gardner et al., in prep.) compels the conclusion that *Ficus beccarii* var. *latifolia* Corner, recognised as distinct by Corner (1960) and informally by Berg & Corner (2005), must be raised to species level, restricting *Ficus beccarii* to the type variety. The description above is amended from that of Berg & Corner (2005) to reflect this narrower species concept. *Ficus beccarii* can be distinguished on sight from *F. pseudobeccarii* E.M.Gardner (=*Ficus beccarii* var. *latifolia*) by the narrower (less than 5 cm) leaves, persistent stipules, flat (as opposed to bullate) lamina, and the often filiform caudate apex of the leaf (which may be subcaudate in *F. pseudobeccarii* but not filiform). The indumentum is pale yellow as opposed to reddish in *Ficus pseudobeccarii*.

While we have not yet encountered specimens with intermediate characters between *Ficus beccarii* and *Ficus pseudobeccarii*, the former may hybridise with its close ally *Ficus malayana* C.C.Berg & Chantaras. Two collections from Sg. Seranau, *Gardner et al. 871* and *1192* (SAR, SING) have leaves matching *Ficus beccarii* but figs that more closely resemble those of *F. malayana*, except for their red colour. These two species are the most widespread of the Geocarpicae clade, ranging from Peninsular Thailand to Borneo.

3. *Ficus bukitrayaensis* C.C.Berg, Blumea 52(2): 320 (2007). – TYPE: Indonesia, Kalimantan, Bukit Raya, Batu Badinding, KCT, 50 m, 8 February 1983, *Veldkamp 8601* (holotype L [L0734892]; isotypes BO n.v., L [L0734891], SAR). (Fig. 4)

Ficus uncinata (King) Becc. var. *parva* Corner, Gard. Bull. Singapore 18: 59 (1960). – TYPE: Brunei, Andulau Forest, February 1959, *Corner s.n.* (holotype CGE n.v.; isotypes K n.v., SAR [2 duplicates], US [US00955729]).

Distribution and habitat. Borneo (Sabah, Sarawak, Kalimantan) in lowland and hill forest from 100 m to 500 m in elevation.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Bukit Patong, Sg. Talong, 19 Jul. 2023, *Gardner et al. 1408* (SAR, SING [SING0389199]); Kapit District, Sg. Sebatu, near Rh. Nading Nanga Senantang, 14 Feb. 2020, *Gardner et al. 882* (SAR, SING [SING0401882]), *884* (SAR, SING [SING0401884]); Kapit District, Ulu Sg. Bena, 16 Jul. 2023, *Gardner et al. 1327* (SAR, SING [SING0389197]), *1345* (SAR, SING [SING0389196]); Kapit District, Sg. Senantang, 18 Jul. 2023, *Gardner et al. 1378* (SAR, SING [SING0389194]), *1392* (SAR, SING [SING0389198]); Nanga Merit, Sg. Raya, 13 Jul. 2023, *Gardner et al. 1290* (SAR, SING [SING0389195]).

Notes. The description in Berg & Chantarasuwan (2007) includes some material here assigned to *Ficus rubrostellata* E.M.Gardner and must be revised. Stipules rarely persist past the second node. The leaves have 8–12(–14) lateral veins, and the broad side of the base usually covers the petiole at least partially. The lateral bracts on the figs are always (sub)appressed and never reflexed.

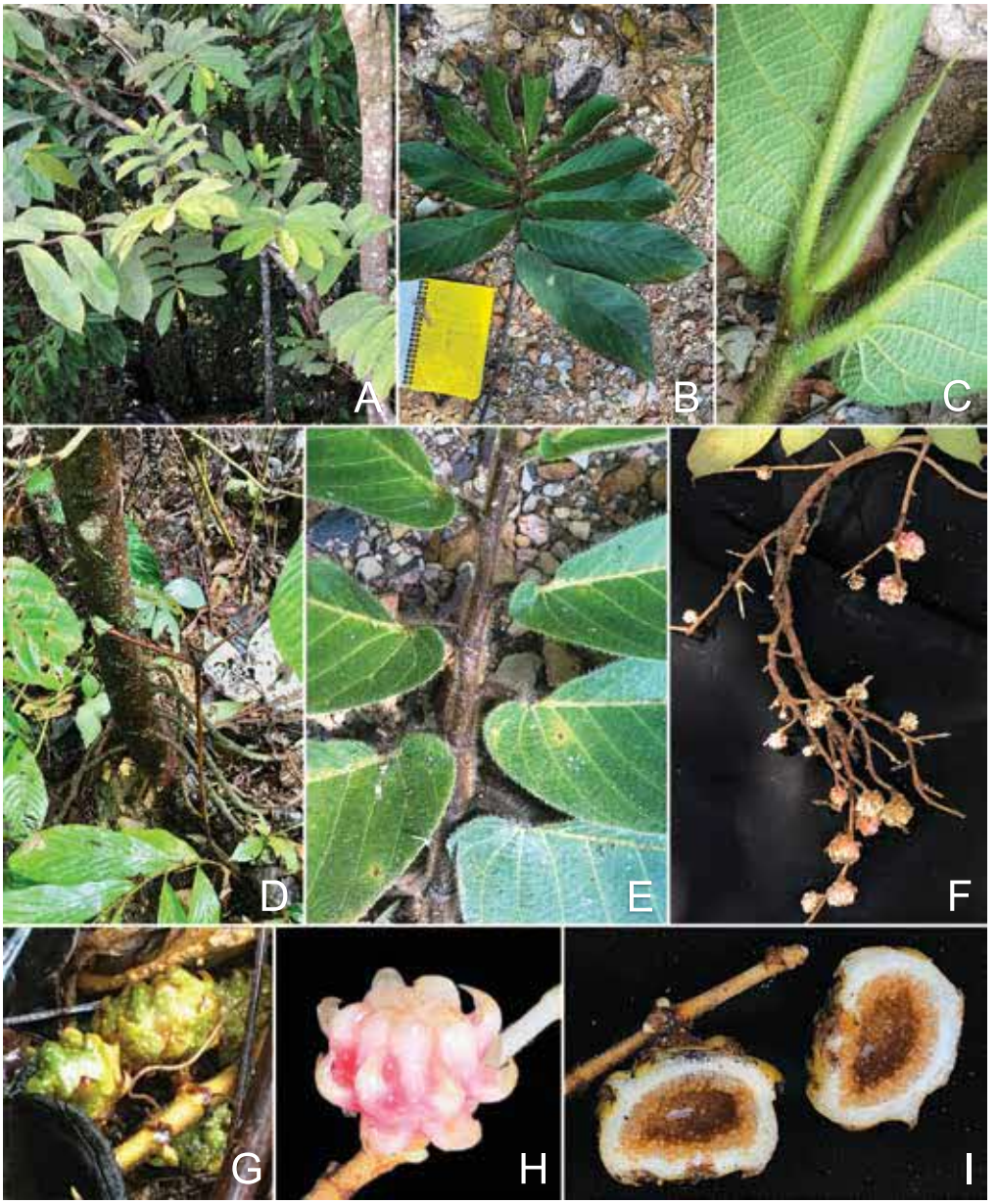

Fig. 4. *Ficus bukitrayaensis* C.C.Berg. **A.** Habit. **B.** Leafy twig, upper surface. **C.** Stipule and leaf lower surface. **D.** Base of trunk with stolons. **E.** Twig showing indumentum and leaf bases. **F.** Stolon with figs. **G.** Green figs. **H.** Pink figs. **I.** Fig interior with seeds. (Photos: E.M. Gardner)

Ficus bukitrayaensis can be recognised at once by the cuneate narrow side of the rather densely hirtellous leaf, which in mature plants is never as large as that of *Ficus megaleia*. The figs are invariably (sub)glabrous, pale and dotted but can be tinged green or red.

4. *Ficus geocharis* Corner, Gard. Bull. Singapore 18: 60 (1960); Corner, Gard. Bull. Singapore 21: 92 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 277 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 424 (2005); Berg & Chantarasuwan, Blumea 52(2): 319 (2007). – TYPE: Malaysia, Sarawak, Upper Rejang River, *Clemens 21912* (holotype BM n.v.; isotype K [K001050605, K001050606 – a single specimen over 2 sheets]). (Fig. 5)

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Bukit Patong, Sg. Talong, 19 Jul. 2023, *Gardner et al. 1400* (SAR, SING [SING0398053]); Nanga Merit, Sg. Raya, 13 Jul. 2023, *Gardner et al. 1299* (SAR, SING [SING0397710]); Kuching District, Matang, Indian Temple Trail, 17 Feb. 2020, *Gardner et al. 890* (SAR, SING [SING0401873]), *902* (SAR, SING [SING0401870]).

Notes. The description in Berg & Corner (2005) needs no emendation but could be clarified to note that the auricle at the broad side of the leaf base is minute compared to that of other species (up to 7 mm long).

Ficus geocharis can be recognised instantly by the minutely auriculate base of the leaf. The figs are essentially indistinguishable from those of *Ficus pseudobeccarii* (= *F. beccarii* var. *latifolia*).

5. *Ficus malayana* C.C.Berg & Chantaras., Blumea 52(2): 315 (2007). – *Ficus uncinata* (King) Becc. var. *strigosa* Corner, Gard. Bull. Singapore 18: 59 (1960); Corner, J. Malayan Branch Roy. Asiat. Soc. 11: 17, f. 5–7 (1933) (as *F. geocarpa*). – TYPE: Peninsular Malaysia, Bukit Kajang, Sungai Nipoh, Kenaman, 29 June 1932, *Corner SFN 25946* (holotype SING [SING0054641]; isotype K [K000227613, K000227614 – a single specimen over 2 sheets]). (Figs 6, 7)

Ficus uncinata (King) Becc. var. *truncata* Corner, Gard. Bull. Singapore 18: 59 (1960); Corner, Gard. Bull. Singapore 21: 92 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 313 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 461 (2005); Berg & Chantarasuwan, Blumea 52(2): 315 (2007) (as *F. malayana* C.C.Berg & Chantaras., p.p.) – TYPE: Borneo, Brunei, Ulu Belalong, *Corner BRUN 5329* (holotype CGE n.v.; isotypes K [K000229236], SAR).

Ficus uncinata (King) Becc. var. *subbeccarii* Corner, Gard. Bull. Singapore 19: 401 (1962); Corner, Gard. Bull. Singapore 21: 92 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 312 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 461 (2005); Berg &

Chantarasuwan, Blumea 52(2): 315 (2007) (as *F. malayana* C.C.Berg & Chantaras., p.p.). – TYPE: Borneo, Sabah, Mount Kinabalu, Ulu Langanani, 4 August 1961, *Corner 1619* (holotype K [K000229238]; isotypes A [A00034648], L [L0281456], SAN, SAR).

Trees to at least 8 m tall; bark medium brown, sparsely to densely covered with small raised lenticels; latex white. ***Leafy twigs*** 2–4 mm wide, with sparsely scattered elongate whitish lenticels, whitish to yellowish strigose to subappressed puberulent, often rather densely so; a single waxy gland usually present just below the node. ***Stipules*** amplexicaul, 2–3 cm long, yellow to brownish subappressed puberulent, caducous. ***Leaves*** distichous; lamina elliptical-oblong to slightly obovate, 17–35 × 7–15 cm, asymmetric, chartaceous, apex acuminate to subcaudate, acumen 2.5–3.5 cm long, base strongly inequilateral, the narrow side rounded to subcordate, the broad side cordate to ± auriculate, only occasionally overlapping the petiole but sometimes overlapping the twig, margin entire or finely denticulate on young leaves; upper surface whitish strigillose, scabrid to the touch, the indumentum somewhat denser on the midrib and secondary veins; lower surface whitish to brownish strigillose, the indumentum somewhat denser on the midrib and secondary veins; secondary veins 9–13 pairs, rather strongly ascending in the upper half, rarely furcate before reaching the margin, tertiary venation scalariform; petiole 1–3.5 cm long, brownish subappressed puberulent, often rather densely so; young leaves with a silvery sheen when very small. ***Figs*** on branched rooting stolons up to at least 6 m long arising from the base of the tree, the stolons often strikingly abundant and rampant, internodes up to at least 8 cm long; stipules c. 1 cm long and subpersistent (or caducous); peduncle 1–3(–10) mm long, puberulent; basal bracts several, subverticillate; receptacle subglobose, c. 2 cm wide at maturity, densely yellowish puberulent; lateral bracts scattered, at least 10, triangular, to c. 3 mm long, white to green and fairly thin, curved inwards but not tightly appressed; ostiole flat to concave, covered by bracts. ***Short-styled and long-styled flowers*** pedicellate with glabrous styles.

Distribution and habitat. Peninsular Thailand, Sumatra (Lingga), Peninsular Malaysia, Borneo, in wet forest from sea level up to 1,200 m (in Kapit, up to 480 m in elevation, especially along small rivers).

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Ulu Sg. Bena, 16 Jul. 2023, *Gardner et al. 1330* (SAR, SING [SING0389167]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023 *Gardner et al. 1362* (SAR, SING [SING0389166]), *1366* (SAR, SING [SING0397917]); Kapit District, Sg. Sebiruk, 10 Aug. 2022, *Gardner et al. 1162* (SAR, SING [SING0397936]); Kapit District, Sg. Senantang, 18 Jul. 2023, *Gardner et al. 1382* (SAR, SING [SING0389164]), *1385* (SAR, SING [SING0389165]); Sri Aman District, Lingga, Gunung Lesong, 27 Nov. 1981, *Lee S 43240* (L [L.1609040], SAN, SAR n.v.); Lubok Antu District, Lanjak Entimau PF, Sungai Jelok, near Bukit Sengkajang, 18 Mar. 1974, *Chai S 34002* (L [L.1609035], SAR n.v.), *S 34012* (L [L.1609033], MO [MO103938799], SAR n.v.).

Fig. 5. *Ficus geocharis* Corner. **A.** Habit and riverside habitat. **B.** Leafy twig, upper surface. **C.** Leafy twig, lower surface. **D.** Leaf base with minute auricle, upper surface. **E.** Leaf base with minute auricle, lower surface. **F.** Trunk and bark slash. **G.** Base of trunk with stolons. **H.** Stolon with figs. **I.** Fig. (Photos: E.M. Gardner)

Fig. 6. *Ficus malayana* C.C.Berg & Chantaras. **A.** Base of trunk with stolons. **B.** Leafy twig, lower surface. **C.** Leafy twig, upper surface. **D.** Stipule and petiole showing indumentum. **E.** Trunk and bark slash. **F.** Branching stolon. **G.** Abundant branching stolons arising from a single individual. **H–J.** Young figs on stolon. **K.** Fig interior with long-styled flowers. (Photos: E.M. Gardner)

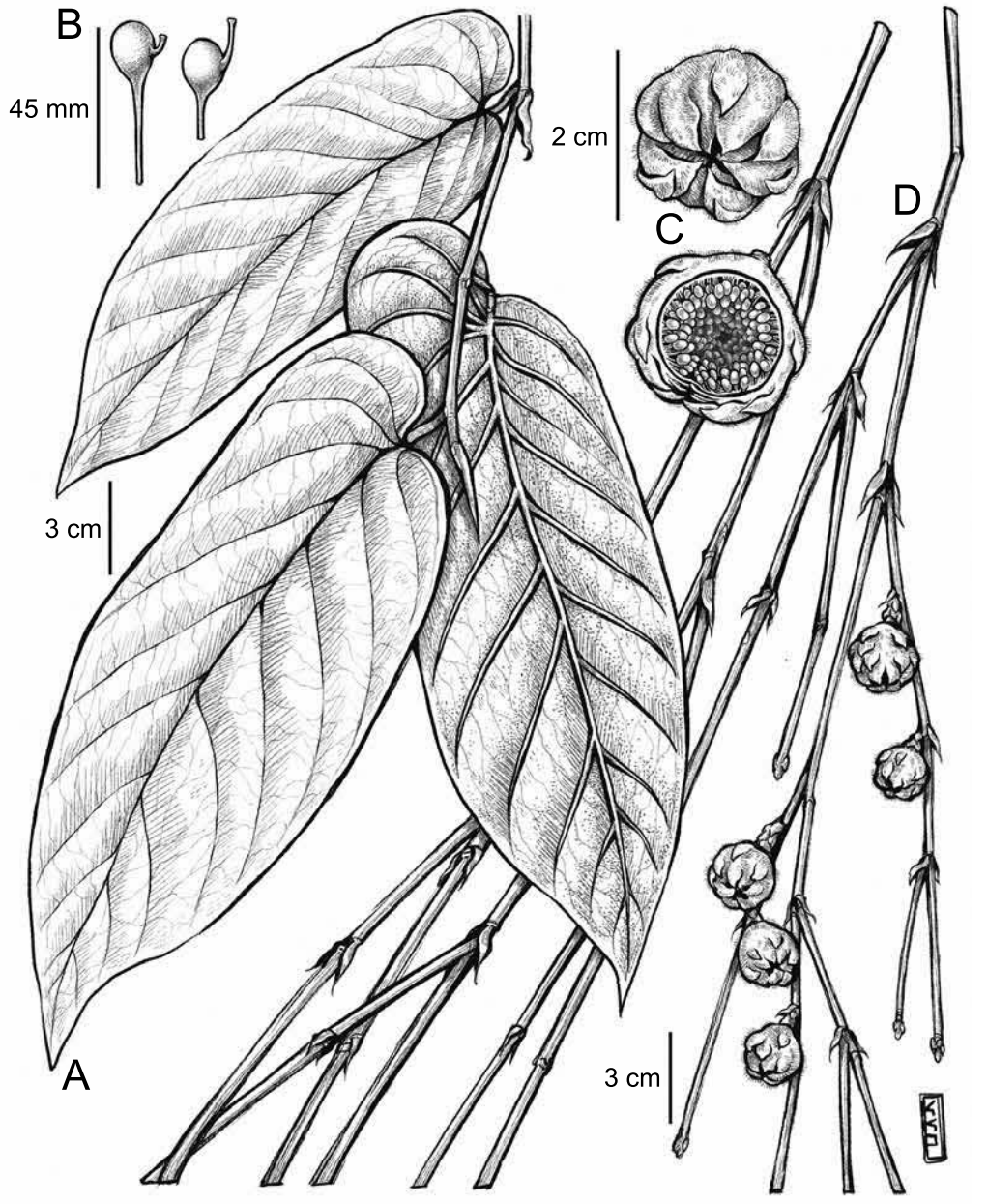

Fig. 7. *Ficus malayana* C.C.Berg & Chantaras. **A.** Leafy shoot. **B.** Short- and long-styled flowers. **C.** Seed fig exterior and interior. **D.** Stolon with figs. Drawn by K. Pham.

Notes. Berg & Chantarasuwan (2007) recognised a broad *Ficus malayana*, based on the type of *Ficus uncinata* var. *strigosa* Corner (from Terengganu in northern Peninsular Malaysia) and also including *F. uncinata* var. *subbeccarii* Corner from Mount Kinabalu in Sabah and *F. uncinata* var. *truncata* Corner from Brunei. The material

from Kapit all corresponds to *F. uncinata* var. *truncata*, which is endemic to Borneo, and the description above reflects this. It differs from the other two varieties in the minute appressed indumentum on vegetative parts, entire margin of the leaf, cordate to auriculate broad side of the leaf base, and greater number of lateral veins (9–13 vs 6–10). The dense abundance of stolons on some individuals (Fig. 6) is striking.

6. *Ficus megaleia* Corner, Gard. Bull. Singapore 18: 57 (1960); Kochummen, Tree Fl. Sabah & Sarawak 3: 286 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 433 (2005); Berg & Chantarasuwan, Blumea 52(2): 322 (2007). – TYPE: Brunei, Ulu Belalong, *Corner BRUN 5301* (holotype CGE n.v.; isotypes L [L.1608956], SAR).

Notes. Berg & Chantarasuwan (2007) circumscribed a broad concept of *Ficus megaleia* that includes some material assigned here to *F. rubrostellata* and must be amended as follows: leafy twigs with an indumentum always of two lengths, minutely puberulous with a yellowish to brownish hirtellous to subhirsute overlayer, the longer hairs with swollen bases; leaves with the base asymmetrical, the broad side auriculate and always at least partly covering the petiole.

Corner recognised three varieties of *Ficus megaleia*, the type from Brunei and the others from Mount Kinabalu (Corner, 1962). Berg & Chantarasuwan (2007) reduced these to two informal forms distinguishable by leaf size. In Kapit these are quite distinct, warranting formal divisions.

1a. Lamina 18–42 × 7–15 cm, secondary veins 10–12 ..... var. *megaleia*
1b. Lamina 47–68 × 12–28 cm, secondary veins 16–20 (or more) ..... var. *multinervia*

6.1. *Ficus megaleia* Corner **var. *megaleia*** (Fig. 8)

Distribution and habitat. Borneo (Sabah, Sarawak, Brunei, Kalimantan) in primary and secondary forest up to 2,000 m in elevation.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Ulu Sg. Bena, 16 Jul. 2023, *Gardner et al. 1329* (SAR, SING [SING0389181]), *1333* (SAR, SING [SING0389174]), *1334* (SAR, SING [SING0389173]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1346* (SAR, SING [SING0389172]), *1363* (SAR, SING [SING0389180]); Kapit District, Bukit Patong, 19 Aug. 2023, *Gardner et al. 1398* (SAR, SING [SING0389175]), *1407* (SAR, SING [SING0389183]); Kapit District, Sg. Senantang, 18 Jul. 2023, *Gardner et al. 1369* (SAR, SING [SING0389176]); Nanga Merit, Sg. Raya, 13 Jul. 2023, *Gardner et al. 1288* (SAR, SING [SING0389179]), *1292* (SAR, SING [SING0389177]), *1295* (SAR, SING [SING0389182]), *1302* (SAR, SING [SING0389178]).

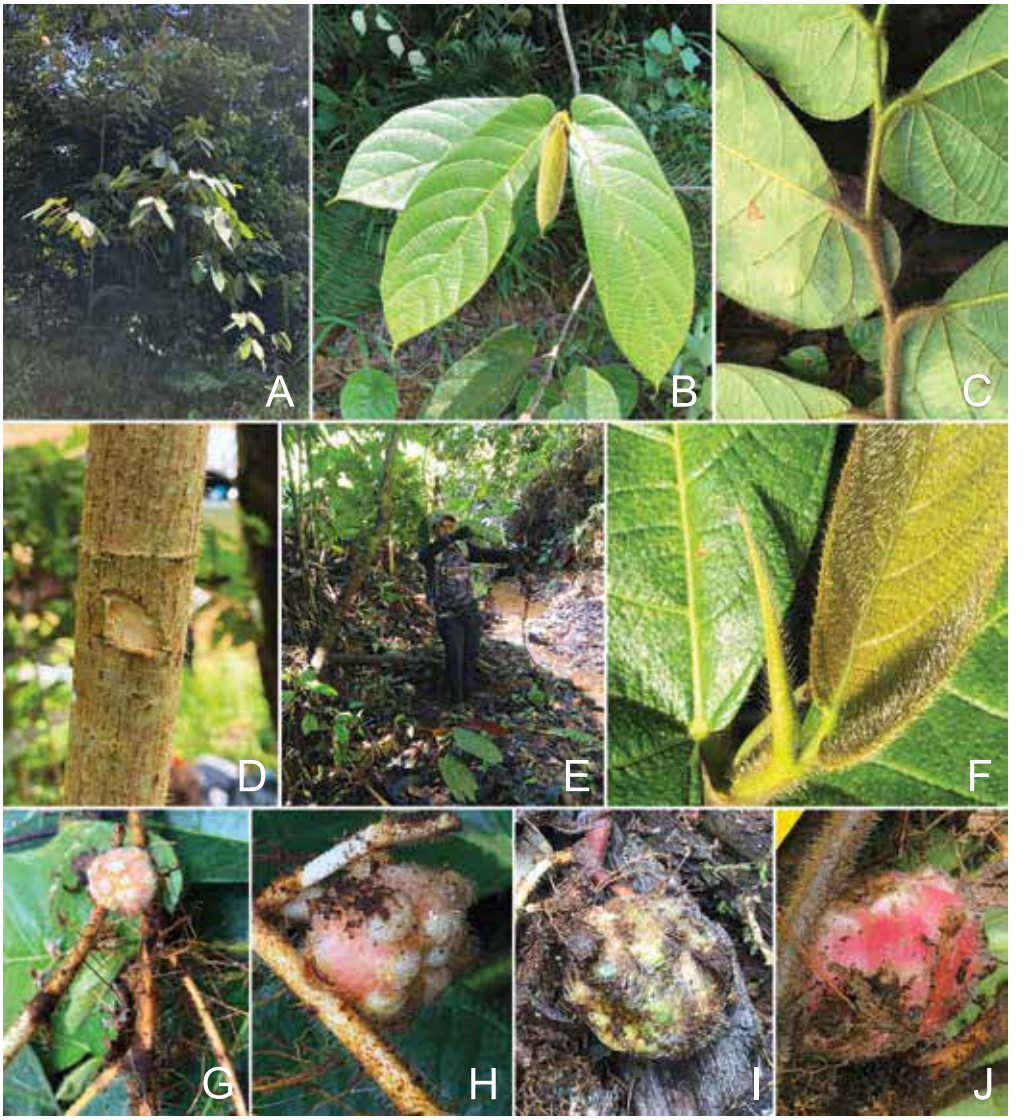

Fig. 8. *Ficus megaleia* Corner var. *megaleia*. **A.** Habit. **B.** Leafy twig, upper surface. **C.** Leafy twig, lower surface, showing auricled leaf bases. **D.** Trunk and bark slash. **E.** Habit with branching stolon. **F.** Stipule and indumentum. **G.** Rooting stolon with fig. **H–J.** Figs. (Photos: E.M. Gardner)

Notes. This variety corresponds in part to the small-leaved form of *Ficus megaleia* recognised by Berg & Chantarasuwan (2007). It has a rather uniform appearance in Kapit, and the figs are invariably quite like those on the type from Brunei: rather densely hairy, maturing pink and white, with thin scattered bracts. It can be distinguished at a glance from *Ficus bukitrayaensis* by the larger leaves (18–42 × 7–15 cm, with 10–12 secondary veins, several forking), rounded to cordate narrow side of the leaf, and the larger auriculate broad side of the leaf base, which always covers the petiole.

6.2. *Ficus megaleia* Corner var. ***multinervia*** Corner, Gard. Bull. Singapore 19: 400 (1962); Gard. Bull. Singapore 21: 91 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 287 (2000). – TYPE: Malaysia, Sabah, Mount Kinabalu, 25 July 1961, *Corner RSNB 970* (holotype K [K001050612, K001050613, K001050614 – a single specimen over 3 sheets]; isotype L [L.3973135]). (Fig. 9)

Distribution and habitat. Borneo (Sabah, Sarawak), in primary and secondary forest up to 1,000 m in elevation.

Vernacular name. Entimau badak, *Entimau raya* (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Sg. Balang, 9 Aug. 2022, *Gardner et al. 1146* (SAR, SING [SING0397955]); ibidem, 12 Jul. 2023, *Gardner et al. 1262* (SAR, SING [SING0397877]); Kapit District, Ulu Sg. Bena, 16 Jul. 2023, *Gardner et al. 1344* (SAR, SING [SING0389169]); Kapit District, Bukit Goram, Sg. Apoh, 17 Aug. 2023, *Gardner et al. 1356* (SAR, SING [SING0389168]); Kapit District, Sg. Senantang, 18 Aug. 2023, *Gardner et al. 1384* (SAR, SING [SING0389171]); Nanga Merit, Sg. Raya, 13 Jul. 2023, *Gardner et al. 1306* (SAR, SING [SING0389170]).

Notes. A large-leaved form of *Ficus megaleia* is also present in Kapit, with leaves 47–68 × 12–28 cm, with 16–20 secondary veins, many forking, and reddish when young. While the large-leaved form entity certainly represents a distinct species-level taxon, additional fertile material must be collected in both Sarawak and Sabah to resolve its status. We therefore provisionally assign this material to *Ficus megaleia* var. *multinervia* Corner, described from sterile type material collected on Mount Kinabalu. Our Kapit specimens are all sterile except for two anomalous collections from Sungai Balang, which have large, minutely puberulent (but appearing ± glabrous) figs covered with numerous inflexed, keeled, lateral bracts (Fig. 7G–I), not unlike some collections from Sabah (*Saw FRI 36256*). However, the petioles of the specimens from Sungai Balang have long hairs with echinate inflated bases, a character otherwise seen only in *Ficus stolonifera* and *F. salangii*. The Sungai Balang specimens therefore may either have a hybrid origin or may represent yet another distinct taxon. These two collections may relate to *Ficus megaleia* var. *subuncinata* Corner from Mount Kinabalu, with large leaves and glabrous figs; however, additional investigation and more material is required before drawing any conclusions.

7. *Ficus pseudobeccarii* E.M.Gardner, **stat. et nom. nov.**, based on *Ficus beccarii* King var. *latifolia* Corner, Gard. Bull. Singapore 18: 60 (1960); Corner, Gard. Bull. Singapore 21: 92 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 262 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 398 (2005), as *F. beccarii*, p.p. – TYPE: Borneo, Brunei, Sungai Belalong, February 1959, *Corner BRUN 5322* (holotype CGE; isotypes P [P06823456], SAR, US [US00955864]). (Fig. 10)

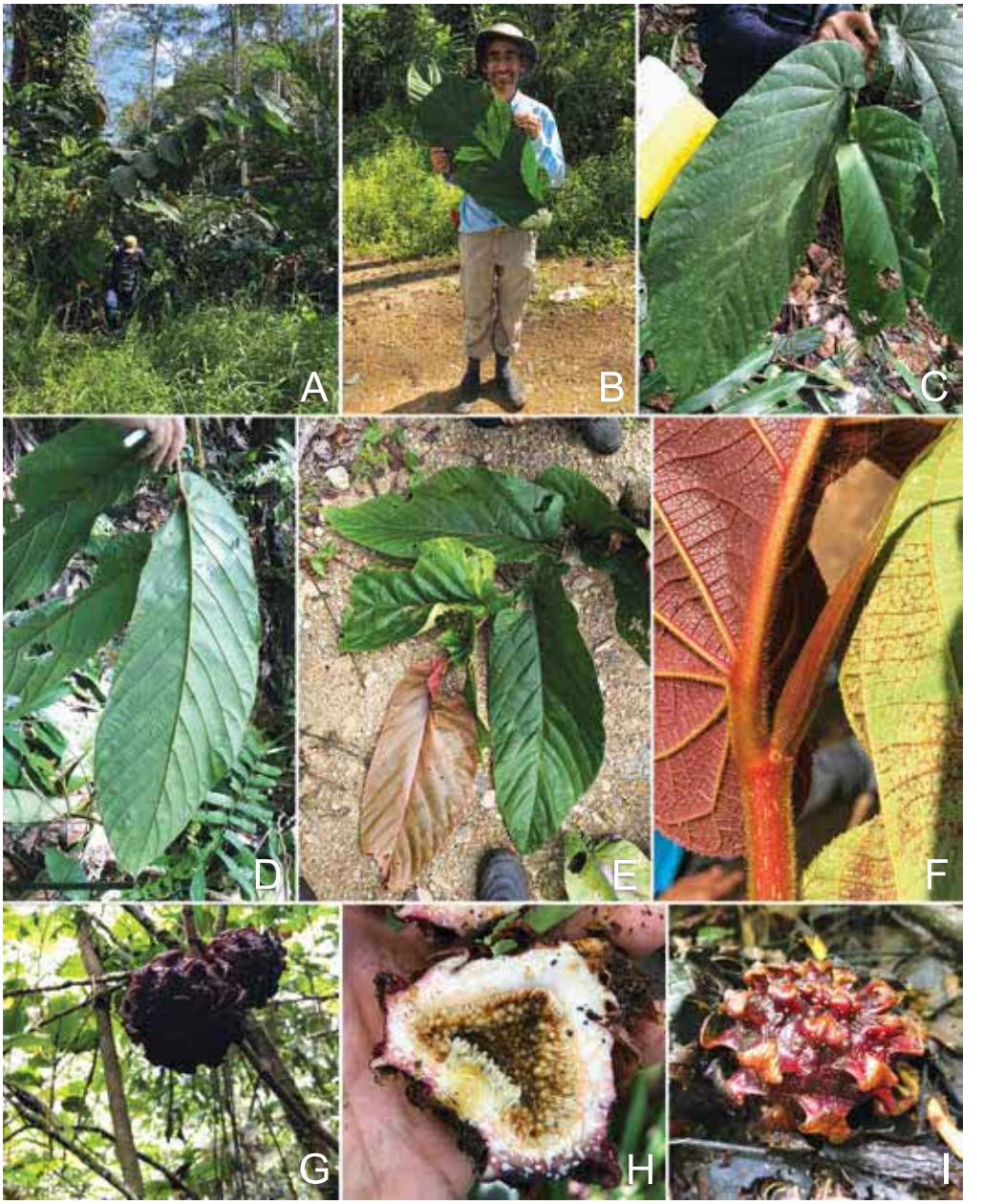

Fig. 9. *Ficus megaleia* Corner var. *multinervia* Corner. **A.** Habit. **B.** Large leaf. **C.** Leaf upper surface. **D.** Leaf lower surface. **E.** Leafy shoot with red young leaf, upper surface. **F.** Stipule and leaf base, lower surface. **G.** Figs on aerial flagellum. **H.** Interior of gall fig. **I.** Fig on stolon. (Photos: E.M. Gardner)

Fig. 10. *Ficus pseudobeccarii* E.M.Gardner. **A.** Habit **B.** Leafy twig, upper surface. **C.** Leafy twig, lower surface. **D.** Trunk. **E.** Reddish new leaves and stipule. **F.** Twig and stipule showing reddish indumentum and leaf base, upper surface. **G.** Stolon with young figs (inset: close-up of young fig). **H, I.** Figs. (Photos: E.M. Gardner)

Ficus beccarii King var. *asymmetrica* Corner, Gard. Bull. Singapore 18: 60 (1960). – TYPE: Malaysia, Sarawak, Kuching Division, Bukit Kuap, January 1959, *Corner s.n.* (holotype CGE n.v.; isotypes K [K001050607], L [L0039972], US [US00955863]).

Shrub or treelet up to 6(–10) m tall. ***Leafy twigs*** 3–6 mm thick, yellowish to reddish strigose, with nodal waxy glands; internodes hollow; periderm persistent. ***Stipules*** 4–6.5 cm long, caudate and margin often inflexed, yellowish to reddish strigose to subsericeous, caducous. ***Leaves*** distichous; lamina lanceolate to oblong, 31–53 × (5–)9–12 cm, nearly symmetrical, chartaceous, apex narrowly acuminate to caudate but not filiform, base rounded to subcordate, margin entire; upper surface glabrous (also the midrib), smooth, bullate; lower surface yellowish to reddish strigose to strigillose on the veins, smooth to scabridulous, cystoliths only beneath; lateral veins (11–)12–13(–14) pairs (in the lower part more closely together than more upwards), none of them branched or furcate far from the margin, tertiary venation scalariform, in the upper part of the lamina running perpendicular to the midrib; waxy glands in the axils of the upper lateral veins; petiole 1–1.5 cm long, yellowish strig(ill)ose, the epidermis persistent. ***Figs*** flagelliflorous on up to 3 m long slender stolons with up to 10 cm long internodes; subsessile or with a peduncle up to 0.5 cm long; basal bracts 3 and verticillate or up to 6 and subverticillate, 3–4 mm long; receptacle subglobose, 1–2 cm diam. when dry, brown hirtellous, reddish at maturity, with greenish recurved lateral bracts, these with a prominent thickened keel, apex convex to flat; ostiole 3–4 mm diam., surrounded by a rosette of apical bracts. ***Long- and short-styled flowers*** without perianth; styles glabrous.

Distribution and habitat. Borneo (Sarawak and Brunei) in primary and secondary forest, especially along riverbanks and roads, from sea level to 500 m in elevation.

Etymology. The epithet refers to the morphological similarity of this species to *Ficus beccarii*, reflected in its former status as a variety of that species.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Ulu Sg. Bena, 16 Jul. 2023, *Gardner et al. 1337* (SAR, SING [SING0389190]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1347* (SAR, SING [SING0389193]), *1361* (SAR, SING [SING0389188]); Kapit District, Sg. Pinih, 14 Jul. 2023, *Gardner et al. 1322* (SAR, SING [SING0389192]); Nanga Merit, Sg. Raya, 13 Jul. 2023, *Gardner et al. 1293* (SAR, SING [SING0389189]), *1300* (SAR, SING [SING0389191]).

Notes. This species is closely related to *Ficus geocharis*; while the leaves differ substantially in the minute auricle and stronger indumentum of the latter, they are difficult to distinguish based on the figs alone. The characters distinguishing *Ficus pseudobeccarii* from *F. beccarii* appear in the notes on the former, above. The type of *Ficus beccarii* var. *asymmetrica* differs in the slightly asymmetrical base of the leaf but otherwise agrees well with *F. pseudobeccarii*; we therefore provisionally include it as a synonym here.

Although this species is based on Corner's *Ficus beccarii* var. *latifolia*, his varietal epithet was not available for combination at the species level, already having been taking up twice, as *F. latifolia* Oken (= *F. altissima* Blume) and *F. latifolia* Salisb. (= *F. carica* L.).

8. *Ficus pulchrifolia* E.M.Gardner, **sp. nov.**
Differs from *Ficus subterranea* Corner in the shiny, larger leaves, cordate leaf bases, and puberulent figs. – TYPE: Malaysia, Sarawak, Kapit Division, Sg. Senantang, 18 July 2023, *E. Gardner et al. 1387* (holotype SING [SING0397871]; isotype SAR). (Figs 11, 12)

Trees to at least 5 m tall; bark medium to orangish brown with raised lenticels; latex white to watery. ***Leafy twigs*** c. 4 mm thick, (sub)glabrous, dark green and shiny, with scattered pale lenticels; a single waxy gland below the petiole attachment at each node. ***Stipules*** amplexicaul, 3.5–5 cm long, subglabrous, caducous. ***Leaves*** distichous; lamina oblong-elliptical, 37–42 × 12–15 cm, slightly asymmetric, subcoriaceous, apex acuminate, base subcordate to cordate and slightly to moderately inequilateral, the broad side sometimes minutely auriculate and overlapping the petiole, margin entire; upper surface (sub)glabrous; lower surface appressed yellow puberulent on the main veins but otherwise thinly puberulent, soon glabrescent, cystoliths apparent on the lower surface; secondary veins 17–20, only slightly curved, markedly ascending in the upper third of the lamina but otherwise shallowly angled, waxy glands in the axils of most of the secondary veins, tertiary venation scalariform; new leaves reddish and somewhat flaccid; petiole 4–8 mm long, (sub)glabrous. ***Figs*** on branched rooting stolons arising from the base of the trunk, at ground level or slightly underground, white to green; peduncle c. 3 mm long; basal bracts 3, (sub)verticillate; receptacle subglobose, c. 1 cm diam. when dry, moderately to densely subappressed yellow puberulent; lateral bracts c. 6–8, scattered, thin, appressed, triangular, c. 2 mm long and thinly appressed puberulent; apex convex; ostiole surrounded by c. 4 appressed triangular bracts, fleshier than the lateral ones, c. 2 mm long, (very) sparsely appressed puberulent. ***Longstyled flowers*** pedicellate, without perianth; styles glabrous, stigma funnel-shaped. ***Short-styled flowers*** not seen.

Distribution and habitat. Borneo (Sarawak), in wet secondary forest along small rivers, up to at least 500 m in elevation.

Vernacular name. Entimau (Iban).

Etymology. The epithet refers to the strikingly ornamental leaves.

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit Division, Ulu Sungai Bena, 16 Jul. 2023, *Gardner et al. 1342* (SAR, SING [SING0397869]); Kapit Division, Bukit Goram, 17 Jul. 2023, *Gardner et al. 1365* (SAR, SING [SING0397870]); Kapit Division, Sg. Senantang, 11 Aug. 2022, *Gardner et al. 1179* (SAR, SING).

Fig. 11. *Ficus pulchrifolia* E.M.Gardner. **A.** Leafy twig with red new leaf, lower surface. **B.** Leaves, upper surface. **C.** Stipule and leaf bases, lower surface. **D.** Twig and stipule. **E.** Trunk and bark slash. **F.** Leaf base, upper surface. **G.** Stolon with figs. **H, I.** Young figs. (Photos: E.M. Gardner)

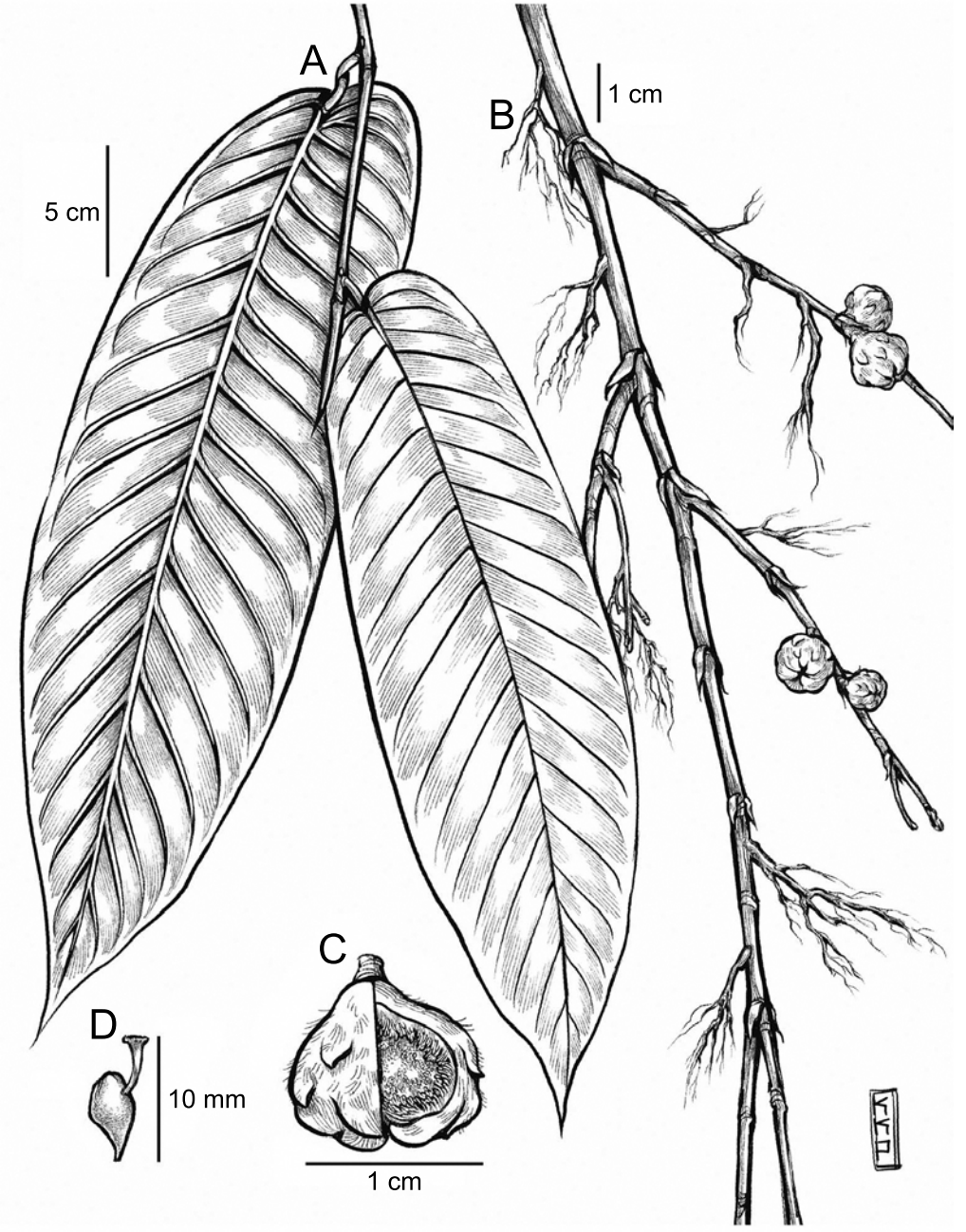

Fig. 12. *Ficus pulchrifolia* E.M.Gardner. **A.** Leafy shoot. **B.** Stolon with figs. **C.** Seed fig. **D.** Long-styled flower. Drawn by K. Pham.

Notes. This species can be instantly recognised by the striking glossy, coriaceous leaves, which are red when young.

9. *Ficus rubrostellata* E.M.Gardner, **sp. nov.**
Differs from *Ficus uncinata* (King) Becc. in the base of the lamina (the two sides of equal length along the petiole and the broad side never cordate or auriculate) and in the bracts of the fig (not hooked; usually glabrous except for a few hispid hairs at their apices). – TYPE: Malaysia, Sarawak, Bintulu Division, Tatau District, Ulu Merirai, Gua Spring, 6 July 2005, *Julia et al. S 93388* (holotype SING [SING0071682]; isotype SAR n.v.). (Figs 13, 14)

Ficus uncinata (King) Becc. var. "C" in Kochummen, Tree Fl. Sabah & Sarawak 3: 311 (2000).

Shrubs or small trees up to 5 m tall, often forming rhizomatous clonal patches; latex white. ***Leafy twigs*** 1.5–2.5 mm thick, moderately to densely covered with patent pale yellow to colourless hairs (rarely brownish), the surface of the hairs slightly punctate and the bases somewhat darker and inflated; waxy glands often present just below the node. ***Stipules*** amplexicaul, 10–21 mm long, rather densely subappressed whitish to yellowish pubescent, persistent for at least the first few nodes. ***Leaves*** distichous, lamina elliptical, 16–32 × 5–12 cm, chartaceous, apex acuminate, base obtuse to rounded on the broad side, acute on the narrow side, both sides the same length measured from the petiole, margin serrulate; upper surface moderately hispidulous to hirtellous; lower surface somewhat more densely so, the hairs pale yellow to colourless, the hairs with a punctate surface and slightly darker inflated bases, occasionally very short hairs present, cystoliths present and more prominent on the lower surface; lateral veins 5–7(–8), curved and ascending, some of them furcate about 2 cm from the margins; waxy glands usually present in the axils of 2–4 of the middle ones and sometimes in the furcations; petiole 3–8 mm long, indumentum as on twigs. ***Figs*** on branched rooting stolons up to at least 5 m long arising from the base of the stem; peduncle 2–5 mm long, subglabrous subtended by a few thin overlapping bracts; basal bracts 3, (sub)verticillate at the apex of the peduncle, triangular, c. 1.5 mm long, hispidulous, subappressed to patent, subtending a stipe, 1–2.5 mm long; receptacle subglobose obovoid, 1.5–2.5 cm diam. (including the patent bracts) when fresh, drying 0.8–1.3 cm, glabrous when mature except for a few yellowish hispid hairs at the apex of each bract (rarely thinly hispidulous throughout), red at maturity, apex more or less flat; bracts numerous, often reflexed (to incurved); ostiole c. 1 mm diam., surrounded by a few appressed triangular bracts; internal hairs absent. ***Long-styled flowers*** pedicellate, without perianth; styles glabrous. ***Short-styled flowers*** (seen only in the gall phase) pedicellate, without perianth; styles glabrous.

Distribution and habitat. Borneo (Sarawak, Sabah, Kalimantan), in wet primary and secondary forest, especially along rivers, up to c. 650 m in elevation; also on limestone.

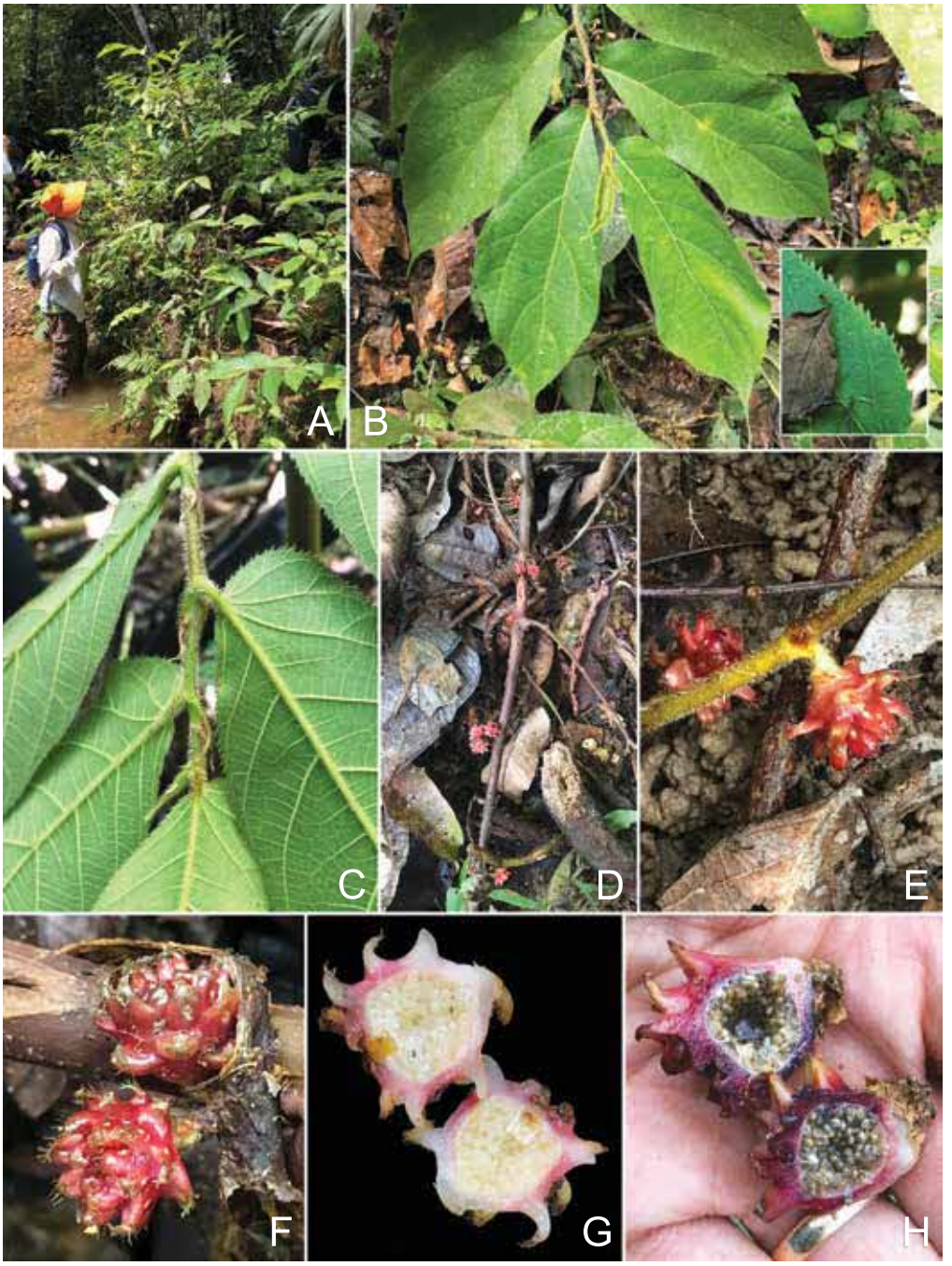

Fig. 13. *Ficus rubrostellata* E.M.Gardner. **A.** Habit and riverside habitat. **B.** Leafy twig, upper surface (inset: leaf margin). **C.** Leafy twig, lower surface. **D.** Stolon with figs. **E, F.** Figs. **G.** Fig with developing galls and staminate flowers. **H.** Fig with mature galls and staminate flowers. (Photos: E.M. Gardner)

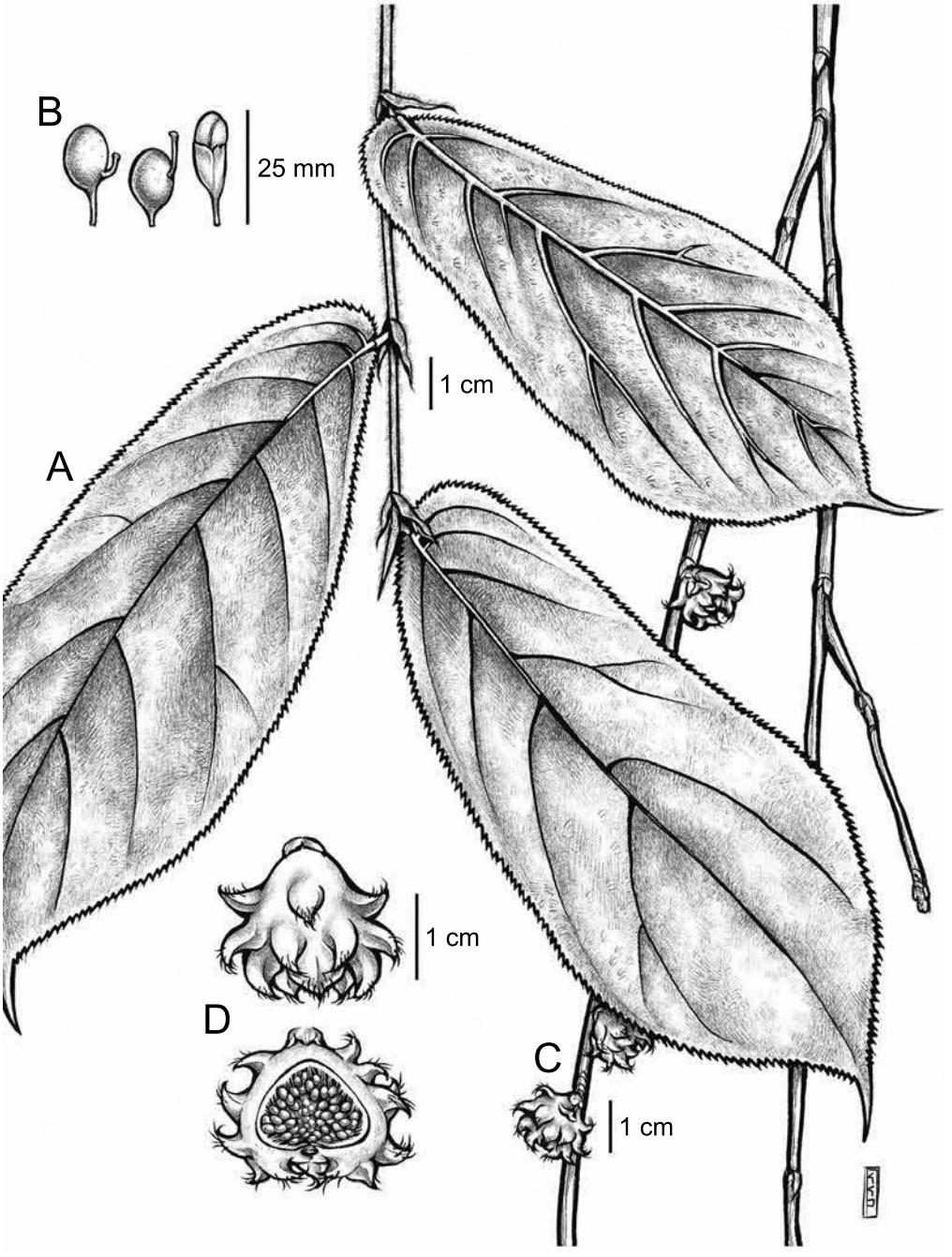

Fig. 14. *Ficus rubrostellata* E.M.Gardner. **A.** Leafy shoot. **B.** Short- and long-styled flowers, staminate flower. **C.** Stolon with figs. **D.** Gall fig exterior and interior. Drawn by K. Pham.

Etymology. The epithet refers to the figs, which resemble red stars.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Sg. Balang, 12 Jul. 2023, *Gardner et al. 1258* (SAR, SING [SING0397863]), *1266* (SAR, SING [SING0397788]), *1267* (SAR, SING [SING0397867]), *1272* (SAR, SING [SING0397787]), *1282* (SAR, SING [SING0397786]), *1283* (SAR, SING [SING0397789]), *1284* (SAR, SING [SING0397866]); Kapit District, Sg. Bena, 11 Jul. 2023, *Gardner et al. 1252* (SAR, SING [SING0397784]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1359* (SAR, SING [SING0397779]); Kapit District, Sg. Pinih, 14 Jul. 2023, *Gardner et al. 1313.2* (SAR, SING [SING0397785]); Kapit District, Sg. Senantang, 18 Jul. 2023, *Gardner et al. 1371* (SAR, SING [SING0397868]), *1372* (SAR, SING [SING0397790]), *1373* (SAR, SING [SING0397780]), *1379* (SAR, SING [SING0397783]), *1380* (SAR, SING [SING0397782]); Kapit District, Sg. Seranau, 13 Feb. 2020, *Gardner et al. 867* (SAR, SING); Kuching District, Mt Matang, Indian Temple Trail, 2 Feb. 2020, *Gardner et al. 891* (SAR, SING [SING0401872]); Kuching District, Mt Matang, Beccari Trail, 14 Aug. 2022, *Gardner et al. 1214* (SAR, SING [SING0397865]); Kuching District, Matang Wildlife Centre, 4 Aug. 2022, *Gardner et al. 1129* (SAR, SING [SING0397937]); Kuching District, Semenggoh Arboretum, 5 Aug. 2022, *Gardner et al. 1135* (SAR, SING [SING0397925]); Kuching District, Tiang Bekap [Teng Bukap], 25 Jul. 1962, *Chew 662* (A [A02406613], L [L.1608974], SING); Serian District, Sabal Tapang F.R., 70th Mile, Serian Road, 12 May 1974, *Tong et al. S 34268* (L [L.2058598], MO [MO2352682], SAR); Song District, Lanjak Entimau Wildlife Sanctuary, Sungai Pedawak near its confluence with Sungai Katibas, 33 km upriver from Camp A, 23 November 1997, *Pearce & Wiriadinata ITTO/ BB 0769* (SAR, BO n.v.); Sri Aman Division, Lubok Antu District, Lanjak Entimau Protected Forest, Sg. Jelok, near Bukit Sengkajang, 13 Mar. 1974, *Chai S 34003* (L [L.1596016], MO [MO3552713]). **Sabah:** Beluran District, Ulu Tongod, 3 Aug. 2024, *Suzana et al. SAN 162220* (IBSC, SAN, SING).
INDONESIA: **Central Kalimantan:** Sintang, 7 Apr. 1994, *Church et al. 726* (A, [A02406609], L [L.1612814, L.1612815]). **South Kalimantan:** Kabupaten Tabalong, Missim River, PT. Aya Yayang Indonesia, Jul. 2000, *Sidiyasa & Arifin 2130* (L [L.1596010]).

Notes. This species is common in Kapit and around Kuching and has been the subject of considerable uncertainty. Berg & Chantarasuwan (2007) included specimens in both *Ficus bukitrayaensis* (*Chai et al. S 34003*) and *Ficus megaleia* (*Beccari P.B. 2798*) but noted in the latter case that the indumentum, all the same length, was not consistent with other specimens of *F. megaleia*. Beccari's specimen is a syntype of *Ficus hypogaea* King, but Corner (1960) designated *Forbes 2505* from Sumatra as the lectotype, bringing *F. hypogaea* into synonymy with *Ficus gilapong* Miq. Our entity thus requires a new name.

The vegetative characters of this species appear to be quite constant, but some variation in the fig indumentum is apparent. While most collections have lateral bracts that are essentially glabrous but for a tuft of hispidulous hairs at the tips, some collections have an indumentum more or less throughout the fig exterior (*Church et al. 726* from Central Kalimantan and *Tong et al. S 34268* from Sarawak).

Ficus rubrostellata includes a paratype of *Ficus uncinata* var. *pilosior* Corner (*Beccari P.B. 2798*). However, the type of that variety (*Corner BRUN 5302*, L [L.1608977]) and another collection from Lambir Hills National Park, Sarawak (*Sibat S 24304*, L [L.2058593]) appear to represent a distinct entity. They have proportionally more elongate leaves, apparently coriaceous, with up to 13 secondary veins, and the bracts of the figs are inflexed without hispidulous apices. We agree with Kochummen (2000) who considered them distinct entities, treating *Ficus rubrostellata* as an unnamed "var. C" under *F. uncinata.* Further research and additional material are necessary to clarify the status of *Ficus uncinata* var. *pilosior*. Also worthy of additional investigation are specimens collected on limestone, represented here by *Chew 662* from the Padawan limestone area in Sarawak. Given the high endemism of limestone areas, that specimen, whose leaves are atypically large, with more lateral veins (10) and a more auriculate broad side of the lamina base, may ultimately prove to represent a distinct taxon.

The designated type, which is the best available specimen, could not be located at SAR, and we have therefore designated the SING duplicate as the holotype.

10. *Ficus salangii* E.M.Gardner, **sp. nov.**

Differs from *Ficus stolonifera* King in the more strongly asymmetrical leaf base with one side auricled, reddish new leaves, and larger figs (1.5–1.8 cm vs 0.8–1.2 cm diam. when dry) with a minute indumentum (not scabrid) and sparse, thin (not fleshy), appressed triangular bracts. – TYPE: Malaysia, Sarawak, Kapit Division, Bukit Patong, Sungai Semerah, 19 July 2023, *E. Gardner et al. 1393* (holotype SING [SING0397879]; isotype SAR). (Figs 15, 16)

Trees, up to at least 10 m tall; bark grey-brown with scattered lenticels; latex white. ***Leafy twigs*** 2.5–3 mm wide, densely whitish puberulous with an overlayer of longer rust-coloured hispid hairs, the bases of the latter inflated and echinate; waxy glands present just below the petiole attachment. ***Stipules*** amplexicaul, c. 1 cm long, caducous, densely subappressed whitish pubescent, with longer more or less patent rust-coloured hairs on the keel. ***Leaves*** subdistichous to ± spirally arranged, but the petioles bent so that the general aspect is distichous, lamina elliptical to sub-ovate, 23–31 × 8–13 cm, inequilateral, base asymmetric, cordate to auriculate on the broad side, sometimes partially overlapping the petiole, and subcordate to rounded on the narrow side, margin crenulate and denticulate; upper surface whitish hispidulous with scattered longer rust-coloured hispid hairs, some of them with echinate inflated bases, scabrid to the touch, the indumentum denser on the midrib and secondary veins; lower surface moderately to densely whitish puberulous with a yellowish to rust-coloured hirtellous overlayer, rather soft to the touch, the hairs denser on the midrib and secondary veins and the bases of the longer hairs often inflated and echinate; new leaves deep red on the lower surface; secondary veins 4–7, bright yellow on both sides, a few of them usually forking at a distance from the margin, tertiary venation scalariform. ***Figs*** on branching stolons at least 3 m long with persistent triangular stipules c. 6 mm long; peduncle 2–3 mm long; basal bracts 4–7 (at least), subverticillate to spirally arranged; receptacle

Fig. 15. *Ficus salangii* E.M.Gardner. **A.** Habit. **B.** Leafy twig, upper surface. **C.** Leafy twig, lower surface. **D.** Trunk and bark slash. **E.** Stipule and leaf base. **F.** Stolon with figs. **G, H.** Figs on stolons. **I.** Fig interior showing developing long-styled flowers. **J.** Fig interior with mature long-styled flowers. (Photos: E.M. Gardner)

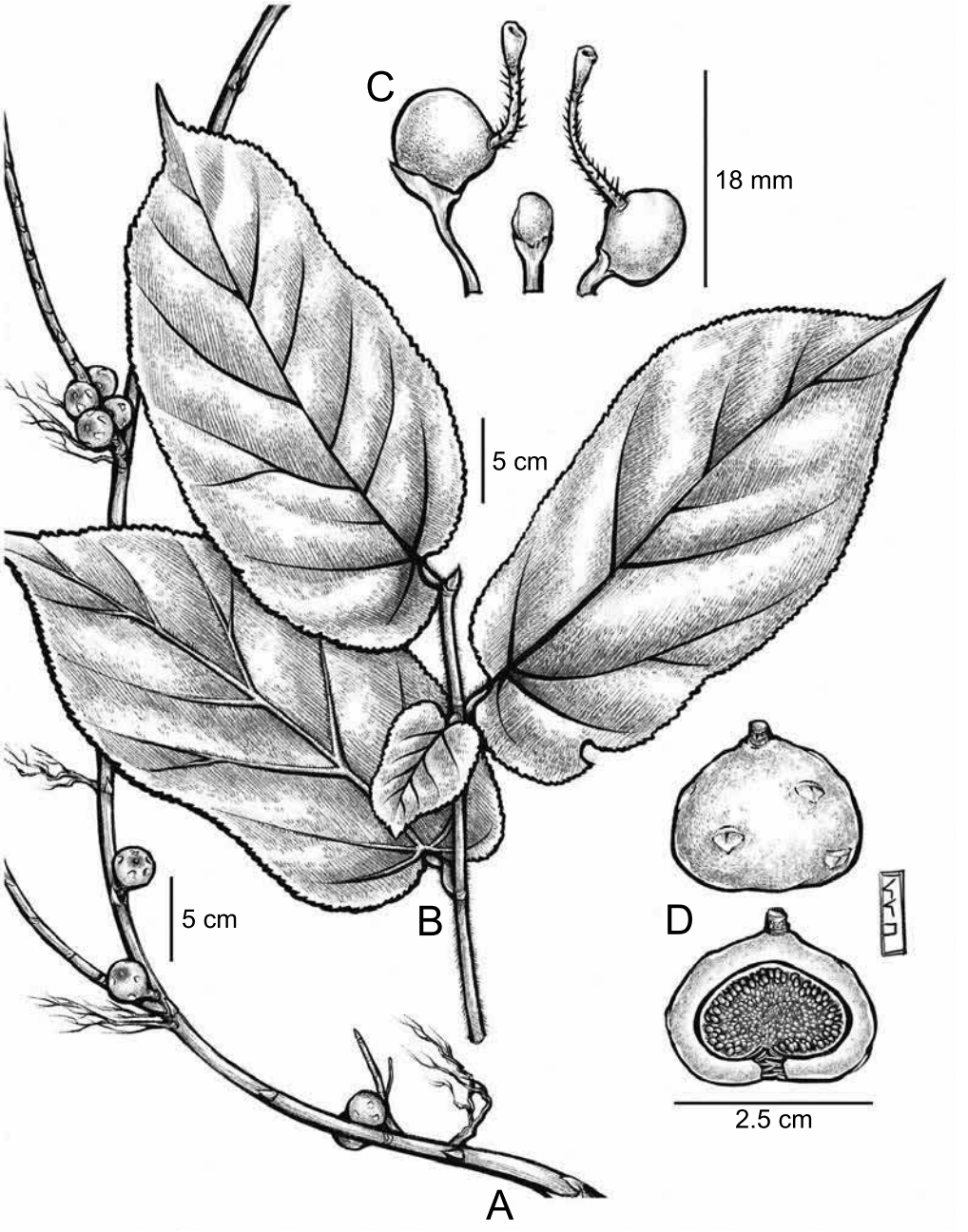

Fig. 16. *Ficus salangii* E.M.Gardner. **A.** Stolon with figs. **B.** Leafy twig. **C.** Long-styled flowers and sterile staminate flower. **D.** Seed fig exterior and interior. Drawn by K. Pham.

subglobose, bright to dark red, 1.5–1.8 cm diam. when dry, minutely brownish subappressed puberulous; lateral bracts thin and sparsely scattered, triangular, (sub) appressed, c. 1.5 mm long, and (sub)appressed brownish puberulent; ostiole c. 1 mm diam. (c. 2 mm in section including the internal bracts), flat to convex, surrounded by numerous (c. 10) appressed triangular bracts. ***Long-styled flowers*** pedicellate; perianth reduced to a collar around the base of the ovary; styles pubescent; fruits distinctly keeled. ***Short-styled flowers*** not seen.

Distribution and habitat. Borneo (Sarawak, Kapit), along roads in secondary hill dipterocarp forest up to c. 500 m in elevation.

Etymology. The epithet honours our lead field guide, Salang anak Nyegang of Rumah Manggai in Kapit. Mr. Salang recalled seeing this species when he was a child.

Vernacular name. Entimau merah (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Along the road towards Ulu Sg. Bena 16 Jul. 2023, *Gardner et al. 1326* (SAR, SING [SING0397878]); Kapit District, Bukit Patong, Sungai Semerah, 19 Jul. 2023, *Gardner et al. 1397* (SAR, SING [SING0397880]).

Notes. The bright to deep red figs alone are sufficient to identify this species. Its alliance with *Ficus stolonifera* (Borneo) and *F. geocarpa* Teijsm. (Sulawesi) is apparent from the tall upright habit, sparse lateral bracts, vestigial pistillate perianth, and pubescent styles (Corner, 1978). Additionally, it shares with *Ficus stolonifera* the echinate swollen bases of the long hairs. The figs are apparently not sweet but can be eaten in salads (S. Nyegang, pers. comm.).

11. ***Ficus stolonifera*** King, Ann. Roy. Bot. Gard. (Calcutta) 1: 104, t. 132 (1888); Merrill, Bibliogr. Enum. Born. Pl.: 227 (1921); Corner, Gard. Bull. Singapore 21: 91 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 306 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 455 (2005); Berg & Chantarasuwan, Blumea 52(2): 313 (2007). – TYPE: Borneo [Malaysia], Sarawak, Pangkalan Ampat, *Beccari P.B. 2799* (lectotype FI [FI013377], designated by Kochummen, Tree Fl. Sabah & Sarawak 3: 306 (2000); isolectotype K [K001050617]). (Fig. 17)

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Sg. Balang, 12 Jul. 2023, *Gardner et al. 1279* (SAR, SING [SING0397770]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1358* (SAR, SING [SING0397773]); Kapit District, Bukit Patong, 19 Jul. 2023, *Gardner et al. 1394* (SAR, SING [SING0397767]), *1395* (SAR, SING [SING0397771]), *1401* (SAR, SING [SING0397772]), *1409* (SAR, SING [SING0397696]); Nanga Merit, Sg. Raya, 13 Jul. 2023, *Gardner et al. 1294* (SAR, SING [SING0397769]); Kuching District, Mt Matang, Beccari Trail, 14 Aug. 2022, *Gardner et al. 1206* (SAR, SING [SING0397768]); Kuching District, Mt Matang, Indian Temple Trail, *Gardner et al. 906* (SAR, SING); Kuching District, Semenggoh Arboretum, 5 Aug. 2022, *Gardner et al. 1136* (SAR, SING [SING0397926]).

Fig. 17. *Ficus stolonifera* King. **A.** Habit. **B.** Leafy twig, upper surface. **C.** Leafy twig, lower surface. **D.** Trunk and bark slash. **E.** Twig, stipule, and leaf bases, upper surface. **F, G.** Figs on stolons. **H.** Fig interior showing fruits developing from long-styled flowers. (Photos: E.M. Gardner)

Notes. The description in Berg & Corner (2005) needs no emendation.

12. ***Ficus subterranea*** Corner, Gard. Bull. Singapore 18: 60 (1960); Gard. Bull. Singapore 21: 92 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 307 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 457 (2005). – TYPE: Brunei, Sg. Belalong, February 1959, *Corner BRUN 5327* (holotype CGE n.v.; isotypes K [K001050604], L [L0040314], SAR [2 duplicates]).

1a. Vegetative parts (sub)glabrous ..... var. *subterranea*
1b. Vegetative parts pubescent ..... var. *pubescens*

12.1. ***Ficus subterranea*** var. ***subterranea*** (Fig. 18, 20F)

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Sg. Senantang, 11 Aug. 2022, *Gardner et al. 1173* (SAR, SING [SING0397957]); Kapit District, Sg. Balang, 12 Jul. 2023, *Gardner et al. 1268* (SAR, SING [SING0389161]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1364* (SAR, SING [SING0389163]), *1367* (SAR, SING [SING0389162]).

Notes. The description in Berg & Corner (2005) needs no emendation.

12.2. ***Ficus subterranea*** var. ***pubescens*** E.M.Gardner, **var. nov.**
Differs from *Ficus subterranea* var. *subterranea* in the scabrid red-brown pubescence throughout the vegetative parts, more strongly asymmetric leaf base, and the numerous bracts present along the fig peduncle. – TYPE: Malaysia, Sarawak, Kapit Division, Sungai Senantang, 18 July 2023, *E. Gardner et al. 1386* (holotype SING [SING0397774]; isotype SAR). (Figs 19, 20)

Trees or shrubs up to 8 m tall; bark orange-brown; latex white. ***Leafy twigs*** 1.5–3 mm wide, dark green to purplish when fresh, moderately yellowish-brownish hirtellous (to subappressed, in that case subpatent at the nodes), the hairs patent and sparse enough to see the twig through them, all the same length or with an underlayer of minute subappressed rust-coloured hairs; waxy glands present at the nodes, lenticels scattered, white when fresh. ***Stipules*** amplexicaul, 3–5 cm long, densely subappressed yellowish to rust-coloured pubescent on the keel, more or less glabrous at the edges, caducous; axillary buds sometimes with protruding stipule up to 1.5 cm long. ***Leaves*** distichous; lamina oblong elliptical to obovate, asymmetrical, apex acuminate, base inequilateral, the broad side obtuse to subcordate, the narrow side subcuneate to obtuse, 16–29 × 4–9 cm; upper surface hirtellous and rough, midrib sunken, densely yellowish hirtellous; lower surface thinly yellowish to yellow-brownish pubescent,

Fig. 18. *Ficus subterranea* Corner var. *subterranea*. **A.** Habit. **B.** Leafy twigs. **C.** Trunk and bark slash. **D.** Stolons with figs. **E.** Leafy twig and stipule, upper surface. **F.** Leafy twig and stipule, lower surface. **G–I.** Figs. **J.** Fig interior with immature flowers. (Photos: E.M. Gardner)

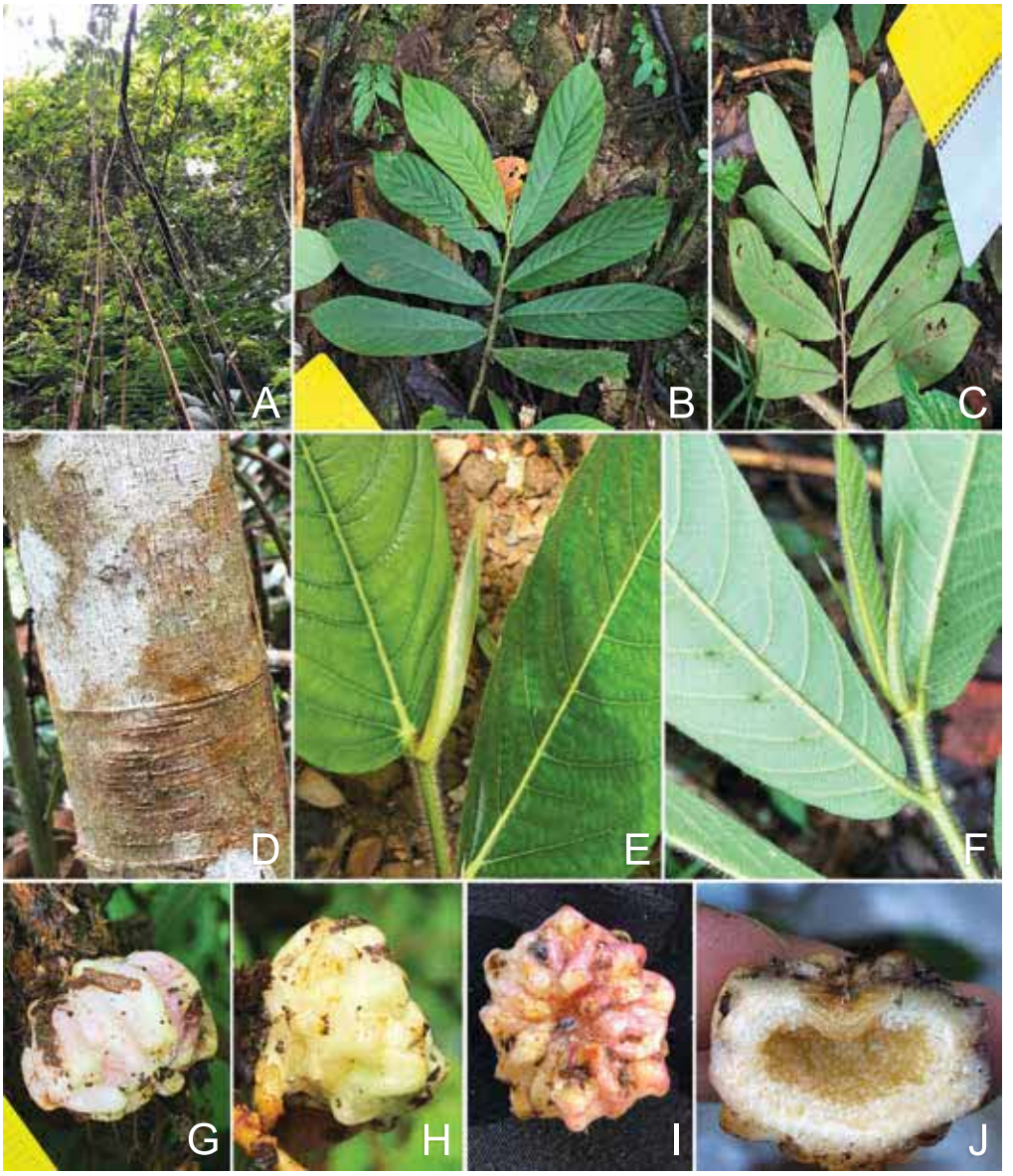

Fig. 19. *Ficus subterranea* Corner var. *pubescens* E.M.Gardner. **A.** Habit. **B.** Leafy twig, upper surface. **C.** Leafy twig, lower surface. **D.** Trunk. **E.** Stipule and leaf bases, upper surface. **F.** Stipule and leaf bases, lower surface. **G–I.** Figs. **J.** Fig interior with long-styled flowers. (Photos: E.M. Gardner)

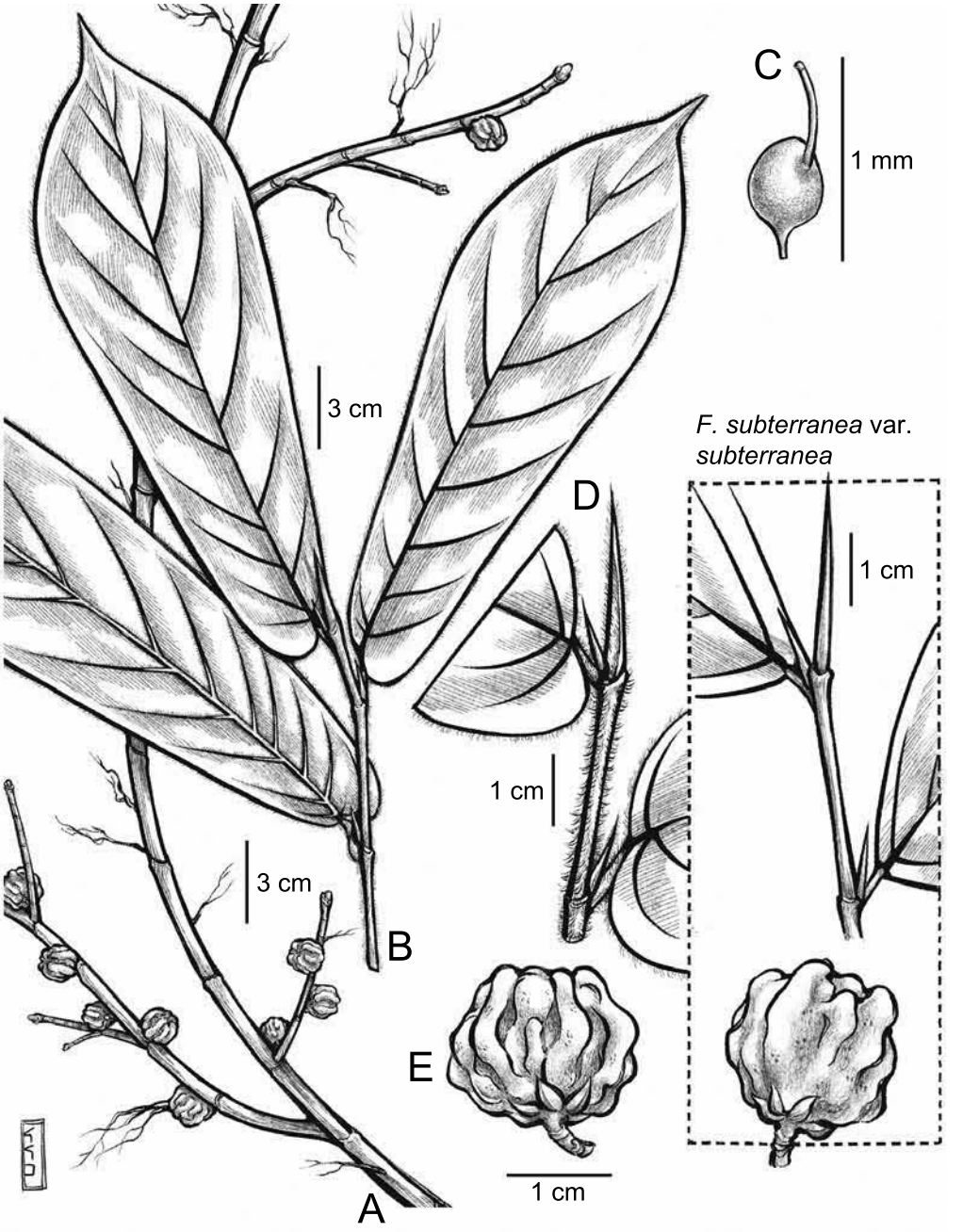

Fig. 20. *Ficus subterranea* Corner var. *pubescens* E.M.Gardner. **A.** Stolon with figs. **B.** Leafy twig. **C.** Long-styled flower. **D.** Twig showing leaf bases, stipule and pubescence. **E.** Fig. Inset: *Ficus subterranea* Corner var. *subterranea*, showing glabrous twig with almost symmetrical leaf bases and fig. Drawn by K. Pham.

hirtellous on the main veins, scabrid, venation drying dark brown below, cystoliths visible beneath; secondary veins 10–14, curved and ascending glands present in at least a few axils, the veins usually not furcate away from the margin except in very large leaves; petiole 3–5 mm long, indumentum same as twig but slightly denser. ***Figs*** on branching stolons up to at least 5 m long originating from the base of the stem or sometimes on flagellae originating from the upper parts of the tree, internodes up to 5 cm long; stipules persistent; peduncle 3–4(–15) mm long; basal bracts 8–10, spirally arranged on the peduncle; receptacle subglobose, 9–13 mm diam. when dry, often keeled, sparsely yellowish to rust-coloured subappressed puberulent to subglabrous; lateral bracts triangular, subappressed, fairly thin when dry, c. 3.5 mm long, and scattered throughout the surface of the receptacle; ostiole convex to concave, tightly covered with many overlapping bracts, c. 0.5 mm diam. (c. 3 mm in section including the internal bracts). ***Long-styled flowers*** without perianth; style glabrous, stigma funnel-shaped; fruits keeled. ***Short-styled flowers*** not seen.

Distribution and habitat. Borneo (Sarawak, Kapit), in secondary hill dipterocarp forest, in wet areas along small streams or at the bottom of slopes, up to c. 500 m in elevation.

Etymology. The epithet refers to the indumentum on the vegetative parts of this variety.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Ulu Sungai Bena, 16 Jul. 2023, *Gardner et al. 1335* (SAR, SING [SING0397775]), *1340* (SAR, SING [SING0397778]), *1341* (SAR, SING [SING0397776]); Kapit District, Sungai Senantang, 18 Jul. 2023, *Gardner et al. 1390* (SAR, SING [SING0397777]).

Notes. The pollinator has not yet been identified. If further investigation reveals variety-specific pollinating wasps, then species-level treatment would likely be warranted. The two varieties of *Ficus subterranea* may hybridise. One collection, *E. Gardner et al. 1341*, is intermediate between var. *subterranea* and var. *pubescens*, with pale sparse appressed hairs instead of the darker patent hairs.

13. *Ficus uncinata* (King) Becc., For. Borneo 527 (1902); Merrill, Bibliogr. Enum. Born. Pl.: 228 (1921); Corner, Gard. Bull. Singapore 18: 58 (1960); Corner, Gard. Bull. Singapore 21: 91 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 310 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 461 (2005); Berg & Chantarasuwan, Blumea 52(2): 324 (2007) – *Ficus geocarpa* Teijsm. ex Miq. var. *uncinata* King, Ann. Roy. Bot. Gard. (Calcutta) 1: 102, t. 129 (1888); Winkler, Bot. Jahrb. Syst. 49: 363 (1913). – TYPE: Borneo [Malaysia], Sarawak, September 1866, *Beccari P.B. 2458* (lectotype FI [FI013358 – a single specimen over 2 sheets], designated by Kochummen, Tree Fl. Sabah & Sarawak 3: 310 (2000); isolectotype K [K001050609]). (Fig. 21)

Fig. 21. *Ficus uncinata* (King) Becc. **A.** Habit with leafy twigs, upper surface. **B.** Leafy twig, lower surface. **C.** Trunk with figs at base of stolon. **D.** Stipule and young leaf. **E, F.** Figs on stolons. **G.** Mature fig. **H.** Fig interior with developing fruits. (Photos: E.M. Gardner)

Distribution and habitat. Borneo (Sarawak, Brunei, Sabah, and Kalimantan), in evergreen forests up to c. 1,100 m in elevation.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Sg. Balang, 12 Jul. 2023, *Gardner et al. 1276* (SAR, SING [SING0397756]), *1277* (SAR, SING [SING0397754); Kapit District, Sungai Bena, 10 Jul. 2023, *Gardner et al. 1244* (SAR, SING [SING0397864]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1348* (SAR, SING [SING0397757]); Kapit District, Sg. Sebatu, 14 Feb. 2020, *Gardner et al. 878* (SAR, SING), *880* (SAR, SING [SING0401883]); Kapit District, Sg. Senantang, 18 Aug. 2023, *Gardner et al. 1389* (SAR, SING [SING0397759]); Kapit District, Sungai Sulubok, 10 Aug. 2022, *Gardner et al. 1153* (SAR, SING [SING0397953]); Nanga Merit, Sungai Raya, 13 Jul. 2023, *Gardner*

et al. 1289 (SAR, SING [SING0397753]), *1291* (SAR, SING [SING0397755]), *1296* (SAR, SING [SING0397758]), *1297* (SAR, SING [SING0397752]); Nanga Merit, Ulu Aya, 13 Jul. 2023, *Gardner et al. 1287* (SAR, SING [SING0397760]).

Notes. The description in Berg & Chantarasuwan (2007) needs no emendation and reflects a narrowing of that taxon to the rather homogenous type variety.

Ficus uncinata is the commonest earth fig in Kapit, particularly common along roadsides. Its leaves can be instantly recognised by the small number of secondary veins, strongly asymmetrical and auriculate base, and long acumen. The figs are equally distinctive, rather densely hispidulous with stiff, patent, hooked (uncinate) bracts, with filiform apices. The seed figs are delicious when ripe, not unlike strawberry jam.

The following species belongs not to the Geocarpicae clade but to a sister clade containing mostly cauliflorous species. It is included here because it has a stoloniflorous habit similar to that of the Geocarpicae species is often found growing in the same habitats.

14. *Ficus treubii* King, Ann. Roy. Bot. Gard. (Calcutta) 1: 105, t. 134 (1888); Merrill, Bibliogr. Enum. Born.: Pl.: 228 (1921); Corner, Gard. Bull. Singapore 21: 91 (1965); Kochummen, Tree Fl. Sabah & Sarawak 3: 310 (2000); Berg & Corner, Fl. Males., ser. I, 17(2): 460 (2005). – TYPE: Borneo [Malaysia], Sarawak, Pangkalan Ampat, November 1866, *Beccari P.B. 2800* (lectotype FI [FI013356], designated by Kochummen, Tree Fl. Sabah & Sarawak 3: 310 (2000); isolectotypes K [K001050618], P [P06755179]). (Fig. 22)

Distribution. Borneo, in evergreen forests up to 1,600(–2,000) m in elevation.

Vernacular name. Entimau (Iban).

Additional specimens examined. MALAYSIA: **Sarawak:** Kapit District, Sg. Balang, 9 Aug. 2022, *Gardner et al. 1150* (SAR, SING [SING0397938]), *1151* (SAR, SING [SING0397940]); ibidem, 12 Jul. 2023, *1273* (SAR, SING [SING0389186]), *1274* (SAR, SING [SING0389187]); Kapit District, Bukit Goram, Sg. Apoh, 17 Jul. 2023, *Gardner et al. 1357* (SAR, SING [SING0397897]); Kapit District, Sg. Senantang, 11 Aug. 2022, *Gardner et al. 1174* (SAR, SING [SING0397954]); ibidem, 18 Aug. 2023, *1381* (SAR, SING [SING0397898]); Nanga Merit, Ulu Aya, 13 Jul. 2023, *Gardner et al. 1286* (SAR, SING [SING0389185]).

Notes. The description in Berg & Corner (2005) needs no emendation. The cut twigs of *Ficus treubii* quickly oxidise purple. It is also the only species present in Kapit with long stolons but with only one or two lateral bracts on the figs. The figs are not always borne on stolons at ground level; they can also arise from aerial flagellae arising from the lower part (c. 1 m) of the trunk. *Ficus treubii* is (so far) the only stoloniflorous fig in Kapit that does not belong to the Geocarpicae clade.

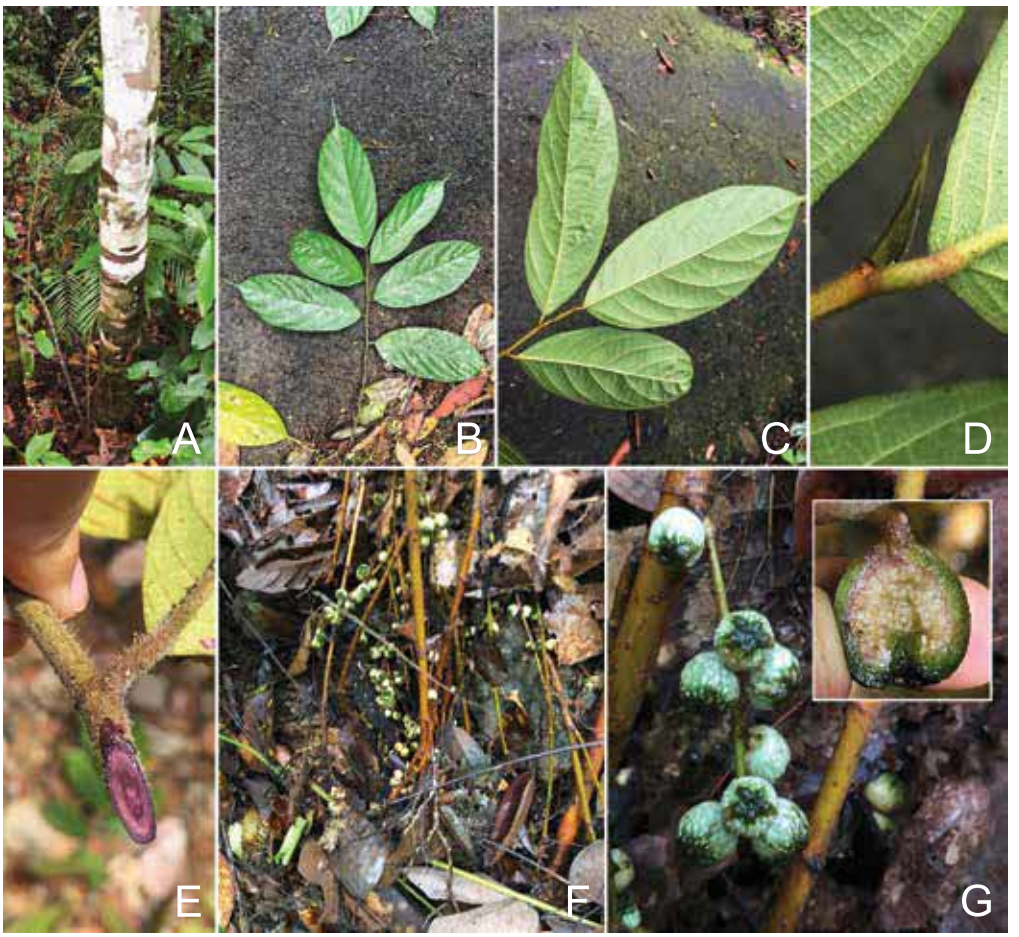

Fig. 22. *Ficus treubii* King. **A.** Trunk. **B.** Leafy twig, upper surface. **C.** Leafy twig, lower surface. **D.** Stipule and petiole. **E.** Cut twig oxidising purple. **F.** Stolons with figs. **G.** Close-up of figs on stolon (inset: cut fig with developing fruits). (Photos: E.M. Gardner)

Conclusion

This study highlights Kapit as a major centre of diversity for earth figs, provides an updated guide for field identification, and serves as a baseline for further study. Additional studies focusing on Sabah (currently underway) and other areas will provide a fuller picture of the still-underappreciated diversity of these figs.

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