

## FIGS OF GUNUNG PALUNG NATIONAL PARK (WEST KALIMANTAN, INDONESIA)

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### ABSTRACT

*Ficus* species (Moraceae) are diverse and ecologically important plants in the forests of Indonesia, and have been a focus of research during the past ten years at Gunung Palung National Park, West Kalimantan. Fifty-six species and five varieties of figs at Gunung Palung (GP) are described, including a new species, *F. palungensis*, and a new variety, *F. binnendykii* v. *pallescens*. Accompanying the paper is an interactive key to species identification, available by internet at [www.herbaria.harvard.edu/software/navikey/figkey](http://www.herbaria.harvard.edu/software/navikey/figkey). In addition, we review the ecology of figs at GP in terms of pollination, dispersal and growth. Patterns of species abundance are outlined and the major ecological role of hemiepiphytic strangler figs in lowland dipterocarp forests is discussed. Comparisons of species composition at GP to other regional sites suggest biogeographic patterns and strategies for species conservation in Indonesia.

Keywords: Figs, *Ficus*, Kalimantan, ecology, taxonomy, interactive key

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### INTRODUCTION

Figs (*Ficus* spp., Moraceae) are species rich and ecologically important plants in the forests of Borneo. Research at Gunung Palung National Park (GP) in West Kalimantan, Indonesia has focused on aspects of fig ecology including seedling establishment (Laman, 1995a, 1995b), seed dispersal (Laman, 1996a, 1996b) and host preferences in hemiepiphytes (Laman, 1996c), as well as phenology and frugivory. For example, figs play an important role in the diets of endangered vertebrates such as orangutans that are also being studied at GP (Knott, 1998).

Due to the extreme species richness of figs at GP, we believe that tools for the identification of species will be useful to current and future research projects. We have developed a computerized, interactive key to the figs of GP and this paper serves as a reference for identification. We include taxonomic descriptions and ecological notes for 56 species and five varieties, including a new species *F. palungensis*, and a new variety, *F. binnendykii* v. *pallescens*. Based on ten years of experience and extensive collecting during 1996-1997, we are confident that we have accurately documented the figs of GP, especially in primary lowland forest. We estimate that nearly half of the 130 fig species known from Borneo are found at GP (Corner, 1958). Although more species may await discovery, we believe that it is an appropriate time to review the figs of GP and

to present a key to their identification. To supplement the key and species descriptions, we discuss ecological aspects of the fig community at GP and compare the species composition at GP to other sites in Borneo and in the region as a whole.

### Study Site

Gunung Palung National Park, located in West Kalimantan Province, Indonesia (Fig. 1) is unique in that it protects a wide range of contiguous habitat types. The park covers an area of approximately 90,000 ha close to the west coast of Kalimantan, and completely encompassing Mount Palung with its range of concentric habitats from sea level to 1100 m. Although the mountain is not high compared with some others in Borneo, due to its isolation and proximity to the coast, vegetation zones are compressed on this peak (MacKinnon, 1996). Thus the summit ridges at 1000 to 1100 m above sea level (asl) are covered with a mossy montane forest formation not found below 1800 m asl on Mt. Kinabalu. Within the park's borders, eight distinct forest formations or habitats can be distinguished. This is why the park is of such great botanical interest and conservation importance.

**Mangrove forest** occurs mostly outside the park, along the larger river courses and coastline. Some small areas of mangrove fall within the park. **Peat swamp forest** occurs in flood plains and in poorly drained areas where lenses of peat have formed between river courses. Large tracts of **freshwater swamp forest** are interdigitated with peat swamp forest, usually nearer to the rivers in better-drained areas. **Lowland mixed dipterocarp forest on alluvium** is also sometimes called *Dipterocarpus* forest because the genus is common here and this habitat also supports the largest trees in the park. **Lowland mixed dipterocarp forest on sandstone** is contiguous with alluvial forest and extends to an elevation of about 150 m asl on the lower foothills of the mountain. This forest grows on sandy clay soils derived from sedimentary rocks such as sandstone or mudstone. **Lowland hill dipterocarp forest on granite** occurs at slightly higher elevations, from 150 to 400 m asl, on granite-derived podzolic soils. In **submontane hill forest on granite**, found between 400 and 800 m asl, dipterocarps become less dominant and tree size declines. The largest trees in this zone are conifers in the genus *Agathis*. In **montane forest** from 800 m to the highest point in the park just over 1100 m asl, *Casuarina*, *Leptospermum*, Ericaceae and tree ferns can be found. Often covered in clouds, this forest zone supports rich bryophyte communities. Along the highest ridge tops, the trees are stunted and densely cloaked in moss.

Our principal focus was on undisturbed primary forest. Gunung Palung is one of the few remaining areas in Borneo with intact lowland vegetation. We based our field work and most of our collecting at the Cabang Panti Research Site located at the base of the west side of Mt. Palung (1°13'S, 110°7'E), within boat or foot access to all of the above habitats. The climate at this site is perhumid according to Whitmore (1985). The mean annual rainfall of 4300 mm is relatively evenly distributed throughout the year, although one or more dry months have occurred in drought years.

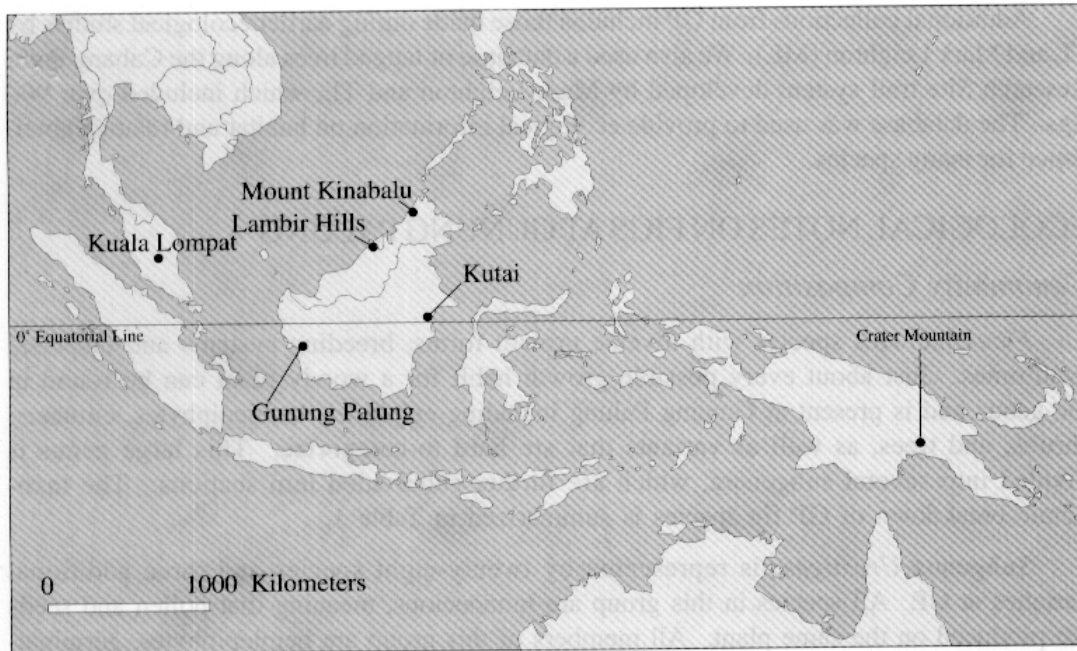


Figure 1. Location of Gunung Palung National Park (West Kalimantan, Indonesia) and five other conservation areas in the region. Figs at GP are compared to Kutai National Park (East Kalimantan); Mount Kinabalu National Park in (Sabah, Malaysia); Lambir Hills National Park (Sarawak, Malaysia); Kuala Lumpur Reserve (Peninsular Malaysia); and Crater Mountain Wildlife Management Area (Papua New Guinea) in Table 2.

## METHODS

Most of our specimens and observations were gathered during intensive collecting trips to GP in 1996 and 1997. We used a small longboat to explore the rivers and we traveled on foot along streams, ridges and the trail system of the Cabang Panti Research Site. Our collecting ranged from coastal forest, where the park extends to the sea near Sukadana, to the highest ridge tops of Mount Palung.

We attempted to be as comprehensive as possible in gathering information using a variety of approaches and techniques. Fertile specimens from plants less than 12 m in height were harvested using a pole pruner. Specimens under 30 cm dbh that could not be reached with a pole pruner were free climbed by local assistants. We accessed larger trees using the single rope technique. This technique involves shooting a small line over a branch with a slingshot or bow and pulling up a climbing rope which is then ascended using mountaineering equipment. As this technique was more time consuming, it was used selectively to obtain specimens that would have otherwise been inaccessible. Specimens were deposited at Herbarium Bogoriense and up to ten duplicates were distributed to the following herbaria: A, AAU, CANB, E, K, L, TI, WAN, SING .

Additional collections from GP included those made during earlier ecological studies by TL and Mark Leighton (ML). We also used a database of tagged trees along the Cabang Panti Research Site trail system developed by Mark Leighton and TL, which included over 900 figs. The database was used to provide ecological information on habitat and relative abundance for many species.

## ECOLOGICAL NOTES ON FIGS AT GUNUNG PALUNG

### *Community Composition*

*Ficus* includes species with diverse growth forms, breeding systems and dispersal syndromes. Just about every possible growth habit for a woody plant can be found in the genus and is present at Gunung Palung including epiphytes, hemiepiphytes, climbers, shrubs, and trees, as well as variants that are hard to categorize. This large genus is divided into several subgenera, which are further subdivided into sections. The taxonomic breakdown of GP fig species is summarized in Table 1.

Subgenus *Urostigma* is represented by twenty-eight species and three additional varieties at GP. All species in this group are monoecious, meaning that pollen and seeds are produced on the same plant. All members of this group are hemiepiphytes, germinating on other trees and sending roots to the ground. They vary in their ultimate size, however. Some species strangle and kill their host tree and become free-standing. Others remain dependent on their hosts for support throughout life, producing crowns rivaling those of the largest dipterocarps or smaller crowns in the middle canopy.

Subgenus *Ficus* is represented by twenty-eight species and two additional varieties at GP. Five different sections of this group are represented at GP. Section *Ficus* includes the epiphytic *F. deltoidea* and several species of shrubs or small trees. Sections *Rhizocladus* and *Kalosyce* include climbers which germinate on the ground and ascend their hosts. Section *Sycidium* is represented at GP by small hemiepiphytes and shrubs in the understory. Lastly, sections *Neomorphe* and *Sycocarpus* include small to medium-sized trees with cauliflorous or geocarpic figs. All species in subg. *Ficus* are dioecious, meaning that pollen and seed are produced on separate plants. Pollen-producing plants serve as hosts for mutualistic fig wasps that carry the pollen to the seed-producing plants. Monoecious and dioecious fig species at GP are nearly equal in number.

### *Fig Pollination*

Fig pollination is one of the most studied examples of obligate mutualism and comprehensive reviews include Bronstein (1992) and articles in Compton (1996). GP provides a natural laboratory in which to study interactions between figs and their pollinators. We provide a sketch of fig pollination in general, a summary of pollination observations from GP, and an outline of questions for future research at GP.

The pollination syndrome and specialized inflorescence are unique features of *Ficus* (Berg, 1990). The fig is an enlarged receptacle bearing hundreds of unisexual florets and enclosed by a bract-lined opening. Figs are exclusively pollinated by female fig wasps in the subfamily Agaoninae of parasitic Hymenoptera, which actively pollinate the florets while

galling a fraction of the fig ovaries (Galil and Eisikowitch, 1968). As larvae, fig wasps are seed predators, destroying the ovaries they occupy. The ultimate fate of the ovaries as either seeds or larval galls is determined by the interaction of style lengths and ovipositors (Ganeshaiah *et al.*, 1995). In monoecious fig species, seeds and wasps develop within each fig due to the combination of long and short-styled florets (Berg, 1989). In dioecious species, seeds and wasps develop in different figs on separate plants (Weiblen *et al.*, 1995). Functionally speaking, female figs contain long-styled, seed-producing florets and male figs contain short-styled gall florets and staminate florets.

In general, the associations between figs and their pollinators are host-specific. In other words, each fig species is pollinated by a unique fig wasp species (Ramirez, 1970 but see Michaloud *et al.*, 1996). We have reared pollinators from 12 fig species at GP (Table 1), including five fig species with previously unknown pollinators. However, pollinator associations are still unknown for one third of the figs at GP.

Based on our observations and those of Wiebes (1994), the fig wasp assemblage at GP reflects the general pattern of taxonomic congruence between *Ficus* sections and pollinating genera. For example, dioecious section *Ficus* and section *Sycidium* subsect. *Paleomorphe* are pollinated by *Blastophaga* and *Liporrhopalum*, respectively. Climbers in sects. *Rhizocladus* and *Kalosyce* are pollinated by *Wiebesia* while cauliflorous trees in sects. *Neomorphe* and *Sycocarpus* are pollinated by *Ceratosolen*. Agreement between fig and pollinator classification is suggestive of coevolution (Wiebes, 1987) but detailed field studies of pollination among sympatric and closely related fig species are needed. Monoecious figs in sect. *Conosycea* at GP are ideal for comparative studies of pollination. Of 27 species at GP, the majority are pollinated by *Waterstoniella* and we need to know their patterns of association in more detail. For example, is the pollinator of *F. sundaica* v. *beccariana* distinct from the pollinator of *F. sundaica* v. *impressicostata*? Instances of figs with multiple pollinators or pollinators with multiple hosts require further investigation. For example, we reared two species of *Waterstoniella* from *F. pellucido-punctata* at GP. Also, *Wiebesia minuta* was recorded from *F. excavata* and *F. villosa* (Wiebes, 1994). *Ficus deltoidea* is represented by three varieties at GP and we do not know the host range of the pollinator *Blastophaga quadrupes*. Reproductive morphology should also be studied in relation to pollinators. Species in series *Perforatae* sect. *Conosycea* (*F. binnendykii*, *F. pellucido-punctata* and *F. pisocarpa*) have internal ostiolar bracts that do not overlap, leaving an open passage for the entry and exit of pollinators from figs. Also, *F. retusa* is unique in that the styles completely fill the fig interior and form a column leading to the ostiole where pollinators are trapped in a small cavity below the ostiolar bracts.

The pollination mutualism is also impacted by non-pollinating fig wasps, including gallers and parasitoids (Compton, 1994). At GP, gall-making subfamilies Otitesellinae and Epichrysomallinae were reared from figs in section *Conosycea*. Among the parasitic fig wasps in the subfamily Sycoryctinae, *Sycoscapter* were found to attack pollinators in most figs. However, *Watshamiella* were reared only from *Conosycea* figs, while *Apocrypta* were found only in figs belonging to sections *Neomorphe* and *Sycocarpus*. The host-specificity of non-pollinating fig wasps and their impact on the pollination mutualism are interesting areas for exploration.

## 250. Figs of Gunung Palung.

Table 1. *Ficus* species in Gunung Palung National Park (Kalimantan, Indonesia) arranged according to the subgenera and sections of Corner (1965). Some characters listed for each species are coded [1] breeding system (m)onoecious or (d)ioecious; [2] growth habit (h)emipiphyte, (e)piphyte, (c)limber, (s)hrub or (t)ree; [3] fig position (a)xillary, (c)auliflorous or (g)eocarpic; [4] • indicates pollinators collected at Gunung Palung. Names of pollinators are based on Wiebes (1994).

<i>Ficus</i>	1	2	3	4	pollinator
subg. <i>Urostigma</i>					
sect. <i>Urostigma</i>					
<i>caulocarpa</i> Miq.	m	h	a		<i>Platyscapa fisheri</i> Wiebes
sect. <i>Conosycea</i>					
<i>acamptophylla</i> Miq.	m	h	a		<i>Waterstoniella obvenata</i> Wiebes
<i>annulata</i> Bl.	m	h	a		<i>Deilagaon annulatae</i> Wiebes
<i>benjamina</i> L.	m	h	a		<i>Eupristina koningsbergeri</i> Grand
<i>binnendykii</i> Miq.	m	h	a	•	<i>Waterstoniella borneana</i> Wiebes
v. <i>pallescens</i> Weiblen v. nov.	m	h	a		
<i>callophylla</i> Bl.	m	h	a	•	indet.
<i>consociata</i> Bl.	m	h	a		<i>Waterstoniella malayana</i> Wiebes
<i>crassiramea</i> Miq.	m	h	a		<i>Waterstoniella cuspidis</i> Wiebes
<i>cucurbitina</i> King	m	h	a		
<i>delosyce</i> Corner	m	h	a	•	<i>Waterstoniella delicata</i> Wiebes
<i>dubia</i> Wall. ex King	m	h	a	•	<i>Waterstoniella</i> sp.
<i>globosa</i> Bl.	m	h	a		
<i>kerkhovenii</i> Val.	m	h	a		<i>Eupristina leightoni</i> Wiebes
<i>lowii</i> King v. <i>minor</i> Corner	m	h	a		
<i>microcarpa</i> L.	m	h	a		<i>Eupristina verticillata</i> Waterson
<i>palungensis</i> Weiblen sp. nov.	m	h	a		
<i>paracamptophylla</i> Corner	m	h	a		
<i>pellucido-punctata</i> Griff.	m	h	a	•	<i>Waterstoniella brevigena</i> Wiebes
<i>pisocarpa</i> Bl.	m	h	a		
<i>retusa</i> L. v. <i>borneensis</i> Corner	m	h	a		<i>Waterstoniella javana</i> Wiebes
<i>spathulifolia</i> Corner	m	h	a		
<i>stricta</i> Miq.	m	h	a		
<i>stupenda</i> Miq.	m	h	a	•	<i>Waterstoniella masii</i> (Grandi)
<i>subgelderii</i> Corner v. <i>rigida</i> Corner	m	h	a	•	<i>Waterstoniella</i> sp.
<i>subtecta</i> Corner	m	h	a		
<i>sundaica</i> Bl.	m	h	a		<i>Waterstoniella sundaica</i> Wiebes
v. <i>beccariana</i> (King) Corner	m	h	a		
v. <i>impressicostata</i> Kochummen	m	h	a	•	<i>Waterstoniella</i> sp.
<i>tristanifolia</i> Corner	m	h	a		
<i>xylophylla</i> Wall. ex Miq.	m	h	a		<i>Waterstoniella grandii</i> Wiebes
subg. <i>Ficus</i>					
sect. <i>Ficus</i>					
<i>aurata</i> Miq.	d	st	a		<i>Blastophaga auratae</i> Wiebes
<i>deltoidea</i> Jack	d	e	a		<i>Blastophaga quadrupes</i> Mayr
v. <i>borneensis</i> Corner	d	e	a		
v. <i>motleyana</i> (Miq.) Corner	d	s	a		

Table 1. (Continued).

<b>Ficus</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>pollinator</b>
<i>glandulifera</i> (Wall. ex Miq.) King	d	t	a		<i>Blastophaga sensillata</i> Wiebes
<i>grossularioides</i> Burm f.	d	st	a	•	<i>Blastophaga malayana</i> Wiebes
sect. <i>Rhizocladus</i>					
<i>callicarpides</i> Corner	d	c	a		
<i>disticha</i> Bl.	d	c	a		<i>Wiebesia corneri</i> Wiebes
<i>excavata</i> King	d	c	a		<i>Wiebesia minuta</i> Wiebes
<i>lanata</i> Bl.	d	c	a		<i>Wiebesia boldinghi</i> (Grandi)
<i>recurva</i> Bl. v. <i>bridelioides</i> Corner	d	c	a		
<i>sagittata</i> Vahl	d	c	ac		<i>Wiebesia flava</i> Wiebes
<i>trichocarpa</i> Bl.	d	c	ac		<i>Wiebesia vechti</i> Wiebes
<i>urnigera</i> Miq.	d	c	a		<i>Wiebesia sensillata</i> Wiebes
<i>villosa</i> Bl.	d	c	a		<i>Wiebesia minuta</i> Wiebes
sect. <i>Kalosyce</i>					
<i>punctata</i> Thunb.	d	c	ac	•	<i>Wiebesia punctatae</i> Wiebes
<i>ruginerva</i> Corner	d	c	ac	•	<i>Wiebesia</i> sp.
sect. <i>Sycidium</i>					
<i>hemsleyana</i> King	d	h	c		<i>Liporrhopalum hemsleyanae</i> Hill
<i>heteropleura</i> Bl.	d	hc	a		<i>Liporrhopalum dubium</i> (Grandi)
<i>obscura</i> Bl. v. <i>borneensis</i> (Miq.) Corner	d	hc	a		
<i>parietalis</i> Bl.	d	hs	a		
<i>sinuata</i> Thunb.	d	hs	a		<i>Liporrhopalum longicornus</i> (Grar
<i>subulata</i> Bl.	d	hc	a		<i>Liporrhopalum erythropareiae</i> Hi
sect. <i>Neomorphe</i>					
<i>variegata</i> Bl.	d	t	c	•	<i>Ceratosolen appendiculatus</i> (Ma
sect. <i>Sycocarpus</i>					
<i>beccarii</i> King	d	t	g		<i>Ceratosolen humatus</i> Wiebes
<i>geocharis</i> Corner	d	t	g		
<i>schwartzii</i> Koord.	d	t	c		<i>Ceratosolen vetustus</i> Wiebes
<i>stolonifera</i> King	d	t	g		<i>Ceratosolen</i> sp.
<i>tarennifolia</i> Corner	d	t	ac		
<i>uncinata</i> Becc.	d	t	g		<i>Ceratosolen albulus</i> Wiebes

### *Frugivores and Fig Seed Dispersal*

In contrast to the host-specific associations between *Ficus* species and their pollinators, seed dispersal is accomplished through more generalized associations with vertebrate frugivores. Figs are eaten by many different animals, who mostly pass the seeds undamaged through their digestive tracts and disperse them in the process. Most ripe crops of figs are visited by more than one animal species and different fig species may attract different guilds of animals. Animal feeding preferences appear to be influenced by traits including the position of the figs on the plant as well as fig color, size, and nutritional content.

The distinctive geocarpic species bear figs on runners at the soil surface or just below it. These species are presumably fed on and dispersed by terrestrial vertebrates such as pigs and deer (Corner, 1940), but this aspect requires further study. A second dispersal syndrome occurs in the cauliflorous species that bear figs in clusters along the trunk and branches. Figs positioned away from dense foliage are accessible to large fruit bats that feed on cauliflorous species such as *F. variegata* (Spencer *et al.*, 1996). However, monkeys, other mammals and birds also feed on cauliflorous figs. Lastly, figs positioned at the tips of leafy branches are fed on largely by birds but also by primates, squirrels, and other mammals (Lambert, 1989, 1990). Major fig consumers at GP include birds such as hornbills, barbets, pigeons, and bulbuls, and mammals such as orangutans, gibbons, leaf monkeys, macaques, squirrels, binturongs, and bats (pers. obs.).

The dioecious fig species face an interesting problem related to pollination and seed dispersal. Seed production requires that wasps pollinate female figs but there is an advantage in wasps' recognizing and avoiding female figs, where pollinators are entombed and do not reproduce. Prior to pollination, male and female figs are indistinguishable to wasps from the outside. After pollination, it is advantageous for female figs to be dispersed by frugivores while uneaten male figs produce more pollinators. Studies suggest that although male and female figs appear similar prior to pollination, they ultimately differ in size, coloration and palatability when ripe (Lambert, 1992, Weiblen *et al.*, 1995). Ripe male figs are often ignored by frugivores that prefer to eat female figs of the same species, even though male figs tend to be larger than female figs when ripe (Lambert, 1992 and pers. obs.). The possibility of opposing selection pressures on dioecious pollination and dispersal is an interesting evolutionary hypothesis.

Dioecious species in sections *Sycidium* and *Sycocarpus* generally occupy the moist and shady lower forest strata at GP, in contrast to monoecious species in subgenus *Urostigma*, which are generally larger, light-demanding plants in the middle to upper canopy. The dioecious species produce relatively small fig crops compared to *Urostigma* species that produce millions of seeds per crop (Laman, 1996a). Perhaps the abundance of upper canopy hemiepiphytic species is limited by the rarity of suitable establishment sites in the crowns of host trees, which may have selected for extremely large crop sizes in *Urostigma* (Laman, 1996a). In contrast, the understory hemiepiphytes and shrubs in subgenus *Ficus* have smaller crop sizes and may be less limited by the availability of suitable establishment sites. In either case, seed dispersal may be a critical factor limiting fig populations but this deserves further study.



In terms of the overall rain forest community at GP, *Urostigma* species play a more dominant role than species in subgenus *Ficus*. This is due to their greater biomass, abundance, and fruit production. They are an important resource for many species of birds and mammals, particularly due to asynchronous reproduction that ensures the year around availability of figs (reviewed in Spencer *et al.*, 1996). *Urostigma* species support vertebrates during periods when little else is available and these vertebrates may, in turn, be important dispersal agents for other tree species that fruit less regularly. Described as "keystone mutualists", *Urostigma* figs are the center of a web of interactions (Lambert and Marshall, 1991, Leighton and Leighton, 1983).

### *Growth Habits in Subgenus Urostigma*

Although the twenty-eight species of *Urostigma* figs at GP share the hemiepiphytic growth habit, they differ considerably in their ecology. One major difference among these species is the position they occupy in the forest canopy. In a comparison of five of the most common *Urostigma* species, Laman (1996c) showed significant differences in the height of establishment on host trees and in canopy position. For example, *F. stupenda* and *F. dubia* grow almost exclusively on large trees with crowns in the high canopy, while *F. xylophylla* preferentially occupies smaller trees with crowns in the lower canopy. It appears that to some extent, *Urostigma* species are specialized for distinct canopy microhabitats and this is an interesting area for further comparison.

The growth patterns of descending aerial roots in *Urostigma* species relates to the tendency of some species to become free-standing. We have observed only seven out of the twenty-eight species that regularly become free-standing. *Ficus benjamina* and *F. microcarpa*, two rare species at GP, have not been observed as free-standing trees, although they are known to become free-standing elsewhere. More common species, such as *F. stupenda* and *F. sundaica*, are reported to become free-standing (Corner, 1940) but we have not observed this at GP. For example, we have examined over 75 individuals of *F. stupenda*, many of which have enormous crowns, and not one is free-standing. These plants have one to several roots that are much smaller than the host trunk and incapable of supporting the fig. It may be the case that some species become free-standing in more open or disturbed habitats but do not become free-standing in primary forest, where the only way to meet their demand for light is to colonize canopy trees.

Among free-standing species, the way in which the roots support the crown varies considerably. In *F. caulocarpa*, numerous roots encircle the host trunk in a fused network. When the host tree dies and rots away, a hollow center remains. *F. kerkhovenii*, on the other hand, sends down one or more roots that expand along the host trunk. Instead of forming a rigid network around the host trunk, these roots develop flying buttresses that extend several meters above the ground and form a supporting base for the plant after the host dies. Another contrasting example is *F. tristanifolia*, which usually produces a single descending root that expands until it is larger than the host trunk and is capable of supporting the plant. Often the only indications that the plant began as an epiphyte are small, horizontal hoops that once wrapped around the bole of the host. In the evolution of the hemiepiphytic growth habit, it appears that different species have arrived at different solutions to the problems imposed by this unusual life history. This is another open area for research at GP.

### *Patterns of Habitat Distribution*

Our observations in primary forest habitats at the Cabang Panti Research Site indicate that fig species differ in terms of the habitats they occupy. Although we did not quantify fig abundance, we gathered data on the habitat distributions of species from field notes and from a list of over 900 hemiepiphytes along the Cabang Panti trail system. The total numbers of species collected or observed in each habitat shows a strong pattern. Numbers of taxa (including 56 species and 5 varieties) found in each habitat were as follows: peat swamp (19), freshwater swamp (34), alluvial bench (29), lowland sandstone (38), lowland granite (13), submontane granite (8), montane (2). Alluvial bench and lowland sandstone habitats, where the soils are the highest quality, were most rich in species. The higher count in the lowland sandstone is due to a number of geocarpic species which were absent from the alluvial bench. The richness of freshwater swamp is partly explained by its proximity to the Air Putih river, considering that riparian zones support many fig species.

The distribution of individual species also showed interesting patterns. Some species seem to be habitat generalists, such as *F. consociata*, which was common across the four lowland habitats. In other cases, we noted broad distributions with apparent preferences for particular habitats. For instance, *F. stupenda*, the most common large hemiepiphyte, is most abundant in the lowland sandstone and alluvial bench habitats but was less common in adjoining habitats. *Ficus binnendykii* was found in six different habitats but increased in abundance with elevation up to the submontane granite where it was the most common species. Other widely distributed species showed the opposite pattern. For example, *F. spathulifolia* was most abundant in the peat swamp forest and declined in abundance with respect to elevation. Some of the most restricted species occurred in swamp forest. For example, all twelve individuals of *F. tristanifolia* trees occurred in peat swamp. Also, *F. palungensis* was only found in peat and freshwater swamp. *F. xylophylla* was the only species observed in every habitat type and had the most intriguing distribution. Unlike other widespread species that showed a gradual decline in abundance away from their most common habitat, *F. xylophylla* was common in peat swamp and on the mountain but uncommon between these habitats. The mechanisms through which habitat specialization could be operating is potentially interesting, since hemiepiphytes colonize hosts prior to contacting the soil.

### *Species Composition Across Regional Sites*

We compared species found at Gunung Palung with other conservation sites in the region (Table 2). The sites range from Kuala Lompat in Peninsular Malaysia, to Crater Mountain in Papua New Guinea, and also include three sites from the island of Borneo; Kutai National Park in East Kalimantan, Mount Kinabalu in Sabah, and Lambir Hills National Park in Sarawak (Fig. 1). The similarity in the total number of species is quite remarkable across the three most comparable sites in lowland Borneo. At GP, Kutai, and Lambir, 56, 52, and 54 species were recorded, respectively (Table 2). Although the sites have similar species richness, there are substantial differences in species composition. In contrast, 78 species were recorded across the extreme range of habitats at Mt. Kinabalu. The slightly higher species richness at GP compared with the other two lowland Bornean sites may be due to the greater habitat diversity in GP, and especially swamp forests not present at the other sites. However,

not a single site encompasses all fig diversity in Borneo and this is likely to be true for other groups of organisms as well. In order to conserve biodiversity on a regional scale, we advocate the design of protected areas that are broadly distributed across the island.

Kutai has the greatest proportion of species in common with GP (68%), which may be due to the presence of lowland dipterocarp forest on sandstone hills at both sites. Fewer species are shared between GP and Kuala Lompat. The 25% in common may be due to the Sundaland connection between Peninsular Malaysia and Borneo or alternatively to long distance dispersal. In contrast, only three species are shared with the Papua New Guinea site, located on the other side of Wallace's Line.

The higher taxonomic distribution of *Ficus* across the sites shows geographic variation in the relative richness of different sections (Table 2). While Mt. Kinabalu is rather poor in subgenus *Urostigma*, it is most rich in subgenus *Ficus*, especially sections *Sycidium* and *Sycocarpus*. Lambir is also noticeably richer in subgenus *Ficus* than the

Table 2. Fig species richness in Gunung Palung compared to five other conservation sites in the region. We report the total richness per site, the number of species in common with GP, and the percentage in common. The number of species per section is listed according to the classification of Corner (1965). Other sites include Kutai National Park (KP) in East Kalimantan (M. Leighton, unpublished data); Mount Kinabalu National Park (MK) in Sabah, Malaysia (Corner, 1962); Lambir Hills National Park (LH) in Sarawak, Malaysia (Harrison, 1997); Kuala Lompat Reserve (KL) in Peninsular Malaysia (Lambert, 1989); and Crater Mountain Wildlife Management Area (CM) in Papua New Guinea (D. Wright, unpublished data).

	GP	KP	MK	LH	KL	CM
subg. <i>Urostigma</i>						
sect. <i>Urostigma</i>	1	2	2	1	2	0
sect. <i>Conosycea</i>	27	23	16	19	20	5
sect. <i>Malvanthera</i>	0	0	0	0	0	1
subg. <i>Pharmacosycea</i>						
sect. <i>Oreosycea</i>	0	1	0	0	0	6
subg. <i>Sycomorus</i>						
sect. <i>Sycomorus</i>	0	1	0	0	0	0
subg. <i>Ficus</i>						
sect. <i>Ficus</i>	4	3	10	7	1	0
sect. <i>Rhizocladus</i>	9	10	11	5	3	7
sect. <i>Kalosyce</i>	2	1	7	3	2	1
sect. <i>Sycidium</i>	6	6	14	8	5	13
sect. <i>Adenosperma</i>	0	0	0	0	0	10
sect. <i>Neomorphe</i>	1	1	1	0	1	3
sect. <i>Sycocarpus</i>	6	4	17	11	2	9
total species	56	52	78	54	36	55
species in common with GP		39	34	33	25	3
% of GP species in common		68	60	58	44	5

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other lowland Borneo sites, which may reflect the occurrence of more secondary forest species. GP and Kutai, on the other hand, are most rich in subgenus *Urostigma*, with 28 and 25 species, respectively. This richness is associated with undisturbed lowland dipterocarp forest at elevations below 100 m, also having with the highest vertebrate abundance and diversity in Borneo (Laman *et al.*, 1996, MacKinnon, 1996). This complementary diversity is not a coincidence because *Urostigma* species are important in the diets of many vertebrates, and this points to the importance of conserving the few remaining areas of lowland dipterocarp forest in Indonesia.

### INTERACTIVE KEY TO THE FIGS OF GUNUNG PALUNG

The interactive key which accompanies this paper resides on the internet at: [www.herbaria.harvard.edu/software/navikey/figkey](http://www.herbaria.harvard.edu/software/navikey/figkey)

The key can be displayed using Navikey, a Java applet developed at the Harvard University Herbaria. Alternatively, data can be downloaded from the web site and used with other taxonomic software such as Intkey (Dallwitz *et al.*, 1993). Interactive keys have many advantages over traditional keys, being accessible to users with a limited knowledge of botany. Interactive keys can also be automatically updated to incorporate new information and can be used in the field with laptop computers. We believe that the "figkey" has the potential to be expanded to include all the fig species of Borneo or perhaps all figs of Indonesia.

For each fig species and variety at GP, we coded information on aspects of growth, branching, leaves, stipules and figs in DELTA format (Dallwitz *et al.*, 1993). We also included detailed information on reproductive morphology that may be of interest to systematists. In the interest of making our key applicable to other localities, we have compared our descriptions to those of Primack (1983), Harrison (1997), Kochummen

Figure 2. Illustrations of fig characters and states redrawn from Corner (1967). (1) hollow twig in cross section; (2) twig with a waxy gland below each node; (3) leaf gland at the base of the midrib; (4) leaf glands paired in the axils of the basal veins; (5) solitary leaf gland in the axil of a basal vein; (6) leaf glands in the axils of secondary veins; (7) midrib; (8) basal vein; (9) secondary vein; (10) tertiary veins; (11) fine venation; (12) sessile fig; (13) peduncle with bracts at the bottom; (14) peduncle with bracts between the bottom and the top; (15) peduncle with bracts at the top; (16) fig basal bracts; (17) lateral bracts; (18) apical bracts; (19) ostiolar bracts; (20) monoecious fig with staminate florets dispersed; (21) dioecious seed fig with long-styled pistillate florets; (22) dioecious gall fig with short-styled pistillate florets and staminate florets around the ostiole; (23) pistillate floret with free tepals; (24) pistillate floret with tepals fused at the base; (25) pistillate floret with tepals fused and enclosing the ovary; (26) pistillate floret without tepals; (27) glabrous and entire perianth; (28) abaxial pubescence on perianth; (29) ciliate perianth margin; (30) dentate perianth margin; (31) glabrous and simple style; (32) setose style; (33) divided style; (34) funnelform style; (35) lenticular seed with a single ridge; (36) compressed seed; (37) tuberculate seed; (38) seed with two ridges arising from the hilum; (39) unistaminate floret; (40) bistaminate floret; (41) staminate floret with a pistillode; (42) staminate floret with a functional gall ovary; (43) filament with epidermal hairs at the base; (44) mucronate anther.

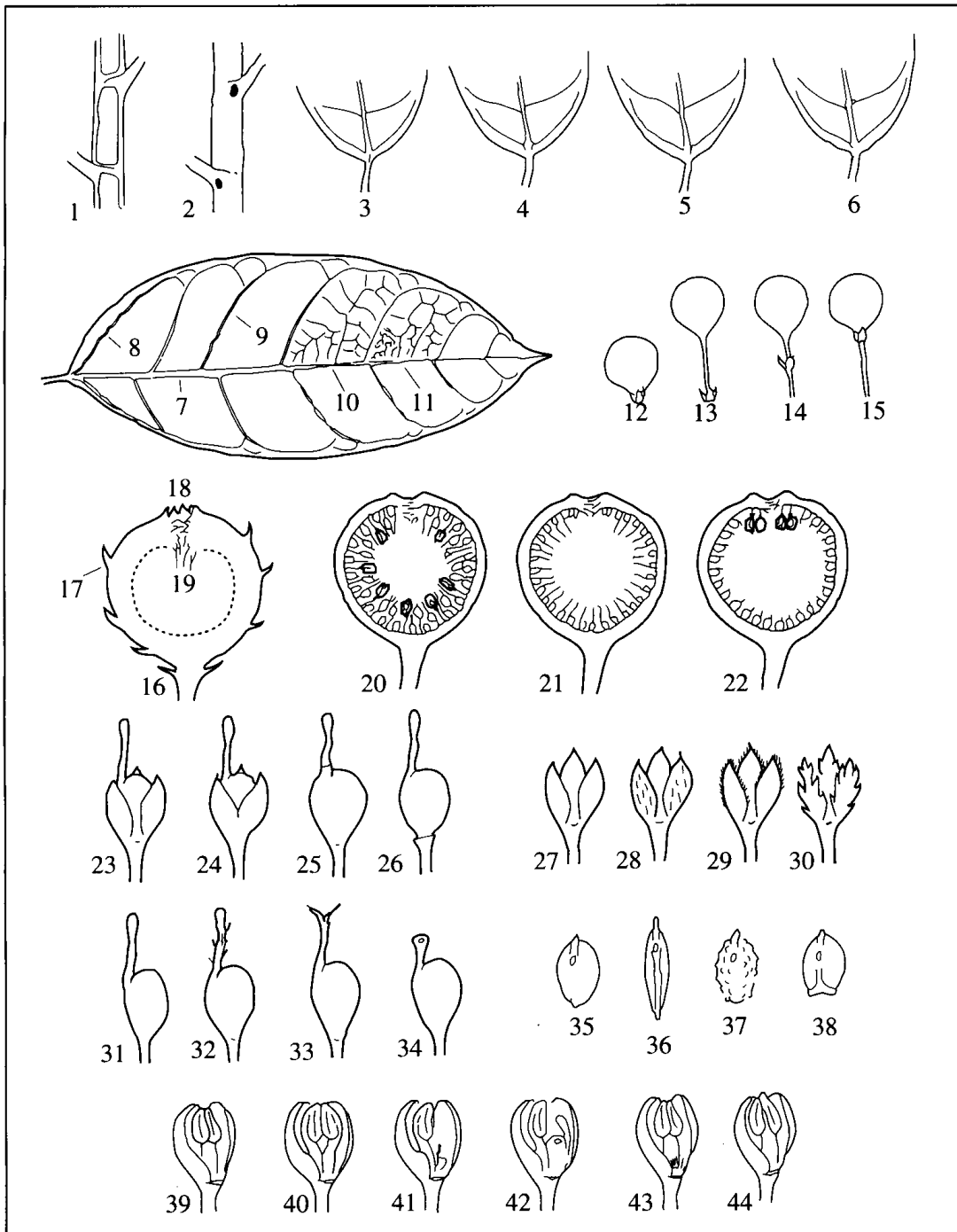


Figure 2. (caption on opposite page)

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(1978, 1998) from Malaysia. In very few cases, it was necessary to expand the ranges of measurements and qualitative characters to encompass broader geographic variation. We believe that our data encompass much of the morphological variation within each species' geographic distribution, however we urge caution when applying our descriptions outside of Kalimantan.

Measurements were taken from dried GP collections at the Harvard University Herbaria. In cases where fertile material was not available from GP, collections from elsewhere in Borneo were measured. Also note that the information contained in the key and in descriptions is based on mature plants and ripe figs. If working with fresh material, measures on figs can be converted to values approximating the dried condition by multiplying by 0.6. This "fresh fig factor" is taken from a regression of 240 ripe figs across a broad range of species and fig sizes ( $r^2 = 0.9$ ).

### *Characters and States*

This section provides definitions of fig characters and states for readers who are less familiar with botanical terminology. We included a total of 86 qualitative and quantitative characters in the interactive key. Fig. 2 illustrates some of the unique characters and states of figs which may not be familiar to readers.

**Growth habit:** [1] epiphyte with roots attached to host plant and not reaching the ground; [2] hemiepiphyte or strangler (established as an epiphyte with aerial roots descending to the ground); [3] climber (established at ground level and ascending host); [4] shrub (branching near the ground) or [5] tree (branching above breast height). Hemiepiphytic species may become free-standing and field notes often do not describe growth habit in precise terms. For these reasons, this character should be used with caution.

**Aerial roots** in mature hemiepiphytes or stranglers: [1] large compared to host tree or free-standing or [2] small compared to host tree and not free-standing. Not applicable to epiphytes, climbers, trees or shrubs. Hemiepiphytic stranglers with large aerial roots may become free-standing at maturity while other hemiepiphytes never become free-standing.

**Height** from ground to top of fig crown in m. **Diameter** at breast height (dbh in cm) is only applicable to trees. **Buttresses** in mature trees: [1] none or less than 0.5 m in height or [2] more than 1 m in height. This character is not applicable to epiphytes, hemiepiphytes, climbers, shrubs or immature trees. Buttresses increase in size with age and this character should only be considered in mature trees.

**Twig surface:** [1] glabrous (or glabrescent; without persistent hairs); [2] pubescent (with persistent hairs but not rough like sandpaper) or [3] scabrid (rough like sandpaper due to raised cystoliths). **Twig diameter** in mm. Measured along leaf-bearing twigs between five and ten nodes below the apical bud. **Twigs in cross section:** [1] not hollow (and without spongy pith); [2] hollow or with spongy pith. In some species, the expanded and spongy pith between the nodes may separate, forming a hollow twig (Fig. 2.1). **Twig glands:** [1] without a waxy gland below the node or [2] with a waxy gland below the node (Fig. 2.2). **Latex:** [1] white or [2] pale yellow to yellow.

**Stipules:** [1] caducous (falling) or [2] persistent. Stipules occurring at more than five nodes below the apical bud are considered to be persistent. **Stipule surface:** [1] glabrous or [2] pubescent. **Stipule length** in cm.

**Leaf arrangement:** [1] spiral; [2] distichous or [3] opposite.

**Petiole surface:** [1] glabrous; [2] pubescent or [3] scabrid. **Petiole length** in cm. Measured from the twig to the base of the lamina (leaf).

**Leaf (lamina) shape:** [1] elliptic (broadest in the middle, tapering toward the ends); [2] ovate (egg shaped, broadest toward the base, tapering toward the apex); [3] lanceolate (narrow, broadest toward the base); [4] obovate (ovate in shape but narrow at the base or spatulate); [5] cordate (heart-shaped) or [6] trilobed (with three lobes).

**Leaf surface:** [1] glabrous; [2] pubescent or [3] scabrid. **Leaf thickness:** [1] chartaceous (thin or papery) or [2] coriaceous (thick or leathery). **Leaf length** in cm. Measured along the midrib from the base of the leaf up to and including the apex (Fig. 2.7). **Leaf width** in cm. Measured at the widest point. **Length:width ratio** of leaf. **Leaf bud in cross-section:** [1] convolute (rolled in bud); [2] plicate (folded in bud).

**Leaf margin:** [1] entire (without teeth) or [2] serrate or dentate (with teeth). Leaves with ascending or looping secondary veins tend to have entire margins. Serrate or dentate leaves tend to have secondary veins terminating in the teeth. **Leaf base:** [1] cordate (heart-shaped); [2] cuneate (wedge-shaped) or [3] rounded. **Leaf base:** [1] symmetric or [2] asymmetric. Leaves that are unequal in area on either side of the midrib are considered to be asymmetric. **Leaf apex:** [1] pointed (acuminate to acute) or [2] rounded (blunt).

**Leaf venation:** [1] pinnate (with an unbranched midrib) or [2] dichotomous (with a branching midrib). **Basal veins** as in Fig. 2.8: [1] paired or [2] not paired. **Basal veins:** [1] as prominent as the secondary veins or [2] more prominent than the secondary veins. **Basal vein length:leaf length ratio**, varying between 0 and 1. **Basal vein angle** of departure from the midrib in degrees. Number of **secondary vein pairs** not including the basal veins. **Secondary veins** as in Fig. 2.9: [1] as prominent as tertiary veins or [2] more prominent than tertiary veins. **Secondary veins in dried leaves:** [1] not raised; [2] raised above and below; [3] raised below but not above; [4] raised above but not below. **Tertiary veins** as in Fig. 2.10. [1] scalariform (ladder-like, perpendicular to secondary veins) or [2] reticulate (net-like, not perpendicular to secondary veins). **Fine venation** as in Fig. 2.11: [1] areoles of more or less equal size (box-shaped) or [2] areoles of unequal size (irregular or not box-shaped).

**Leaf glands:** [1] none; [2] solitary at the base of the midrib (Fig. 2.3); [3] solitary in the axil of a basal vein (Fig. 2.4); [4] paired in the axils of the basal veins (Fig. 2.5); [5] in the axils of the secondary veins (Fig. 2.6) or [6] in the axil of the dichotomous midrib. A single gland at the base of the midrib is common in subg. *Urostigma*. Glands in the axils of basal or secondary veins are common in other taxa and they may be paired or solitary, as in some members of sect. *Sycidium*. Leaf glands appear to secrete cuticular wax which may be collected by insects.

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**Cystoliths:** [1] none; [2] abaxial (only on the lower surface); [3] paraxial (on the upper and lower surfaces) or [4] adaxial (only on the upper surface). Cystoliths are visible on leaves at 20x magnification. They are secretory cells distributed in the upper and lower epidermis of the leaf that contain calcium oxalate crystals.

**Stomata:** [1] not aggregated or [2] aggregated in sunken and foveate areoles (in hairy depressions). Stomatal pits are visible at 20x magnification in sect. *Kalosyce* and may be associated with the climbing habit, although they are absent in some climbing *Rhizocladus*.

**Fig position:** [1] axillary (in the axils of leaves or on leaf-bearing twigs); [2] cauliflorous (on aerial leafless branches or trunk); [3] geocarpic (on subterranean leafless branches). Figs often occur in the axils of leaves. As is common in Moraceae, paired inflorescences are located in the axils of the two lateral prophylls associated with each leaf, however, figs may also occur on specialized leafless branches borne at or above ground level.

**Fig position:** [1] sessile (without a stalk as in Fig. 2.12); [2] pedunculate (with a stalk as in Figures 2.13-2.15). The peduncle is an elongated inflorescence axis.

**Peduncle surface:** [1] glabrous; [2] pubescent or [3] scabrid. **Peduncle length** in mm. Measured from the twig to the base of the fig. **Fig basal bracts:** [1] at the bottom (Fig. 2.13); [2] between the bottom and the top (Fig. 2.14) or [3] at the top of the peduncle (Fig. 2.15).

**Fig shape:** [1] globose (as long as wide, approximately spherical); [2] oblong (longer than wide, rounded at the apex); [3] fusiform (longer than wide, tapering at both ends); [4] conical (cone-shaped, tapering toward the apex) or [5] obconical (cone-shaped, tapering toward the base). **Fig apex** excluding bracts: [1] rounded; [2] umbonate (protruding) or [3] sunken.

**Fig surface:** [1] glabrous; [2] pubescent or [3] scabrid. **Fig length** in mm. Measured from the base to the apex. **Fig width** in mm (diameter). Measured at the widest point. **Fig color** when immature and when ripe. Applicable only to fresh specimens. **Figs:** [1] without spots or [2] with spots. Applicable only to fresh specimens.

**Fig basal bracts** [1] caducous or [2] persistent in mature figs (Fig. 2.16). Three bracts below the fig or displaced along the peduncle correspond to a modified leaf and two prophylls. **Basal bract surface:** [1] glabrous or [2] pubescent. **Basal bracts:** [1] acuminate or [2] rounded. **Basal bracts:** [1] more or less equal in length or [2] unequal in length (one much shorter than the other two). **Basal bract length** in mm. Measured from the base to the apex. **Lateral bracts** on fig exterior (Fig. 2.17): [1] none or [2] few to many.

**Apical bracts** on fig exterior (Fig. 2.18): [1] 3, forming a flattened disc; [2] 3, forming a cone; [3] more than 3; [4] sunken and not visible on fig exterior. The number of bracts visible at the apex of the fig varies according to their degree of overlap and orientation. Three overlapping bracts forming a flat disc or cone are found in members of subg. *Urostigma*. More than three apical bracts are found throughout subg. *Ficus*, although it may not be possible to count them when they are sunken.



**Ostiolar bracts** (in cross-section of figs; Fig. 2.19): [1] overlapping or [2] not overlapping. Ostiolar bracts are involved in facilitating the entry of pollinators but preventing their escape from the fig. Figs have at least some internal ostiolar bracts that overlap except for species in series. *Perforatae* of sect. *Conosycea*.

**Breeding system** (Figures 2.20-2.22): [1] monoecious or [2] gynodioecious (functionally dioecious). Morphologically gynodioecious species are functionally dioecious due to interactions between the heterostylous florets and pollinating fig wasps.

**Fig inner epidermis**: [1] without glandular hairs or [2] with glandular hairs. **Pistillate florets**: [1] all without pedicels (sessile) or [2] varying from sessile to pedicellate. Most species have sessile and pedicellate florets within a single fig that correlate with style lengths to form a level stigmatic surface.

**Pistillate perianth** with: [1] tepals free (Fig. 2.23); [2] tepals fused at the base (Fig. 2.24); [3] tepals fused completely along their length (Fig. 2.25); [4] without tepals in seed figs (Fig. 2.26). The following three characters are not applicable to figs without tepals. **Pistillate perianth surface**: [1] glabrous (Fig. 2.27); [2] pubescent on the abaxial surface (Fig. 2.28). **Pistillate perianth color**: [1] white or [2] red. **Pistillate perianth margins**: [1] entire; [2] ciliate (hairy; Fig. 2.29) or [3] dentate (toothed; Fig. 2.30). Completely fused perianth may split secondarily due to the swelling of the galled ovaries in sect. *Sycocarpus*.

**Style position**: [1] subterminal to lateral or [2] gynobasic. **Style surface**: [1] glabrous (as in Fig. 2.31) or [2] setose in long-styled florets (hairy as in Fig. 2.31). Only long styles may be hairy so character is not applicable to gall figs in dioecious species. **Style shape**: [1] not divided or [2] divided at the apex (Fig. 2.33).

**Stigma**: [1] clavate (not funnel-shaped) [2] funnellform (funnel-shaped in gall figs; as in Fig. 2.34). Only applicable to gall figs in dioecious species. Short-styled florets in gall figs may be specially adapted to ovipositing fig wasps.

**Ovary position**: [1] superior (not embedded in the fig wall) or [2] inferior in seed-producing florets (embedded in the fig wall). Ovaries of seed-producing florets in sect. *Malvanthera* are embedded in the receptacle and surrounded by a layer of lignin. **Ovary color**: [1] white; [2] with a red spot near the base of the style or [3] red. Ovaries with a red spot on the stylar side occur in sect. *Conosycea*.

**Achene shape**: [1] not flattened (Fig. 2.35) or [2] flattened and more than twice as long as wide (Fig. 2.26). **Achene surface** [1] smooth or [2] tuberculate (rough due to microscopic projections as in Fig. 2.37). Achenes in sect. *Ficus* subsect. *Erioseycea* are tuberculate due to elongated prismatic cells in the endocarp. **Achene**: [1] with a single ridge arising from the hilum (Figures 2.35-2.37) or [2] with a forked, double ridge arising from the hilum (Fig. 2.38). The prominence of single ridges varies but forked ridges are always distinctly raised.

**Staminate floret position**: [1] ostiolar (clustered around the fig opening as in Fig. 2.22) or [2] dispersed (scattered among the pistillate florets as in Fig. 2.20). **Staminate florets**: [1] sessile or [2] pedicellate.

**Number of stamens per floret** (Figures 2.39-2.40). Florets are unistaminate throughout subg. *Urostigma* and bistaminate throughout sects. *Ficus* and *Rhizocladus*. The number of stamens per floret varies within figs in some members of sect. *Sycidium* and sect. *Sycocarpus*. **Staminate florets**: [1] without pistillodes; [2] with pistillodes (Fig. 2.41) or [3] with functional gall ovaries (Fig. 2.42). Apparently hermaphroditic florets occur in the ostiolar position in sect. *Sycidium* subsect. *Paleomorphe*, and although the ovary has an ovule, it does not produce an achene since the ovary is galled.

**Staminodia in seed figs**: [1] absent or [2] present. Not applicable to monoecious species. Some members of sects. *Neomorphe* and *Sycocarpus* have abortive staminate florets around the ostiole in seed figs.

**Perianth in staminate florets**: [1] free (not fused); [2] fused at the base or [3] fused completely along their length and splitting at anthesis. The staminate perianth is partly fused in sects. *Kalosyce* and *Neomorphe* and is completely fused in sect. *Sycocarpus*. **Staminate perianth surface**: [1] glabrous or [2] pubescent on the abaxial surface. **Filaments**: [1] without epidermal hairs at the base or [2] with epidermal hairs at the base (Fig. 2.43). **Anthers**: [1] not mucronate or [2] mucronate (filament or connective projecting beyond the pollen sacs as in Fig. 2.44).

## DESCRIPTIONS OF FIGS AT GUNUNG PALUNG

Taxonomic descriptions were generated using DELTA software (Dallwitz *et al.*, 1993). Complete and parallel descriptions of each species are listed alphabetically. Internal fig characters are included in the key but are omitted from the species descriptions for the sake of brevity. The following additional notes are included: **Spot characters** for rapid identification. **Habitat** distribution and abundance based only on observations at GP. Habitats listed from lowest to highest elevation include: [1] peat swamp, [2] freshwater swamp, [3] alluvial bench (lowland mixed dipterocarp forest on alluvium), [4] lowland sandstone (lowland mixed dipterocarp forest on sandstone), [5] lowland granite (lowland dipterocarp forest on granite), [6] submontane granite (submontane hill forest on granite) and [7] montane forest. Abundance categories range from rare, uncommon, common, to abundant. **Geographic range** updated from Corner (1965). **Vouchers** from GP deposited at the Herbarium Bogoriense and the Arnold Arboretum. All vouchers are fertile unless otherwise indicated. Collectors include: TL = Tim Laman; GW = George Weiblen; ML = Mark Leighton.

### *Ficus acamptophylla* Miq.

Small scrambling hemiepiphyte or climber; aerial roots small compared to host tree. 1-20 m in height. **Twigs** glabrous; 3-5 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; glabrous; 1-2.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.4-2 cm long. **Leaf shape** elliptic to lanceolate; glabrous; coriaceous; 6-15 cm long; 2.5-5 cm wide; 2-3 times as long as wide; convolute in bud. Margin entire. Base rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.2 times as long as the leaf; departing at an angle of 45-80 degrees from the midrib. **Secondary**

**veins** 4-7 pairs; more prominent than tertiary veins; raised above and below or raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose to conical; umbonate; glabrous; 8-12 mm long; 7-10 mm wide; green to yellow; ripening orange to red to purple; with spots. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 3-5 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Habitat:** Common along river edges in disturbed swamp forest. **Geographic range:** Borneo, Bangka. **Vouchers:** GW935, TL357

### *Ficus annulata* Bl.

Hemiepiphyte of the lower and middle canopy, not free-standing; aerial roots small compared to host tree. 5-30 m in height. **Twigs** glabrous; 7-11 mm in diameter; not hollow or hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1.5-3.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.5-3 cm long. **Leaf shape** obovate; pubescent; coriaceous; 15-35 cm long; 4-12.5 cm wide; 2.7-3.2 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.05-0.2 times as long as the leaf; departing at an angle of 30-75 degrees from the midrib. **Secondary veins** 10-20 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths none. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** conical; rounded at the apex; pubescent; 25-37 mm long; 15-25 mm wide; green; ripening green to yellow; with spots. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate to rounded; more or less equal in size; 1-5 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Long obovate leaf with many secondary veins prominent below. Leaves dry shiny dark-brown above, dull light-brown below. **Habitat:** Common in peat swamp through lowland sandstone habitats. **Geographic range:** Indochina, Sumatra, Java, Borneo, Sulawesi. **Voucher:** GW911

### *Ficus aurata* Miq.

Shrub or small tree. 1-9 m in height. **Twigs** pubescent; 3-5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node. **Stipules** caducous; pubescent; 0.5-4.5 cm long.

**Leaves** spiral. **Petioles** pubescent; 1-6 cm long. **Leaf shape** ovate to elliptic to obovate; pubescent; chartaceous; 6-25 cm long; 3-10 cm wide; 2.3-3.1 times as long as wide; plicate in bud. Margin serrate or dentate. Base cuneate; symmetric. Apex pointed.

**Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.3 times as long as the leaf; departing at an angle of 15-30 degrees from the midrib. **Secondary veins** 4-7 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins and in the axils of the secondary veins. Cystoliths none. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; umbonate; pubescent; 9-12 mm long; 8-11 mm wide; green; ripening yellow; without spots. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 1.5-2.5 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Pubescent in all parts. **Habitat:** Along river in lowland sandstone; rare at GP. **Geographic range:** Vietnam, Peninsular Malaysia, Sumatra, Bangka, Riau, Borneo. **Voucher:** TL243

*Ficus beccarii* King

Small tree. 3-8 m in height; 2-10 cm dbh; buttresses absent or less than 0.5 m in height. **Twigs** pubescent; 2-4 mm in diameter; hollow or with spongy pith; with a waxy gland below the node; latex color white. **Stipules** caducous; pubescent; 1-4 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.3-1.5 cm long. **Leaf shape** elliptic to ovate to lanceolate; pubescent; chartaceous; 10-30 cm long; 2-9 cm wide; 2.3-3.5 times as long as wide; plicate in bud. Margin entire. Base cuneate; asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired or not paired; as prominent as the secondary veins; 0-0.1 times as long as the leaf; departing at an angle of 30-60 degrees from the midrib. **Secondary veins** 6-12 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of unequal size. Leaf glands none or in the axils of the secondary veins. Cystoliths abaxial. Stomata not aggregated.

**Figs** geocarpic; pedunculate. Peduncle pubescent; 1-8 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** globose; sunken at the apex; pubescent; 7-17 mm long; 7-17 mm wide; pink; ripening red to brown; with spots. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 1-2 mm long. **Lateral bracts** few to many. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Disturbed slopes in lowland sandstone, uncommon. **Geographic range:** Peninsular Malaysia, Borneo. **Vouchers:** GW895, TL1231

*Ficus benjamina* L.

Large hemiepiphyte becoming free-standing. Aerial roots large compared to host tree. 15-40 m in height. **Twigs** glabrous; 1-3 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.5-1.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.5-1.8 cm long. **Leaf shape** elliptic to ovate; glabrous; chartaceous; 3-11 cm long; 1.5-5 cm wide; 1.7-2.8 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.3 times as long as the leaf; departing at an angle of 35-60 degrees from the midrib. As prominent as tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of unequal size. Leaf glands none. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 6-12 mm long; 6-10 mm wide; green to yellow; ripening white to purple; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 0-1 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Numerous closely parallel secondary veins and small figs ripening white to purple. **Habitat:** Alluvial bench; rare. **Geographic range:** India, Indochina, Indonesia, northern Australia, New Guinea, Solomon Islands. **Voucher:** ML1525

*Ficus binnendykii* Miq.

Small to medium-sized hemiepiphyte, in the middle to upper canopy; with roots to the ground small compared to host trunk; not free-standing. 15-50 m in height. **Twigs** glabrous; 1-4 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.5-1.3 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.6-1.5 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 2.5-9 cm long; 1.2-4.5 cm wide; 1.8-3 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex pointed to rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.6 times as long as the leaf; departing at an angle of 25-45 degrees from the midrib. **Secondary veins** 2-4 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 4-8 mm long; 4-8 mm wide; green to yellow; ripening orange to red; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 1.5-2.5 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or sunken. **Ostiolar bracts** overlapping or not overlapping. **Breeding system** monoecious.

**Spot characters:** Hemiepiphyte with small leaves and figs ripening orange with a perforate ostiole. Differs from *v. pallescens* in fig color when ripe and in having thick, elliptic leaves with less distinct tertiary venation. **Habitat:** Common from peat swamp and freshwater swamp forest to submontane granite where the species is most abundant. By far the most abundant species in lowland and submontane granite habitats. **Geographic range:** Peninsular Malaysia, Java, Borneo. **Vouchers:** GW913, GW928

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*Ficus binnendykii* v. *pallescens* Weiblen v. nov.;

differt a varietate *binnendykii* Miq. in fico subpurpureo haud aurantiaco ubi maturo et foliis plus lanceolatis renuioribus longioribusve cum nervatura tertiaria bene evoluta. Habitat in sylvis palustris et sylvis in lapide arenario. Typus: TL1195, Borneo, Kalimantan, Gunung Palung National Park (holotypus A; isotypi AAU; BOG. CANB, E, K, L, TL, WAN, SING).

Differing from v. *binnendykii* in the following respects. **Twigs** 1.5-3 mm in diameter. **Stipules** 0.5-1.5 cm long. **Petioles** 0.5-1 cm long. **Leaf shape** elliptic to lanceolate; glabrous; chartaceous to coriaceous; 5-11 cm long; 1.5-4 cm wide; 2.5-3.7 times as long as wide. Base cuneate. Apex pointed. Basal veins 0.2-0.4 times as long as the leaf; departing at an angle of 30-50 degrees from the midrib. **Secondary veins** 4-6 pairs. **Figs** 3-6 mm long; 3-6 mm wide; green; ripening white to pink to purple; without spots. **Fig basal bracts** acuminate to rounded, 0.5-2 mm long.

The morphology of the fig interior does not differ from v. *binnendykii* and is described as follows. Fig inner epidermis without glandular hairs. Pistillate florets all without pedicels. Pistillate perianth with tepals free; glabrous; red; margins entire. Style subterminal to lateral; not divided. Ovary superior; with a red spot near the base of the style. Achene not flattened; smooth; with a longitudinal ridge arising from the hilum. Staminate florets dispersed; pedicellate; stamens per floret 1; without pistillodes. Staminate perianth with tepals free; glabrous. Filaments without epidermal hairs at the base. Anthers not mucronate.

**Spot characters:** Distinguished from v. *binnendykii* in fig color when ripe and in having thinner, longer and more lanceolate leaves with well-developed tertiary venation. **Habitat:** Freshwater swamp through lowland sandstone; uncommon. **Geographic range:** Borneo, Java. **Isotype:** TL1195. **Paratypes:** ML3230, GW864 (sterile), Sandakan 110158 (Sabah), Bakhuizen van den Brink 7956 (Java), Rastini 253 (Bogor)

*Ficus callicarpides* Corner

Climber reaching the high canopy. 30-50 m in height. **Twigs** pubescent; 0.5-1.5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.3-0.4 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.2-0.8 cm long. **Leaf shape** cordate; pubescent; coriaceous; 1-3 cm long; 1.2-2.7 cm wide; 0.8-1.2 times as long as wide; plicate in bud. Margin entire. Base cordate; asymmetric. Apex pointed to rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.5-1 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 3-5 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins or in the axils of the secondary veins. Cystoliths paraxial. Stomata aggregated in sunken and foveate areoles.

**Figs** axillary; pedunculate. Peduncle glabrous; 1-2 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** globose; sunken at the apex; glabrous; 2-6 mm long; 2-6 mm wide; ripening red. **Fig basal bracts** 3, cadu-

cous; glabrous; acuminate; more or less equal in size; 0.5-1 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Alluvial bench and lowland sandstone; uncommon. **Geographic range:** Borneo.  
**Voucher:** TL1440 (sterile)

*Ficus callophylla* Bl.

Large hemiepiphyte with plank buttresses and crown in the middle to upper canopy; strangling host and becoming free-standing. 30-50 m in height. **Twigs** glabrous; 2.5-5 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1.5-2.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.7-3.5 cm long. **Leaf shape** obovate; glabrous; coriaceous; 4-22 cm long; 1.7-10 cm wide; 1.8-2.4 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.15-0.35 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 7-12 pairs; more prominent than tertiary veins; raised above and below or raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 9-13 mm long; 9-13 mm wide; green; ripening pink; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 5-7 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Thick obovate leaves with numerous indistinct secondary veins. Figs ripening pink with red spots or streaks. **Habitat:** Freshwater swamp, alluvial bench and lowland sandstone; rare. **Geographic range:** Indochina, Sumatra, Java, Borneo.  
**Voucher:** TL470

*Ficus caulocarpa* Miq.

Large hemiepiphyte with crown in the upper canopy; strangling host and becoming free-standing. 25-50 m in height. **Twigs** glabrous; 2-4 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.5-0.8 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.5-6.5 cm long. **Leaf shape** elliptic to obovate; glabrous; chartaceous to coriaceous; 6-18 cm long; 2.5-7.5 cm wide; 2-2.4 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.2-0.4 times as long as the leaf; departing at an angle of 35-50 degrees from the midrib. **Secondary veins** 6-16 pairs; more prominent than tertiary veins; not raised. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

tion pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 7-11 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of equal or unequal size. Leaf gland solitary at the base of the midrib. Cystoliths abaxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; sunken at the apex; glabrous; 12-18 mm long; 12-18 mm wide; ripening orange; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 3-6 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Large basal bracts on figs, elongate petioles and box-like fine venation. **Habitat:** Freshwater swamp and lowland sandstone. Rare. **Geographic range:** Myanmar, Thailand, Malaysia, Indonesia, Philippines, Papua New Guinea. **Voucher:** GW919 (sterile)

### *Ficus cucurbitina* King

Hemiepiphyte with crown in the middle to upper canopy and aerial roots small compared to host; not free-standing. 20-50 m in height. **Twigs** glabrous; 2-4.5 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; pubescent; 0.8-2 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.5-3 cm long. **Leaf shape** obovate to elliptic; glabrous; chartaceous to coriaceous; 10-20 cm long; 4-9 cm wide; 1.9-2.4 times as long as wide; convolute in bud. Margin entire. Base rounded to cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.25 times as long as the leaf; departing at an angle of 40-60 degrees from the midrib. **Secondary veins** 6-12 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths none. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** oblong; umbonate; pubescent; 30-40 mm long; 14-22 mm wide; green to yellow; ripening orange. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 1-3 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Irritant, silicate hairs on figs. **Habitat:** Uncommon in alluvial bench, rare in freshwater swamp. **Geographic range:** Peninsular Malaysia, Borneo, Philippines. **Voucher:** TL1438

### *Ficus delosyce* Corner

Hemiepiphyte, strangling host and becoming free-standing. 10-30 m in height. **Twigs** glabrous; 1.5-4 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; glabrous; 0.7-1.8 cm long.



tion pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 7-11 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of equal or unequal size. Leaf gland solitary at the base of the midrib. Cystoliths abaxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; sunken at the apex; glabrous; 12-18 mm long; 12-18 mm wide; ripening orange; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 3-6 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Large basal bracts on figs, elongate petioles and box-like fine venation. **Habitat:** Freshwater swamp and lowland sandstone. Rare. **Geographic range:** Myanmar, Thailand, Malaysia, Indonesia, Philippines, Papua New Guinea. **Voucher:** GW919 (sterile)

### *Ficus cucurbitina* King

Hemiepiphyte with crown in the middle to upper canopy and aerial roots small compared to host; not free-standing. 20-50 m in height. **Twigs** glabrous; 2-4.5 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; pubescent; 0.8-2 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.5-3 cm long. **Leaf shape** obovate to elliptic; glabrous; chartaceous to coriaceous; 10-20 cm long; 4-9 cm wide; 1.9-2.4 times as long as wide; convolute in bud. Margin entire. Base rounded to cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.25 times as long as the leaf; departing at an angle of 40-60 degrees from the midrib. **Secondary veins** 6-12 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths none. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** oblong; umbonate; pubescent; 30-40 mm long; 14-22 mm wide; green to yellow; ripening orange. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 1-3 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Irritant, silicate hairs on figs. **Habitat:** Uncommon in alluvial bench, rare in freshwater swamp. **Geographic range:** Peninsular Malaysia, Borneo, Philippines. **Voucher:** TL1438

### *Ficus delosyce* Corner

Hemiepiphyte, strangling host and becoming free-standing. 10-30 m in height. **Twigs** glabrous; 1.5-4 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; glabrous; 0.7-1.8 cm long.

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**Leaves** spiral. **Petioles** glabrous; 0.6-1.8 cm long. **Leaf shape** elliptic to obovate; glabrous; coriaceous; 2.5-8.5 cm long; 1.2-4 cm wide; 1.6-2.9 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex pointed to rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.6 times as long as the leaf; departing at an angle of 25-40 degrees from the midrib. **Secondary veins** 2-6 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** oblong to fusiform; rounded at the apex; glabrous; 6-14 mm long; 5-9 mm wide; green to yellow; ripening orange to red; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 2-4 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Small leaves and figs with apical bracts forming a cone. **Habitat:** Uncommon in freshwater swamp forest along rivers. **Geographic range:** Peninsular Malaysia, Borneo. **Vouchers:** GW934, GW868.

*Ficus deltoidea* Jack

Epiphytic shrub to 3 m in height, usually growing in sunny exposures in the high canopy. **Twigs** glabrous; 1-3 mm in diameter; hollow or with spongy pith; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.25-0.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.3-1 cm long. **Leaf shape** obovate; glabrous; coriaceous; 2.5-5.5 cm long; 1.2-4 cm wide; 1.4-2.2 times as long as wide; plicate in bud. Margin entire. Base cuneate; symmetric. Apex rounded. **Leaf venation** dichotomous; basal veins paired; as prominent as the secondary veins; 0.4-0.6 times as long as the leaf; departing at an angle of 20-40 degrees from the midrib. More prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf glands in the axil of the dichotomous midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle pubescent; 5-9 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** globose; rounded at the apex or umbonate; glabrous or pubescent; 5-9 mm long; 5-8 mm wide; green to yellow; ripening orange. **Fig basal bracts** 3, persistent in mature figs; pubescent; rounded; more or less equal in size; 0.5-1 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Spathulate leaves with a branching midrib. **Habitat:** Abundant in alluvial bench forest, uncommon in all other habitats up to submontane granite. **Geographic range:** Peninsular Malaysia, Sumatra, Bangka, Riau, Borneo. **Vouchers:** TL252, TL738, GW878

*Ficus deltoidea* Jack v. *borneensis* Corner

Differing from v. *deltoidea* in the following respects. **Twigs** 3-6 mm. **Stipules** 0.5-0.9 cm long. **Petioles** 0.8-1.8 cm long. **Leaf shape** 7-10 cm long; 5-7 cm wide; 1.1-1.7 times as long as wide. Leaf glands paired in the axils of the basal veins or in the axils of the secondary veins or in the axil of the dichotomous midrib. Fig peduncle 0.5-3 mm long. **Figs** pubescent; 12-16 mm long; 10-14 mm wide; green; ripening orange to red. **Fig basal bracts** acuminate; 1-2 mm long.

**Spot characters:** Distinguished from v. *deltoidea* in having larger leaves and figs. **Habitat:** Peat swamp and alluvial bench. Rare. **Geographic range:** Borneo. **Vouchers:** ML2068, GW922 (sterile).

*Ficus deltoidea* Jack v. *motleyana* (Miq.) Corner

Differing from v. *deltoidea* in the following respects. Small shrub or treelet. 0.5-2 m in height. **Stipules** pubescent; 0.4-1 cm long. **Petioles** 0.3-1.5 cm long. **Leaf shape** lanceolate; 5-13 cm long; 1-3 cm wide; 3.5-10 times as long as wide. Apex pointed. **Leaf venation** pinnate; basal veins 0.15-0.3 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 5-7 pairs; more prominent than tertiary veins; not raised or raised above and below. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins or in the axils of the secondary veins. Fig peduncle glabrous; 3-6 mm long. **Fig shape** fusiform; umbonate; glabrous; 14-20 mm long; 4-8 mm wide; green; ripening orange to red; without spots. **Fig basal bracts** 0.5-1.5 mm long.

**Spot characters:** Distinguished from v. *deltoidea* and v. *borneensis* by pinnate venation, lanceolate leaves and oblong figs. **Habitat:** Lowland granite to montane forest. Uncommon. **Geographic range:** Peninsular Malaysia, Sumatra, Borneo, Sulawesi. **Vouchers:** TL259, GW903, GW904

*Ficus disticha* Bl.

Large climber in the upper canopy. 20-60 m in height. **Twigs** glabrous; 1-2.5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node. **Stipules** caducous; glabrous; 0.1-0.5 cm long.

**Leaves** distichous. **Petioles** glabrous; 0.1-1.6 cm long. **Leaf shape** obovate; glabrous; coriaceous; 2-5 cm long; 1.5-2.8 cm wide; 1.4-2 times as long as wide; plicate in bud. Margin entire. Base cuneate; symmetric. Apex rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.25-0.5 times as long as the leaf; departing at an angle of 25-40 degrees from the midrib. **Secondary veins** 2-4 pairs; more prominent than tertiary veins; not raised. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins or in the axils of the secondary veins. Cystoliths abaxial. Stomata aggregated in sunken and foveate areoles.

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**Figs** axillary; pedunculate. Peduncle glabrous; 1-3 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** obconical; rounded at the apex; glabrous; 5-10 mm long; 4-7 mm wide; green to yellow; ripening orange to red; with spots. **Fig basal bracts** 3, caducous; glabrous; rounded; more or less equal in size; 0.5-2 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Large climber with small, obconical figs. **Habitat:** Peat swamp and alluvial bench. Uncommon. **Geographic range:** Myanmar, Thailand, Peninsular Malaysia, Sumatra, Borneo, Sulawesi, Philippines, Mollucas (Ternate) **Voucher:** GW921 (sterile)

*Ficus dubia* Wall. ex King

Large hemiepiphyte usually on emergent dipterocarps with small roots compared to host trunk and not free-standing. 30-60 m in height. **Twigs** glabrous; 2-5 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1-2.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.2-3.8 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 6-15 cm long; 2.5-7.5 cm wide; 1.8-2.5 times as long as wide; convolute in bud. Margin entire. Base rounded to cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.3 times as long as the leaf; departing at an angle of 35-70 degrees from the midrib. **Secondary veins** 5-11 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths none. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle glabrous; 5-20 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose to oblong; rounded at the apex; glabrous; 20-30 mm long; 15-30 mm wide; green; ripening red to purple; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 2-3 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Large, pedunculate figs ripening dark red. The only other species in subg. *Urostigma* with pedunculate figs is *F. globosa*, a small understory hemiepiphyte. **Habitat:** Rare in peat and freshwater swamp. More common in alluvial bench to lowland granite. **Geographic range:** Peninsular Malaysia, Sumatra, Borneo. **Voucher:** TL1021

*Ficus excavata* King

Climber. **Twigs** pubescent; 1-3 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; pubescent; 0.3-0.8 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.2-0.5 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 1.5-4 cm long; 1.5-3 cm wide; 1-1.2 times as long as wide; plicate in bud. Margin entire. Base rounded; symmetric. Apex rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.5-0.8 times as long

as the leaf; departing at an angle of 30-50 degrees from the midrib. **Secondary veins** 2-5 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins or in the axils of the secondary veins. Cystoliths abaxial. Stomata aggregated in sunken and foveate areoles.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; pubescent; 3-8 mm long; 3-8 mm wide; orange; ripening red. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 1-3 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Not recorded. **Geographic range:** Peninsular Malaysia, Sumatra, Borneo. **Vouchers:** ML3053 (sterile)

### *Ficus geocharis* Corner

Small tree. 3-10 m in height; 2-8 cm dbh; buttresses absent or less than 0.5 m in height. **Twigs** pubescent; 1-3 mm in diameter; hollow or with spongy pith; with a waxy gland below the node; latex color white. **Stipules** persistent; pubescent; 1-2.5 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.5-1 cm long. **Leaf shape** elliptic; pubescent; chartaceous; 10-30 cm long; 2.5-9 cm wide; 2.6-4.3 times as long as wide; plicate in bud. Margin serrate or dentate. Base cuneate to rounded; asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins not paired. **Secondary veins** 4-10 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of unequal size. Leaf glands in the axils of the secondary veins. Cystoliths abaxial. Stomata not aggregated.

**Figs** geocarpic; pedunculate. Peduncle pubescent; 1-4 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** globose; sunken at the apex; pubescent; 12-20 mm long; 12-20 mm wide; green to brown; ripening orange to pink to red; with spots. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 2-4 mm long. **Lateral bracts** few to many. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Disturbed slopes in lowland sandstone. Uncommon. **Geographic range:** Borneo. **Vouchers:** GW883, GW888, TL1232, TL1233

### *Ficus glandulifera* Wall ex. Miq.

Small to medium sized tree. 5-25 m in height; 5-30 cm dbh; buttresses absent or less than 0.5 m in height. **Twigs** pubescent; 2-4 mm in diameter; hollow or with spongy pith; with a waxy gland below the node; latex color white. **Stipules** caducous; pubescent; 0.2-0.5 cm long.

**Leaves** spiral. **Petioles** pubescent; 1.5-7 cm long. **Leaf shape** elliptic to obovate; pubescent; chartaceous; 4-22 cm long; 2-12 cm wide; 1.6-2.4 times as long as wide; plicate in bud. Margin serrate or dentate. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary

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veins; 0.4-0.6 times as long as the leaf; departing at an angle of 35-55 degrees from the midrib. **Secondary veins** 4-7 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands none. Cystoliths none. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle pubescent; 3-10 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** globose; rounded at the apex; pubescent; 7-12 mm long; 7-12 mm wide; green; ripening yellow to red. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 1-2 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Known from a single collection from river bank in freshwater swamp forest. **Geographic range:** Peninsular Malaysia, Sumatra, Riau, Bangka, Borneo, Sulawesi, Moluccas. **Vouchers:** GW866 (sterile)

*Ficus globosa* Bl.

Small hemiepiphyte in the understory to lower canopy, often looking like a climber; not free-standing. 5-30 m in height. **Twigs** glabrous; 3-5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1-3.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.5-6 cm long. **Leaf shape** elliptic to obovate; glabrous; coriaceous; 7-25 cm long; 5-10 cm wide; 2-3.2 times as long as wide; convolute in bud. Margin entire. Base rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.3 times as long as the leaf; departing at an angle of 40-70 degrees from the midrib. **Secondary veins** 7-10 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle pubescent; 2-10 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** oblong; rounded at the apex; pubescent; 10-20 mm long; 7-15 mm wide; green; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded to acuminate; more or less equal in size; 1-2 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Habitat:** Collected in peat swamp and submontane granite. Rare. **Geographic range:** Myanmar, Thailand, Peninsular Malaysia, Sumatra, Java, Riau, Borneo. **Vouchers:** GW898, TL1399

*Ficus grossularioides* Burm f.

Shrub or small tree. 1-9 m in height. **Twigs** pubescent; 2-5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node; latex color white. **Stipules** caducous; pubescent; 0.3-1 cm long.

**Leaves** spiral. **Petioles** pubescent; 1-10 cm long. **Leaf shape** elliptic to ovate to trilobed; pubescent and scabrid; chartaceous; 5-20 cm long; 2.5-17 cm wide; 1.2-3.4 times as long as wide; plicate in bud. **Margin** serrate or dentate. **Base** cordate to cuneate to rounded; symmetric. **Apex** pointed. **Leaf venation** pinnate; basal veins paired; more prominent than the secondary veins; 0.25-0.75 times as long as the leaf; departing at an angle of 30-40 degrees from the midrib. **Secondary veins** 3-6 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. **Areoles** of more or less equal size. **Leaf glands** paired in the axils of the basal veins. **Cystoliths** none. **Stomata** not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex to umbonate; glabrous or pubescent; 8-13 mm long; 7-13 mm wide; green to yellow; ripening orange to red. **Fig basal bracts** 3, persistent in mature figs; pubescent; rounded; more or less equal in size; 1.5-3 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Trilobed leaves on young plants and dense white pubescence on the underside of leaves. **Habitat:** Secondary forest and degraded areas of the park. **Geographic range:** Thailand, Peninsular Malaysia, Sumatra, Java, Riau, Borneo. **Vouchers:** GW858, GW861

### *Ficus hemsleyana* King

Small hemiepiphyte in the understory or lower canopy; not free-standing. 3-15 m in height. **Twigs** pubescent; 2-4 mm in diameter; hollow or with spongy pith; without a wax gland below the node. **Stipules** caducous or persistent; pubescent; 0.8-2 cm long.

**Leaves** distichous. **Petioles** pubescent; 0-0.5 cm long. **Leaf shape** elliptic; pubescent; chartaceous; 15-35 cm long; 5-14 cm wide; 1.8-3.1 times as long as wide; plicate in bud. **Margin** serrate or dentate to entire. **Base** cordate to rounded; asymmetric. **Apex** pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.2-0.6 times as long as the leaf; departing at an angle of 30-60 degrees from the midrib. **Secondary veins** 5-8 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. **Areoles** of more or less equal size. **Leaf glands** paired in the axils of the basal veins and in the axils of the secondary veins. **Cystoliths** paraxial. **Stomata** not aggregated.

**Figs** cauliflorous; pedunculate. **Peduncle** glabrous; 5-20 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; sunken at the apex; glabrous; 5-10 mm long; 5-10 mm wide; green; ripening orange; with spots. **Fig basal bracts** 3, caducous or persistent in mature figs; glabrous; acuminate; 0-1 mm long. **Lateral bracts** none. **Apical bracts** more than 3 and sunken. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Freshwater swamp and alluvial bench. **Rare.** **Geographic range:** Borneo. **Voucher:** TL1001

*Ficus heteropleura* Bl.

Small scrambling hemiepiphyte or climber in the understory or lower canopy. **Twigs** glabrous; 1-3 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; glabrous; 0.2-0.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.5-1.2 cm long. **Leaf shape** elliptic to obovate; glabrous; coriaceous; 5-22 cm long; 2-6.5 cm wide; 1.9-3 times as long as wide; plicate in bud. Margin entire. Base cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.6 times as long as the leaf; departing at an angle of 30-40 degrees from the midrib. **Secondary veins** 2-5 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of more or less equal size. Leaf gland solitary in the axil of a basal vein. Cystoliths abaxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle scabrid; 4-9 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; sunken at the apex; scabrid; 3-7 mm long; 3-7 mm wide; green; ripening orange to pink. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 0-1 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Leaves with a long, narrow apex and prominent venation below. **Habitat:** Freshwater swamp and along rivers in alluvial bench and lowland sandstone. Rare. **Geographic range:** Bhutan, northeast India, Indochina, Sumatra, Riau, Borneo, Java, Sulawesi, Philippines. **Voucher:** GW873

*Ficus kerkhovenii* Koord. et Valet.

The largest hemiepiphyte in GP with numerous prop roots and flying buttresses; strangling host and becoming free-standing; aerial roots large compared to host tree. 20-50 m in height. **Twigs** glabrous; 3-5 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1-2 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.5-3 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 6.5-19 cm long; 2.5-7 cm wide; 2-3 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired or not paired; as prominent as the secondary veins; 0.01-0.2 times as long as the leaf; departing at an angle of 30-50 degrees from the midrib. **Secondary veins** 5-12 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 8-12 mm long; 8-12 mm wide; green to yellow; ripening orange to red. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; unequal in size (with one much shorter than the other two); 1.5-2.5 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.



**Spot characters:** One of the fig basal bracts much smaller than the other two. **Habitat:** Uncommon in freshwater swamp, common in alluvial bench through lowland granite. **Geographic range:** Peninsular Malaysia, Sumatra, Bangka, Java, Borneo, Philippines. **Voucher:** TL507

*Ficus lanata* Bl.

Climber. **Twigs** pubescent; 2-3 mm in diameter; not hollow; without a waxy gland below the node; latex color yellow. **Stipules** caducous; pubescent; 0.5-2.5 cm long.

**Leaves** spiral. **Petioles** pubescent; 1.3-2 cm long. **Leaf shape** cordate; pubescent; coriaceous; 6-10 cm long; 2.5-5.5 cm wide; 1.7-2.2 times as long as wide; plicate in bud. Margin entire. Base cordate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.4-0.7 times as long as the leaf; departing at an angle of 45-60 degrees from the midrib. **Secondary veins** 3-5 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins. Cystoliths paraxial. Stomata aggregated in sunken and foveate areoles.

**Figs** axillary; pedunculate. Peduncle glabrous; 2-3 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; rounded at the apex; pubescent; 2-5 mm long; 2-5 mm wide; green; ripening red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 0.5-1.5 mm long. **Lateral bracts** none. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Single collection in lowland sandstone. Rare. **Geographic range:** Sumatra, Java, Borneo. **Vouchers:** GW893 (sterile)

*Ficus lowii* King v. *minor* Corner

Medium sized hemiepiphyte, with crown in the middle to upper canopy; aerial roots small compared to host trunk, not free-standing. 15-40 m in height. **Twigs** pubescent; 2-3.5 mm in diameter; not hollow; without a waxy gland below the node; latex color yellow. **Stipules** caducous; pubescent; 1-1.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.2-2 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 7-12 cm long; 3-4.5 cm wide; 2.3-2.9 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; more prominent than the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 35-50 degrees from the midrib. **Secondary veins** 3-8 pairs; as prominent as tertiary veins or more prominent than tertiary veins; not raised or raised above and below. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 7-10 mm long; 9-11 mm wide; green to yellow; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 1-2 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breed-**

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**Spot characters:** Tertiary venation very distinct and box-shaped, leaves dark green above and greyish below. **Habitat:** Rare in alluvial bench and lowland sandstone, common in lowland and submontane granite. **Geographic range:** Peninsular Malaysia, Borneo. **Voucher:** GW917

*Ficus microcarpa* L. f.

Hemiepiphytic strangler; becoming free-standing. 20-30 m in height. **Twigs** glabrous; 1.5-5 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous or pubescent; 1-1.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.4-1 cm long. **Leaf shape** elliptic to ovate; glabrous; coriaceous; 4-9 cm long; 1.5-4 cm wide; 2-2.5 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric or asymmetric. Apex pointed to rounded. **Leaf venation** pinnate; basal veins paired; more prominent than the secondary veins; 0.25-0.4 times as long as the leaf; departing at an angle of 45-60 degrees from the midrib. **Secondary veins** 3-12 pairs; more prominent than tertiary veins; not raised to raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 8-12 mm long; 8-12 mm wide; green to yellow; ripening pink to purple; with spots. **Fig basal bracts** 3, caducous; pubescent; acuminate to rounded; more or less equal in size; 2-3 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Habitat:** Coastal forest. **Geographic range:** Sri Lanka, India, Indochina, Indonesia, New Guinea, Solomon Isl., Australia, Cocos and Christmas Isl. (Indian Ocean), Caroline Isl., New Caledonia, Loyalty, Caroline, Marianas, and Palau Isl. (Pacific Ocean). **Voucher:** GW857

*Ficus obscura* v. *borneensis* (Miq.) Corner

Small hemiepiphyte, climber or shrub in the understory to lower canopy. 1-25 m in height. **Twigs** pubescent; 3-4.5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node. **Stipules** persistent; pubescent; 0.3-0.7 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.3-0.7 cm long. **Leaf shape** obovate; pubescent to scabrid; chartaceous to coriaceous; 8-24 cm long; 3.5-8 cm wide; 1.9-2.7 times as long as wide; plicate in bud. Margin serrate or dentate. Base rounded; asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.25-0.5 times as long as the leaf; departing at an angle of 25-45 degrees from the midrib. **Secondary veins** 3-7 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary in the axil of a basal vein and in the axils of the secondary veins. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle pubescent; 3-7 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; rounded at the apex; glabrous; 3-5 mm long; 3-5 mm wide; green to white; ripening orange to pink; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 0.5-1.5 mm long. **Lateral bracts** none. **Apical bracts** sunken and not visible on fig exterior. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Leaves toothed at the apex, scabrid above, pubescent below, and strongly asymmetrical at the base. **Habitat:** Along rivers in freshwater swamp forest. Uncommon. **Geographic range:** Thailand, Peninsular Malaysia, Sumatra, Riau, Java, Borneo, Sulawesi, Philippines. **Vouchers:** TL348, GW937

*Ficus palungensis* Weiblen sp. nov.

a *paracamptophylla* Corner in stipulis elongatis persistentibus aemulans, in fliis angustioribus cum neventura indistincta et ficis parvioribus. In turbario vulgare. In palude rarus. Typus: TL1420, Borneo, Kalimantan, Gunung Palung National Park (holotypus A; isotypi AAU, BOG, CANB, E, K, L, TI, WAN, SING).

Scrambling hemiepiphyte in the middle canopy; not free-standing. 20 m in height. **Twigs** glabrous; 4-8 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** persistent; glabrous; 2-6 cm long.

**Leaves** spiral. **Petioles** glabrous; 1-2 cm long. **Leaf shape** elliptic to ovate; glabrous; coriaceous; 10-16 cm long; 2.5-5.5 cm wide; 2-4 times as long as wide; convolute in bud. Margin entire. Base cordate to cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.2 times as long as the leaf; departing at an angle of 60-70 degrees from the midrib. **Secondary veins** 6-9 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 10-12 mm long; 10-12 mm wide; yellow; ripening orange to red. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 3-5 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping.

**Breeding system** monoecious. Inner epidermis without glandular hairs. Pistillate florets varying within figs from sessile to pedicellate. Pistillate perianth with tepals free; glabrous; red; margins entire. Style subterminal to lateral; not divided. Ovary superior; with a red spot near the base of the style. Achene not flattened; smooth; with a longitudinal ridge arising from the hilum. Staminate florets dispersed; pedicellate; stamens per floret 1; without pistillodes. Staminate perianth with tepals free; glabrous. Filaments without epidermal hairs at the base. Anthers not mucronate.

**Spot characters:** Similar to *F. paracamptophylla* in having elongated, persistent stipules. Differs in having narrow leaves with indistinct venation and smaller figs. **Habitat:** Common in peat swamp; less common in freshwater swamp. **Geographic range:** Kalimantan. **Isotype:** TL1420. **Paratypes:** GW863, Argent 93162 (Central Kalimantan)

*Ficus paracamptophylla* Corner

Small, scrambling hemiepiphyte in the lower canopy; not free-standing. **Twigs** glabrous; 5-8 mm in diameter; not hollow or hollow; without a waxy gland below the node; latex color white. **Stipules** persistent; glabrous; 1-9 cm long.

**Leaves** spiral. **Petioles** glabrous; 3.5-4.5 cm long. **Leaf shape** elliptic to ovate; glabrous; coriaceous; 15-25 cm long; 4-11.5 cm wide; 2-3 times as long as wide; convolute in bud. Margin entire. Base rounded to cordate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 45-60 degrees from the midrib. **Secondary veins** 7-10 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose to oblong; rounded at the apex to umbonate; glabrous; 14-16 mm long; 13-17 mm wide; yellow to orange; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 4-6 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Elongated, persistent stipules. See also *F. palungensis*. **Habitat:** Rare in peat and freshwater swamp forest. **Geographic range:** Borneo. **Vouchers:** TL1441, TL1442 (sterile)

*Ficus parietalis* Bl.

Lithophytic shrub, scrambling hemiepiphyte or climber. 1-8 m in height. **Twigs** pubescent; 1-3.5 mm in diameter; not hollow or hollow; without a waxy gland below the node; latex color yellow. **Stipules** caducous; pubescent; 0.2-0.6 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.2-1.3 cm long. **Leaf shape** elliptic to ovate; pubescent; coriaceous; 9-30 cm long; 4-12 cm wide; 1.8-2.8 times as long as wide; plicate in bud. Margin entire. Base rounded; symmetric or asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.4-0.7 times as long as the leaf; departing at an angle of 40-55 degrees from the midrib. **Secondary veins** 1-4 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins. Cystoliths abaxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle scabrid; 5-17 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; rounded at the apex; scabrid; 7-14 mm long; 7-14 mm wide; green; ripening yellow to orange; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 0-1.5 mm long. **Lateral bracts** none. **Apical bracts** more than 3 or sunken. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Leaf venation prominently raised below, secondary veins regular, ladder-like. **Habitat:** Boulder outcrops on low ridges. **Geographic range:** Vietnam, Thailand, Peninsular Malaysia, Sumatra, Java, Borneo, Palawan. **Voucher:** TL1251

*Ficus pellucido-punctata* Griff.

Medium to large hemiepiphyte in the middle to upper canopy; strangling and becoming free-standing. 15-50 m in height. **Twigs** glabrous; 2-4 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; pubescent; 0.5-2.2 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.5-3 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 7.5-20 cm long; 2.5-7 cm wide; 2.2-3.2 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.2-0.4 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 4-8 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** oblong; rounded at the apex or umbonate; glabrous; 9-18 mm long; 4-13 mm wide; green to yellow; ripening orange to red; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate to rounded; more or less equal in size; 3-6 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or sunken. **Ostiolar bracts** not overlapping. **Breeding system** monoecious.

**Spot characters:** Triangular perforation in the apex of the figs. **Habitat:** Broad range from peat swamp to submontane granite; uncommon. **Geographic range:** Northeast India, Indochina, Peninsular Malaysia, Sumatra, Borneo, Philippines. **Vouchers:** GW880, TL1199

*Ficus pisocarpa* Bl.

Medium sized hemiepiphyte, occupying middle to upper canopy; aerial roots small compared to host trunk, not free-standing. 20-50 m in height. **Twigs** glabrous; 2-4 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.8-1.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 1-1.7 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 7-19 cm long; 3.5-8 cm wide; 2-2.8 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 20-45 degrees from the midrib. **Secondary veins** 3-7 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

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**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex or umbonate; glabrous to pubescent; 6-13 mm long; 6-13 mm wide; green to yellow; ripening yellow to orange to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous or pubescent; acuminate to rounded; more or less equal in size; 2-4 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** not overlapping. **Breeding system** monoecious.

**Spot characters:** Figs with a thickened disc at the apex, a thin epidermis and papery basal bracts. **Habitat:** Peat swamp to lowland granite; uncommon. **Geographic range:** Southern Thailand, Peninsular Malaysia, Sumatra, Java, Borneo. **Vouchers:** GW912, GW925

*Ficus punctata* Thunb.

Climber reaching the upper canopy; prostrate on boles and major branches of emergent trees. 10-60 m in height. **Twigs** glabrous to pubescent; 1-4 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** persistent; glabrous; 0.3-1 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.3-1 cm long. **Leaf shape** obovate; pubescent to glabrous; coriaceous; 1.5-6 cm long; 1-3.5 cm wide; 1.7-2.8 times as long as wide; plicate in bud. Margin entire. Base cuneate to rounded; asymmetric. Apex rounded. **Leaf venation** pinnate; basal veins not paired. **Secondary veins** 3-4 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins. Cystoliths paraxial. Stomata aggregated in sunken and foveate areoles.

**Figs** axillary or cauliflorous; pedunculate. Peduncle pubescent; 5-35 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** obconical; umbonate; pubescent; 40-100 mm long; 30-80 mm wide; green to brown; ripening yellow to orange to red; with spots. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 2-4 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Leaves appressed to tree trunks; largest figs at GP. **Habitat:** Common on emergent dipterocarps in alluvial bench, freshwater swamp and lowland sandstone. **Geographic range:** Southern Thailand, Peninsular Malaysia, Sumatra, Borneo, southeast Sulawesi. **Vouchers:** GW 896, GW909

*Ficus recurva* v. *brideliodes* Corner

Climber reaching the upper canopy. 10-50 m in height. **Twigs** glabrous; 1.5-3 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; pubescent; 0.05-0.15 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.5-1 cm long. **Leaf shape** elliptic to ovate to obovate; glabrous; chartaceous to coriaceous; 2.5-8 cm long; 1.5-6 cm wide; 1.3-2.6 times as long as wide; plicate in bud. Margin entire. Base cuneate to rounded; symmetric. Apex rounded. **Leaf venation** pinnate; basal veins paired; as prominent

as the secondary veins; 0.4-0.7 times as long as the leaf; departing at an angle of 25-40 degrees from the midrib. **Secondary veins** 2-5 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary in the axil of a basal vein or paired in the axils of the basal veins. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle glabrous; 2-5 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; rounded at the apex; glabrous; 6-8 mm long; 6-9 mm wide; green. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 0.5-1.5 mm long. **Lateral bracts** none. **Apical bracts** sunken and not visible on fig exterior. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Single collection from freshwater swamp. **Geographic range:** Southern Thailand, Peninsular Malaysia, Sumatra, Borneo. **Vouchers:** GW927

#### *Ficus retusa* v. *borneensis* Corner

Medium-sized hemiepiphyte in the lower to middle canopy with aerial roots small compared to host; not free-standing. 10-30 m in height. **Twigs** glabrous; 3-5 mm in diameter; without a waxy gland below the node; latex color yellow. **Stipules** caducous; glabrous; 0.7-1.3 cm long.

**Leaves** spiral. **Petioles** glabrous; 1-2 cm long. **Leaf shape** elliptic to obovate; glabrous; coriaceous; 8-17 cm long; 3-8 cm wide; 2.2-2.5 times as long as wide. Margin entire. Base cuneate to rounded; symmetric. Apex pointed to rounded.

Basal veins paired; as prominent as the secondary veins; 0.2-0.35 times as long as the leaf; departing at an angle of 25-50 degrees from the midrib. **Secondary veins** 4-10 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular or irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths none. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 5-8 mm long; 7-11 mm wide; green to yellow; ripening orange to pink; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate to rounded; more or less equal in size; 2-3 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Leaf venation sunken above, prominently raised below. **Habitat:** Most common in submontane granite habitat; less common in lowland granite and rare in lowland sandstone and alluvial bench. **Geographic range:** Peninsular Malaysia, Sumatra, Java, Borneo. **Voucher:** GW902

#### *Ficus ruginerva* Corner

Climber. 5-20 m in height. **Twigs** glabrous; 1-3 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.4-0.7 cm long.

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**Leaves** distichous. **Petioles** pubescent; 0.3-1.6 cm long. **Leaf shape** elliptic to obovate; pubescent; coriaceous; 2-9 cm long; 1-5.5 cm wide; 1.6-2.2 times as long as wide; plicate in bud. **Margin** entire. **Base** cuneate; symmetric to asymmetric. **Apex** rounded. **Leaf venation** pinnate; basal veins paired or not paired; as prominent as the secondary veins; 0.2-0.5 times as long as the leaf; departing at an angle of 30-50 degrees from the midrib. **Secondary veins** 3-7 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. **Areoles** of more or less equal size. **Leaf gland** solitary in the axil of a basal vein. **Cystoliths** paraxial. **Stomata** aggregated in sunken and foveate areoles.

**Figs** axillary or cauliflorous; pedunculate. **Peduncle** pubescent; 8-30 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** obconical; umbonate; glabrous; 25-60 mm long; 25-50 mm wide; green; ripening orange; with spots. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 3-5 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Single collection from coastal secondary forest. **Geographic range:** Peninsular Malaysia, Sumatra, Borneo. **Voucher:** GW854.

*Ficus sagittata* Vahl.

Climber. **Twigs** glabrous; 1-5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node. **Stipules** caducous; pubescent; 0.5-0.7 cm long.

**Leaves** distichous. **Petioles** glabrous; 1-3.5 cm long. **Leaf shape** elliptic to ovate; glabrous; coriaceous; 9-17 cm long; 4.5-8 cm wide; 1.8-2 times as long as wide; plicate in bud. **Margin** entire. **Base** cordate to rounded to cuneate; symmetric. **Apex** pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.25-0.3 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 5-8 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. **Areoles** of more or less equal size. **Leaf glands** paired in the axils of the basal veins. **Cystoliths** paraxial. **Stomata** aggregated in sunken and foveate areoles.

**Figs** axillary or cauliflorous; pedunculate. **Peduncle** glabrous; 4-8 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** globose; sunken at the apex; glabrous; 7-12 mm long; 7-11 mm wide; ripening red. **Fig basal bracts** 3, caducous; glabrous; acuminate; more or less equal in size; 1-2 mm long. **Lateral bracts** none. **Apical bracts** sunken and not visible on fig exterior. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Not recorded. **Geographic range:** Andaman Isl., Indochina, Indonesia, Philippines, Caroline Isl. (Palau). **Vouchers:** ML2763



*Ficus schwarzii* Koord.

Small to medium-sized tree. 5-15 m in height; 10-30 cm dbh; buttresses absent or less than 0.5 m in height. **Twigs** glabrous; 2-4 mm in diameter; hollow or with spongy pith; with a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.5-0.9 cm long.

**Leaves** spiral. **Petioles** glabrous or pubescent; 0.4-3 cm long. **Leaf shape** obovate; glabrous; chartaceous; 5-22 cm long; 2.5-10 cm wide; 2.4-3.6 times as long as wide; plicate in bud. Margin entire to serrate or dentate. Base cuneate; symmetric to asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins not paired. **Secondary veins** 5-9 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular or regular. Areoles of unequal size. Leaf glands none. Cystoliths abaxial. Stomata not aggregated.

**Figs** cauliflorous; pedunculate. Peduncle glabrous; 8-50 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** globose to obconical; rounded at the apex; scabrid; 9-17 mm long; 10-20 mm wide; green to brown; ripening green to brown; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 2-3 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Cauliflorous tree with leaves 2-3 times longer than wide. **Habitat:** Lowland sandstone; rare. **Geographic range:** Myanmar, Thailand, Peninsular Malaysia, Sumatra, Borneo, Sulawesi. **Vouchers:** GW882, GW884

*Ficus sinuata* Thunb.

Small hemiepiphyte, lithophyte or shrub in the understory. 1-10 m in height. **Twigs** glabrous; 1-3 mm in diameter; hollow or with spongy pith; without a waxy gland below the node. **Stipules** caducous; glabrous; 0.4-2 cm long.

**Leaves** spiral or distichous. **Petioles** glabrous; 0.3-1.5 cm long. **Leaf shape** elliptic to obovate; glabrous; chartaceous; 7.5-22 cm long; 3.5-9.5 cm wide; 2.4-3.5 times as long as wide; plicate in bud. Margin entire to serrate or dentate. Base cuneate; symmetric to asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.3 times as long as the leaf; departing at an angle of 30-50 degrees from the midrib. **Secondary veins** 5-12 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular or irregular. Areoles of more or less equal size. Leaf gland solitary in the axil of a basal vein and in the axils of the secondary veins. Cystoliths abaxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle scabrid; 1-5 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; rounded at the apex; scabrid; 3-7 mm long; 3-7 mm wide; green to yellow; ripening orange to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 0-1 mm long. **Lateral bracts** none. **Apical bracts** more than 3 and sunken. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

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**Habitat:** Common in lowland sandstone habitat along streams; also in freshwater swamp.

**Geographic range:** Northeast India, Thailand, Peninsular Malaysia, Sumatra, Riau, Java, Borneo. **Vouchers:** TL85, TL241, TL981, GW881, GW891

*Ficus spathulifolia* Corner

Medium-sized hemiepiphyte in the middle to upper canopy; aerial roots small compared to host; not free-standing. 20-50 m in height. **Twigs** glabrous; 2-5 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 0.5-1.2 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.8-1.5 cm long. **Leaf shape** obovate; glabrous; coriaceous; 3.5-9 cm long; 2-4.5 cm wide; 1.9-2.5 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.25-0.5 times as long as the leaf; departing at an angle of 20-40 degrees from the midrib. **Secondary veins** 2-7 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex to umbonate; glabrous; 5-8 mm long; 5-8 mm wide; green to yellow; ripening orange to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate to rounded; more or less equal in size; 2-3 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Small, obovate leaves densely clustered near the ends of the thick twigs.

**Habitat:** The most abundant fig species in peat swamp; also common in freshwater swamp through lowland sandstone. **Geographic range:** Peninsular Malaysia, Borneo. **Vouchers:** GW929, GW933, TL1322

*Ficus stolonifera* King

Small tree. 2-25 m in height; 4-15 cm dbh; buttresses absent or less than 0.5 m in height. **Twigs** pubescent; 2-4 mm in diameter; hollow or with spongy pith; with a waxy gland below the node; latex color yellow. **Stipules** caducous; pubescent; 0.6-1 cm long.

**Leaves** spiral. **Petioles** pubescent; 0.4-1 cm long. **Leaf shape** elliptic; scabrid; chartaceous; 9-27 cm long; 4-13 cm wide; 2.3-2.9 times as long as wide; plicate in bud. Margin serrate or dentate. Base rounded; asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.1-0.4 times as long as the leaf; departing at an angle of 45-80 degrees from the midrib. **Secondary veins** 5-7 pairs; more prominent than tertiary veins; raised above and below or raised below but not above. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands in the axils of the secondary veins. Cystoliths paraxial. Stomata not aggregated.

**Figs** geocarpic; pedunculate. Peduncle glabrous; 1-4 mm long; with fig basal bracts at the top of the peduncle or with fig basal bracts between the bottom and the top of the peduncle.

**Fig shape** globose; rounded at the apex; glabrous; 4-12 mm long; 4-12 mm wide; green to white; ripening pink to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 0.5-1.5 mm long. **Lateral bracts** few to many. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Disturbed slopes in lowland sandstone habitat, river banks, and coastal secondary forest; uncommon. **Geographic range:** Borneo. **Vouchers:** GW889, TL1230

*Ficus stricta* Miq.

Large hemiepiphyte with crown in the upper canopy; strangling host and becoming free-standing. 15-40 m in height. **Twigs** glabrous; 2-3.5 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; glabrous; 1-2 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.8-2 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 7-15 cm long; 3.5-6 cm wide; 1.7-2.3 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins not paired. As prominent as tertiary veins or more prominent than tertiary veins; not raised or raised above and below. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 13-17 mm long; 13-17 mm wide; green to yellow; ripening orange to red. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate to rounded; more or less equal in size; 2.5-4 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Numerous secondary veins similar to *F. benjamina* but with larger leaves and larger figs ripening orange. **Habitat:** Single collection in lowland sandstone habitat; rare. **Geographic range:** Indochina, Peninsular Malaysia, Sumatra, Java, Borneo, Sulawesi (Minhasa), Luzon. **Voucher:** TL1443 (sterile)

*Ficus stupenda* Miq.

Large hemiepiphyte in the upper canopy with aerial roots small compared with host trunk; not free-standing. 30-60 m in height. **Twigs** glabrous; 7-12 mm in diameter; hollow or with spongy pith; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1.5-3 cm long.

**Leaves** spiral. **Petioles** glabrous; 2-5 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 10-20(-30) cm long; 4-14 cm wide; 2 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 35-60 degrees from the midrib. **Secondary veins** 4-8 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of more or less equal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** oblong; rounded at the apex; glabrous; 25-40 mm long; 20-30 mm wide; green to yellow; ripening orange to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 5-10 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Large, oblong figs with prominent basal bracts and large leaves with distinct box-like fine venation. **Habitat:** Rare in peat swamp; common in freshwater swamp; the most common hemiepiphytic species in alluvial bench and lowland sandstone; uncommon in lowland granite. **Geographic range:** Peninsular Malaysia, Sumatra, Java, Borneo. **Voucher:** GW907

*Ficus subgelderii* Corner v. *rigida* Corner

Medium sized hemiepiphyte in the middle to upper canopy with aerial roots small compared to host trunk; not free-standing. 20-50 m in height. **Twigs** glabrous; 2-6 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous or pubescent; 1-2.5 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.5-3 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 4-20 cm long; 1.5-8 cm wide; 2.1-2.5 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 20-40 degrees from the midrib. **Secondary veins** 3-7 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose to oblong; rounded at the apex; glabrous; 12-16 mm long; 9-15 mm wide; green to yellow; ripening orange to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous or pubescent; acuminate; more or less equal in size; 6-10 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Leaves with tertiary venation distinctly raised below; drying pale brown. **Habitat:** Common across all habitats from peat swamp to lowland granite. **Geographic range:** Peninsular Malaysia, Borneo. **Vouchers:** GW918, GW930, TL1228, TL1389

*Ficus subtecta* Corner

Large hemiepiphyte in the upper canopy; aerial roots always small compared with host trunk; not free-standing. 30-60 m in height. **Twigs** glabrous to pubescent; 4-10 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; pubescent; 1.5-4 cm long.

**Leaves** spiral. **Petioles** glabrous; 2-3 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 10-19 cm long; 5-9 cm wide; 1.5-2.8 times as long as wide; convolute in bud. Margin

entire. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.25-0.5 times as long as the leaf; departing at an angle of 25-50 degrees from the midrib. **Secondary veins** 4-8 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 12-18 mm long; 13-17 mm wide; green to yellow; ripening orange. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 12-15 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Basal bracts covering half or more than half the fig. **Habitat:** Common in freshwater swamp through lowland sandstone; uncommon in lowland granite. **Geographic range:** Peninsular Malaysia, Sumatra, Java, Borneo. **Vouchers:** ML2528, ML3228

#### *Ficus subulata* Bl.

Climber or hemiepiphyte in the understory to middle canopy. Rarely a small tree. 5-20 m in height. **Twigs** glabrous; 1-4 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; glabrous to pubescent; 1-2 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.3-1.5 cm long. **Leaf shape** elliptic to obovate; glabrous; chartaceous; 8-23 cm long; 1.5-10 cm wide; 1.9-2.4 times as long as wide; plicate in bud. Margin entire. Base cuneate; symmetric or asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0-0.1 times as long as the leaf; departing at an angle of 40-50 degrees from the midrib. **Secondary veins** 9-16 pairs; more prominent than tertiary veins; raised above and below or raised below but not above. **Tertiary veins** regular or irregular. Areoles of more or less equal size. Leaf gland solitary in the axil of a basal vein. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle glabrous; 3-6 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** globose; rounded at the apex to umbonate; glabrous; 4-8 mm long; 4-8 mm wide; green; ripening orange. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 0-1 mm long. **Lateral bracts** none or few to many. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Single collection from lowland sandstone. **Geographic range:** India, Indochina, Malaysia, Indonesia, Papua New Guinea and Solomon Isl. **Voucher:** TL66

#### *Ficus sunaica* Bl.

Large hemiepiphyte in the upper canopy; aerial roots small compared with host trunk, not free-standing. 20-50 m in height. **Twigs** glabrous to pubescent; 2-5 mm in diameter; hollow or with spongy pith; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1-2.2 cm long.

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**Leaves** spiral. **Petioles** glabrous; 1-2.5 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 8-23 cm long; 3.5-11 cm wide; 2.1-3.2 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins or more prominent than the secondary veins; 0.2-0.5 times as long as the leaf; departing at an angle of 30-50 degrees from the midrib. **Secondary veins** 5-10 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose to oblong; rounded at the apex; glabrous; 11-17 mm long; 11-14 mm wide; green to yellow; ripening orange to red; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 5-7 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Coriaceous leaves with distinct but not strongly raised venation; fine venation not box-like. Large basal bracts cover less than half of the globose fig. See also *F. stupenda*, *F. subsecta*, *F. subgelderi*. **Habitat:** Peat swamp to lowland sandstone; uncommon. **Geographic range:** Myanmar, Vietnam, Thailand, Peninsular Malaysia, Sumatra, Java, Borneo. **Vouchers:** GW865, GW867, GW872, TL1274

#### *Ficus sundaica* v. *beccariana* Bl. (King)

Differing from v. *sundaica* in the following respects. Hemiepiphyte 30-60 m in height. **Twigs** 3-7 mm in diameter; not hollow. **Stipules** pubescent; 1.5-3 cm long. **Petioles** glabrous or pubescent; 1.4-3 cm long. **Leaf shape** 12-24 cm long; 3.5-10 cm wide; 1.8-3.5 times as long as wide. Base cuneate. Basal veins 0.3-0.5 times as long as the leaf; departing at an angle of 30-45 degrees from the midrib. **Secondary veins** 4-8 pairs; raised above and below. **Figs** 16-25 mm long; 14-20 mm wide. **Fig basal bracts** acuminate to rounded; 7-9 mm long.

**Spot characters:** Larger figs and generally larger more elongate leaves than in v. *sundaica*. **Habitat:** Most common in peat swamp; also common in freshwater swamp; uncommon in alluvial bench. **Geographic range:** Peninsular Malaysia, Borneo. **Vouchers:** GW932, TL1437

#### *Ficus sundaica* Bl. v. *impressicostata* Kochummen

Sprawling hemiepiphyte that often drapes through several trees in the lower to middle canopy and may drop roots down more than one host. 10-30 m in height. **Twigs** 2-4 mm in diameter; not hollow. **Petioles** 0.8-2.1 cm long. **Leaves** 6-17.5 cm long; 3-7 cm wide; 1.5-2.8 times as long as wide. **Leaf venation** with basal veins more prominent than the secondary veins. **Secondary veins** 3-6 pairs. Cystoliths none. **Fig shape** oblong; rounded at the apex; 15-20 mm long; 7-15 mm wide. **Fig basal bracts** acuminate.

**Spot characters:** Sprawling hemiepiphyte. Leaves drying very dark, thick, elliptical, with a pointed apex and rolled margins. **Habitat:** Common in peat swamp. **Geographic range:** India, Indochina, Sumatra, Borneo. **Voucher:** GW906

*Ficus tarennifolia* Corner

Small tree. 2-8 m in height; 5-10 cm dbh; buttresses absent or less than 0.5 m in height. **Twigs** glabrous; 1-4 mm in diameter; hollow or with spongy pith; with a waxy gland below the node; latex color yellow. **Stipules** caducous; glabrous; 0.8-2 cm long.

**Leaves** spiral or opposite. **Petioles** glabrous; 0.5-2.5 cm long. **Leaf shape** obovate; glabrous; chartaceous; 4-18 cm long; 2-6 cm wide; 2.8-3.3 times as long as wide; plicate in bud. Margin entire to serrate or dentate. Base cuneate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins not paired. **Secondary veins** 3-6 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** irregular. Areoles of unequal size. Leaf glands none. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary and cauliflorous; pedunculate. Peduncle glabrous; 6-12 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** globose to oblong; rounded at the apex; glabrous; 6-12 mm long; 4-8 mm wide; green; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 0.5-1 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Figs born axillary or cauliflorous, small compared to *F. schwartzii*.

**Habitat:** River banks in alluvial bench forest. **Geographic range:** Borneo. **Vouchers:** TL742, TL743

*Ficus trichocarpa* Bl.

Climber. **Twigs** pubescent; 1-3 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; pubescent.

**Leaves** spiral. **Petioles** pubescent; 0.7-2 cm long. **Leaf shape** elliptic to ovate to cordate; pubescent and scabrid; coriaceous; 4.5-14 cm long; 3.3-9.5 cm wide; 1.2-1.5 times as long as wide; plicate in bud. Margin entire. Base cordate to rounded; symmetric. Apex pointed or blunt. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.5 times as long as the leaf; departing at an angle of 45-60 degrees from the midrib. **Secondary veins** 3-7 pairs; as prominent as tertiary veins or more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular to irregular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary or cauliflorous; pedunculate. Peduncle pubescent; 4-8 mm long; with fig basal bracts at the top of the peduncle. **Fig shape** globose; rounded at the apex; pubescent; 8-10 mm long; 8-10 mm wide; ripening red to purple to brown. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate to rounded; more or less equal in size; 0.5-1.5 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Single collection from coastal secondary forest. **Geographic range:** Indochina, Peninsular Malaysia, Sumatra, Java, Borneo. **Voucher:** GW855 (sterile)

*Ficus tristanifolia* Corner

Medium sized hemiepiphyte with crown in the upper canopy; strangling host and becoming free-standing by a single root. 20-35 m in height. **Twigs** glabrous; 2-4 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous; 1.2-2 cm long.

**Leaves** spiral. **Petioles** glabrous; 0.5-2 cm long. **Leaf shape** obovate; glabrous; coriaceous; 6-15 cm long; 3-8 cm wide; 1.7-2.2 times as long as wide; convolute in bud. Margin entire. Base cuneate; symmetric. Apex rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins or more prominent than the secondary veins; departing at an angle of 30-40 degrees from the midrib. **Secondary veins** 10-20 pairs; as prominent as tertiary veins or more prominent than tertiary veins; not raised or raised above but not below. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose; rounded at the apex; glabrous; 5-10 mm long; 5-10 mm wide; green; ripening white. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 2-4 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a flattened disc or forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Leaves thick, obovate; venation not visible in fresh leaves; 10 or more pairs of secondary veins visible in dried leaves. **Habitat:** Restricted to peat swamp. **Geographic range:** Peninsular Malaysia, Sumatra, Borneo. **Vouchers:** GW931, TL1293

*Ficus uncinata* (King) Becc.

Small tree. 3-8 m in height; 3-8 cm dbh; buttresses absent or less than 0.5 m in height. **Twigs** pubescent; 2-3.5 mm in diameter; hollow or with spongy pith; with a waxy gland below the node. **Stipules** caducous; pubescent; 1.5-3.5 cm long.

**Leaves** spiral. **Petioles** pubescent; 0.2-1 cm long. **Leaf shape** elliptic to obovate; pubescent; chartaceous; 10-31 cm long; 2.5-16 cm wide; 2-2.4 times as long as wide; plicate in bud. Margin serrate or dentate. Base cordate to cuneate to rounded; asymmetric. Apex pointed. **Leaf venation** pinnate; basal veins not paired. **Secondary veins** 4-13 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** regular. Areoles of unequal size. Leaf glands in the axils of the secondary veins. Cystoliths paraxial. Stomata not aggregated.

**Figs** geocarpic; pedunculate. Peduncle glabrous; 2-4 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** globose; sunken at the apex; glabrous; 12-25 mm long; 12-25 mm wide; ripening red; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 1-2 mm long. **Lateral bracts** few to many. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.



**Spot characters:** Leaves with an asymmetrical base and a rounded lobe on one side; margins toothed; densely hairy below. **Habitat:** Disturbed slopes in lowland sandstone habitat; uncommon. **Geographic range:** Borneo. **Vouchers:** GW886, GW887

*Ficus urnigera* Miq.

Climber. **Twigs** pubescent; 1.5-3 mm in diameter; not hollow; without a waxy gland below the node. **Stipules** caducous; glabrous; 0.3-1 cm long.

**Leaves** distichous. **Petioles** pubescent; 0.3-1.2 cm long. **Leaf shape** ovate to lanceolate; glabrous to pubescent; coriaceous; 6-12 cm long; 2.5-4.5 cm wide; 2.1-3.1 times as long as wide; plicate in bud. Margin entire. Base rounded to cordate; symmetric. Apex pointed to rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.3-0.6 times as long as the leaf; departing at an angle of 30-40 degrees from the midrib. **Secondary veins** 3-4 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of unequal size. Leaf glands in the axils of the secondary veins. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** globose to obconical; rounded at the apex or sunken at the apex; glabrous; 3-5 mm long; 3-6 mm wide; green; ripening orange to red. **Fig basal bracts** 3, persistent in mature figs; pubescent; acuminate; more or less equal in size; 0-1 mm long. **Lateral bracts** none. **Apical bracts** sunken and not visible on fig exterior. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

**Habitat:** Coastal secondary forest, along disturbed river bank, and in lowland sandstone habitat; rare. **Geographic range:** Southern Thailand, Peninsular Malaysia, Sumatra, Java, Borneo, Philippines. **Voucher:** GW936

*Ficus variegata* Bl.

Medium-sized tree. 10-35 m in height; 10-60 cm dbh; buttresses often more than 1 m in height. **Twigs** glabrous; 2-8 mm in diameter; hollow or with spongy pith; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous to pubescent; 1-1.4 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.5-10 cm long. **Leaf shape** ovate; glabrous; chartaceous; 8-25 cm long; 4.5-12.5 cm wide; 1.8-2.5 times as long as wide; plicate in bud. Margin entire. Base rounded to cordate; symmetric. Apex pointed. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.4-0.6 times as long as the leaf; departing at an angle of 25-40 degrees from the midrib. **Secondary veins** 4-8 pairs; more prominent than tertiary veins; raised above and below. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands paired in the axils of the basal veins. Cystoliths abaxial. Stomata not aggregated.

**Figs** cauliflorous; pedunculate. Peduncle pubescent; 15-60 mm long; with fig basal bracts between the bottom and the top of the peduncle. **Fig shape** globose to obconical; umbonate; glabrous; 10-30 mm long; 10-30 mm wide; green to pink; ripening pink to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous to pubescent; acuminate to rounded; more or less equal in size; 0.5-1 mm long. **Lateral bracts** none. **Apical bracts** more than 3. **Ostiolar bracts** overlapping. **Breeding system** gynodioecious.

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**Spot characters:** Cauliflorous tree with broad leaves and figs ripening with pink or red spots.

**Habitat:** Single collection in lowland sandstone habitat. **Geographic range:** India, Indochina, Indonesia, Philippines, New Guinea, Solomon Isl., Australia. **Voucher:** GW892

*Ficus villosa* Bl.

Moderate-sized climber in the middle canopy. 10-30 m in height. **Twigs** pubescent; 4-8 mm in diameter; hollow or with spongy pith; without a waxy gland below the node. **Stipules** caducous or persistent; pubescent; 1-3.5 cm long.

**Leaves** distichous. **Petioles** pubescent; 1.2-2.5 cm long. **Leaf shape** elliptic to ovate; pubescent; coriaceous; 7-25 cm long; 4-12 cm wide; 1.5-2.7 times as long as wide; plicate in bud. Margin entire. Base rounded to cordate; symmetric. Apex pointed to rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.25-0.5 times as long as the leaf; departing at an angle of 40-65 degrees from the midrib. **Secondary veins** 3-7 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** regular. Areoles of more or less equal size. Leaf glands in the axils of the secondary veins. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; pedunculate. Peduncle glabrous; 2-6 mm long; with fig basal bracts at the bottom of the peduncle. **Fig shape** globose; umbonate; glabrous; 8-15 mm long; 8-15 mm wide; green; ripening orange to red; without spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; rounded; more or less equal in size; 1.5-2.5 mm long. **Lateral bracts** none. **Apical bracts** sunken and not visible on fig exterior. **Ostiole bracts** overlapping. **Breeding system** gynodioecious.

**Spot characters:** Twigs and underside of leaves with reddish brown hairs; venation sunken above. **Habitat:** Streamsides in lowland sandstone and submontane granite; uncommon. **Geographic range:** India, Andaman Isl., Indochina, Peninsular Malaysia, Sumatra, Java, Borneo. **Voucher:** GW899

*Ficus xylophylla* (Miq.) Wall. ex Miq.

Moderate-sized hemiepiphyte in the lower to middle canopy with aerial roots small compared with host trunk; not free-standing. 15-40 m in height. **Twigs** glabrous; 7-10 mm in diameter; not hollow; without a waxy gland below the node; latex color white. **Stipules** caducous; glabrous or pubescent; 1.7-5 cm long.

**Leaves** spiral. **Petioles** glabrous; 1.2-5 cm long. **Leaf shape** elliptic; glabrous; coriaceous; 11-30 cm long; 7-15 cm wide; 1.5-2.1 times as long as wide; convolute in bud. Margin entire. Base cuneate to rounded; symmetric. Apex rounded. **Leaf venation** pinnate; basal veins paired; as prominent as the secondary veins; 0.4-0.6 times as long as the leaf; departing at an angle of 35-55 degrees from the midrib. **Secondary veins** 4-8 pairs; more prominent than tertiary veins; raised below but not above. **Tertiary veins** irregular. Areoles of unequal size. Leaf gland solitary at the base of the midrib. Cystoliths paraxial. Stomata not aggregated.

**Figs** axillary; sessile. **Fig shape** oblong; rounded at the apex; glabrous; 20-35 mm long; 13-25 mm wide; green to yellow; ripening orange to red; with spots. **Fig basal bracts** 3, persistent in mature figs; glabrous; acuminate; more or less equal in size; 4-8 mm long. **Lateral bracts** none. **Apical bracts** 3, forming a cone. **Ostiolar bracts** overlapping. **Breeding system** monoecious.

**Spot characters:** Large, oblong figs with small basal bracts; large, coriaceous leaves with a rounded apex and without box-like venation. **Habitat:** Ranging from peat swamp through all habitats to montane forest; most abundant in peat swamp and submontane forest. **Geographic range:** Laos, Thailand, Peninsular Malaysia, Sumatra, Riau, Bangka, Borneo. **Vouchers:** GW910, TL1421

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