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TAXONOMY, SYSTEMATICS, AND BIOGEOGRAPHY OF *FICUS* SUBSECTION *UROSTIGMA* (MORACEAE)

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TAXONOMY, SYSTEMATICS, AND BIOGEOGRAPHY OF *FICUS* SUBSECTION *UROSTIGMA* (MORACEAE)

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TABLE OF CONTENTS

Chapter 1	General Introduction	*7*
Chapter 2	A Revision of *Ficus* subsection *Urostigma* (Moraceae)	*21*
Chapter 3	Leaf anatomy of *Ficus* subsection *Urostigma* (Moraceae)	*93*
Chapter 4	Pollen morphology of *Ficus* subsection *Urostigma* (Moraceae)	*129*
Chapter 5	A new classification of *Ficus* subsection *Urostigma* (Moraceae) based on four nuclear DNA markers (ITS, ETS, G3pdh, and ncpGS), morphology and leaf anatomy	*143*
Chapter 6	*Ficus cornelisiana*, a new species of *Ficus* subsection *Urostigma* (Moraceae) from the Sino-himalayan Region	*181*
Chapter 7	Historical biogeography of *Ficus* subsection *Urostigma* (Moraceae)	*189*
Chapter 8	Which species of *Ficus* subsection *Urostigma* in Thailand are used as food, ornamental plants or sacred trees?	*207*
	Summary & Conclusions	*217*
	Samenvatting & Conclusies (Dutch summary)	*223*
	References	*231*
	Curriculum Vitae	*241*
	Acknowledgements	*244*

Chapter 1

General Introduction

General Introduction

Ficus L. (Moraceae) is an important plant genus for various and diverse reasons. In Buddhist religion it is prominent, because the Lord Buddha attained enlightenment while meditating under a tree belonging to *Ficus religiosa* L. (Berg & Corner, 2005). Hindus conduct various meditative paces around fig trees, while the sadhus (hindu ascetics) also meditate beneath sacred fig trees (Murty, 2014).

In pollination biology *Ficus* is one of three taxa with an obligatory, symbiotic relationship with its pollinators, whereby the larvae of the pollinators, while feeding on a part of the seeds, are protected by the fruits (or figs). In *Ficus* pollination is carried out by the fig wasps. The other two groups are *Yucca* (Pellmyr et al., 1996; Proctor et al., 1996; Pellmyr, 2003) and Phyllanthaceae (Kawakita and Kato, 2004), both pollinated and the seed predated upon by moths. Pollen loaded female fig wasps enter the fig via the ostiole, loosing their wings in the process due to the scales in the ostiole. They pollinate the pistillate flowers, of which there are two types, those with a long and those with a short stigma. The wasps can only deposit eggs in the flowers with short stigmas. The developing larvae eat the seeds. The male wasps hatch first and gather around the ostiole, where staminate flowers shed their pollen. Once the females hatch from the pupae, they are inseminated by the males and gather pollen while leaving the fig passing the withered scales in the ostiole. The male wasps die in the fig (Ramírez, 1969; Wiebes, 1979; Anstett et al., 1997; Kjellberg et al., 2001).

Ecologically, *Ficus* is important for two reasons. Many species start as slow growing epiphytes in high trees, which, at one stage, send out a root to the soil, after which growth becomes vigorous, making more and more (interconnecting) roots around the host tree. The host tree dies, either because of the competition for food or light or because it is strangled (hence the name strangler figs). In the ecosystem the figs are keystone species to uphold the food chain by producing plentiful food for various wild animals, especially during the dry season when other trees are only present vegetatively or even shed their leaves (Berg & Corner, 2005; Berg et al., 2011; Shanahan et al., 2001, Harrison et al., 2012).

In this thesis the focus is on a group within *Ficus, F.* subsect. *Urostigma* (Gasp.) Berg. The species are found from West Africa and Madagascar through the Asian mainland to Japan and via southern Malesia to Australia and the Pacific. The species have highly variable morphological characters and can exhibit a wide distribution range (Berg & Corner, 2005). The systematic circumscription of the subsection and its classificatory relationships with other subsections are problematic. Furthermore, morphologically some species of subsect. *Urostigma* are very variable and show character combinations that make it difficult to distinguish the species from others. These problems will be addressed, discussed and (partly) solved in this thesis. Also presented will be a hypothesis of the evolution of the group (phylogeny) and its historical biogeography.

General morphology, leaf anatomy, and pollen morphology of *Ficus* subsect. *Urostigma*

The species of subsect. *Urostigma* can be recognised by a combination of various traits: They are mainly hemi-epiphytic trees or shrubs (stranglers; Fig. 1-1A, B). All of them show intermittent growth, whereby long internodes without leaves alternate with short shoots with leaves. The species are often deciduous, and the leaves are clearly articulate or subarticulate in most Asian species. There are two forms of stipules, long ones (more than 2 cm long) that are thin and caducous and which appear on the long shoots (Fig. 1-1C) and short ones (usually less than 2 cm), that are thicker and more persistent and found on the short shoots (Fig. 1-1D).

The figs are often borne below the leaves, sometimes only in the leaf axils (Fig. 1-1E), and in some species on spurs (brachyblasts) on the older wood (Fig. 1-1F). The figs occur solitary, in pairs, or up to eight together on the spurs. The number of basal bracts is usually three. The syconium (fig) is subglobose to subpyriform and varies in size. The syconium changes colour during maturation, from greenish to finally black, but with various pathways via white, pink and purple. Staminate flowers occur near the ostiole (opening of the fig) or they are dispersed among the pistillate flowers, but sometimes they can be abundant around the ostiole with a few dispersed. The staminate flowers are mostly sessile, rarely shortly pedicellate (Fig. 1-1G). Pistillate flowers are sessile or pedicellate. The ovary is white or red brown. The styles differ in length, long-styled flowers are mostly sessile; short-styled ones are generally pedicellate and their ovaries tend to be longer than those of the long-styled flowers. There is only one stigma, which entangles with those of adjacent flowers, thus forming a syn-stigmatic layer.

Leaf anatomy shows the presence of glandular hairs and simple hairs. The glandular hairs are elongate or cylindrical with 1- or 2-celled heads (Fig. 1-2A), or ellipsoid with 4-celled heads. Simple hairs are mostly single-celled with a pointed tip (Fig. 1-2B). Many species have translucent hairs on the inner surface of the syconium among the flowers, these are called “internal hairs”. The epidermis is mostly single-layered and generally thicker at the adaxial side of the leaf (Fig. 1-2C), although it may have proliferated to form a multiple epidermis in some species (Fig. 1-2D). In surface view, the epidermis shows a pattern of 5-16 radiating cells, forming a rosette around the base of every lithocyst (enlarged epidermal cell with a cystolith in it, see below; Fig. 1-2E). The lithocysts are generally cells containing a hanging, short, club-shaped crystal (cystolith), which resembles an abortive hair (Berg and Corner, 2005). The lithocysts come in two forms. “Enlarged lithocysts” consist of very large cells, which deeply intrude into the palisade or spongy mesophyll and which are

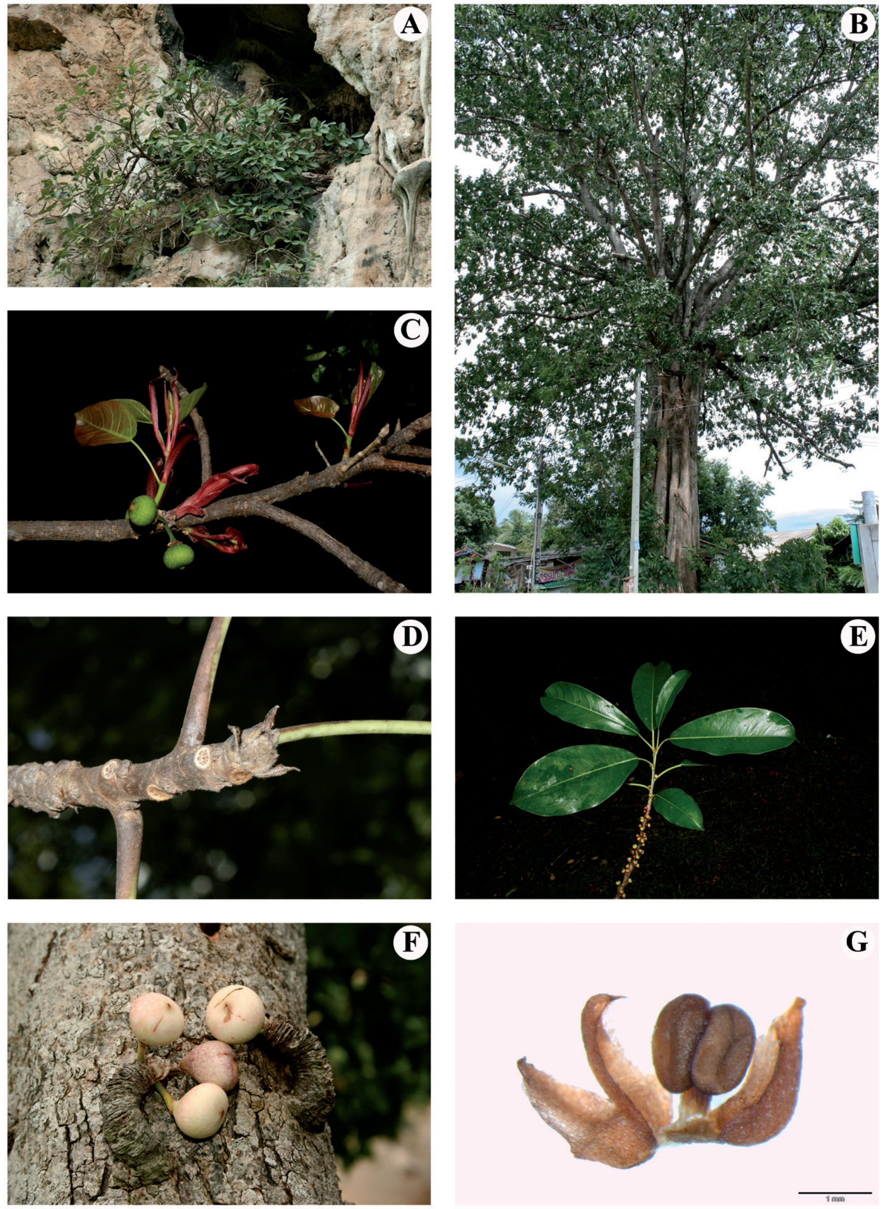

FIGURE 1-1: A. *Ficus orthoneura* in habit. B. *Ficus superba* in habit. C. Long stipulate form of *Ficus subpisocarpa* subsp. *pubipoda*. D. Short stipulate form of *Ficus subpisocarpa* subsp. *pubipoda*. E. Living twig of *Ficus glabella* shows the figs in leaf axils of fallen leaves. F. Figs on the spur of *Ficus superba*. G. Staminate flower of *Ficus saxophila* showing one stamen (*Kostermans 335*). All photographs by B. Chantarasuwan.

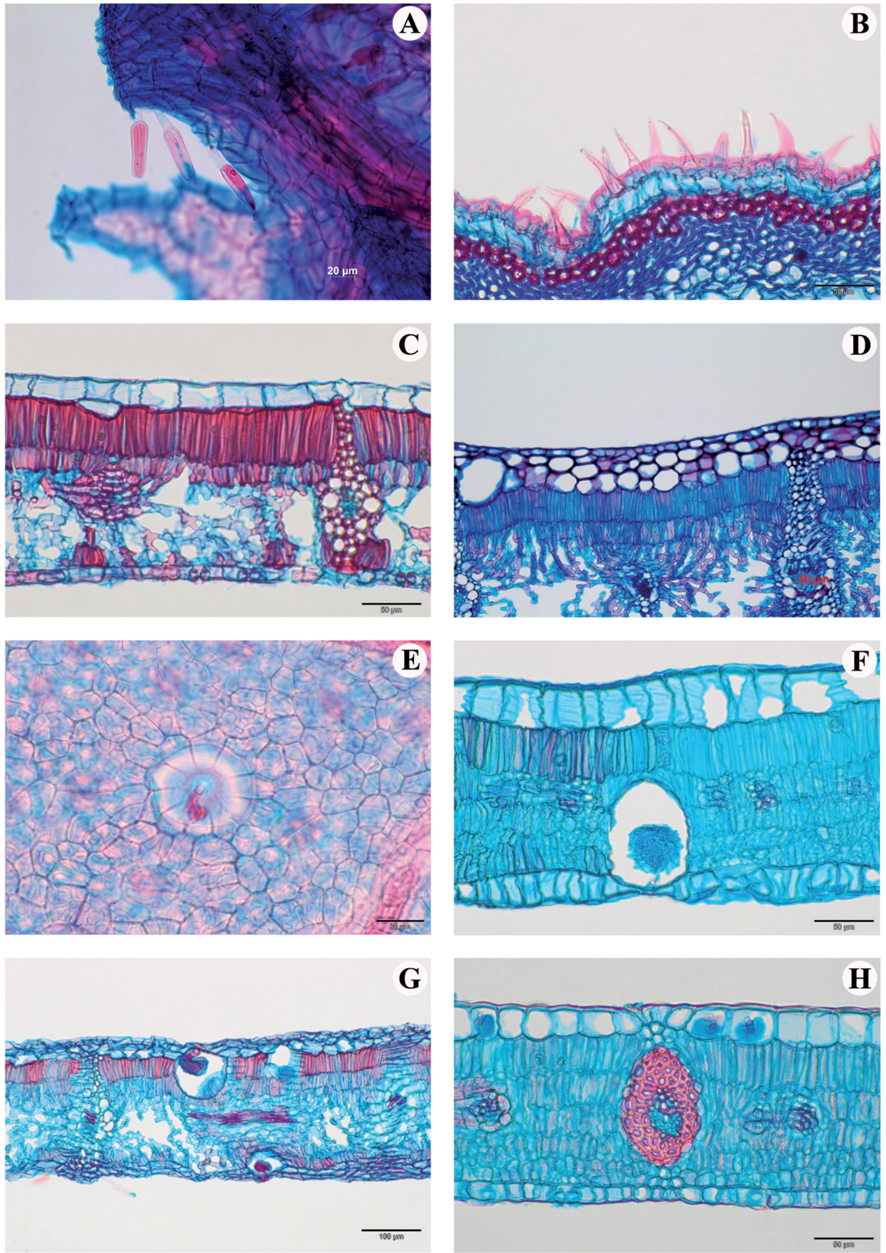

FIGURE 1-2: A. Glandular hairs with two head cells of *Ficus arnottiana* (*Haines 3546*). B. Simple hairs of *Ficus prolixa* (*Fosberg 31278*). C. The single layered epidermal cells of *Ficus caulocarpa* (*Chantarasuwan 071010–2*). D. The multiple layered epidermal cell of *Ficus arnottiana* (*Haines 3546*). E. The rosette-like epidermal cells surrounding the base of a lithocyst of *Ficus caulocarpa* (*Chantarasuwan 071010–2*). F. Enlarged lithocyst abaxially in the epidermis of *Ficus cordata* (*Seydel 3186*). G. Enlarged lithocysts in both abaxial and adaxial epidermis of *Ficus arnottiana* (*Haines 3546*). H. Epidermal lithocysts of *Ficus religiosa* (*Chantarasuwan 150910–2*). All photographs by B. Chantarasuwan.

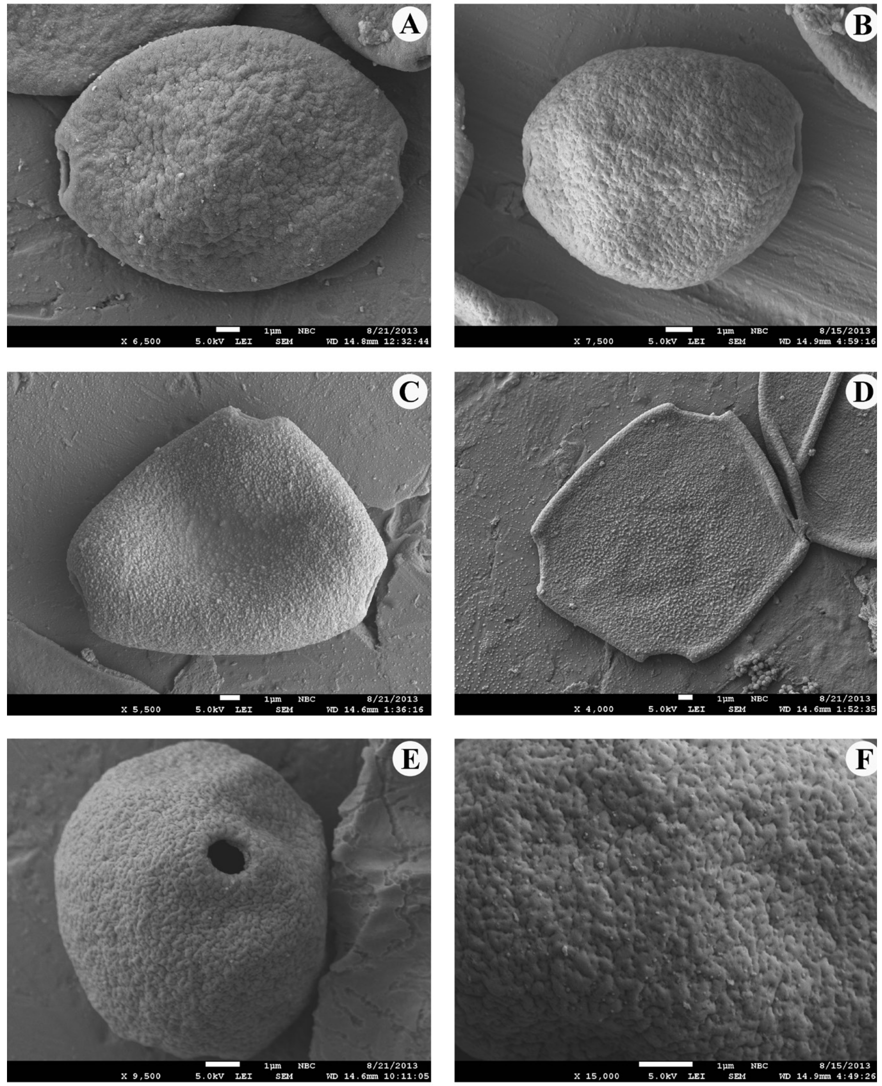

FIGURE 1-3: A. An ellipsoid 2–porate grain of *Ficus religiosa* (*Koelz 4030*). B. A gibbous 2–porate grain of *Ficus densifolia* (*Etienne 5156*). C. In polar view a triangular 3–porate grain of *Ficus salicifolia* (*Léonard 4959*). D. A quadrangular 4–porate grain of *Ficus salicifolia* (*Léonard 4959*) in polar view. E. The circular pore of *Ficus orthoneura* (*Cavalerie & Fortunat 2050*). F. The microrugulate pollen surface of *Ficus densifolia* (*Etienne 5156*). All photographs by B. Chantarasuwan.

surrounded by radiating epidermal cells in surface view. They mostly appear on the abaxial side of the lamina (Fig. 1-2F), except in *F. arnottiana* (Miq.) Miq., which shows abundant enlarged lithocysts adaxially and very few abaxially (Fig. 1-2G). The smaller lithocysts are adaxial epidermal cells of normal size, but they are not always consistently present in all species (Fig. 1-2H).

The pollen grains are very small to small, and they are 2–porate and ellipsoid or asymmetrically ellipsoid ('gibbous') (Fig. 1-3A,B) or sometimes 3–porate with a triangular polar view (Fig. 1-3C), rarely 4–porate monads quadrangular in polar view (Fig. 1-3D). The pores are circular (Fig. 1-3E). The exine is less than 1 μm thick, and the ornamentation is nearly always scabrate (elements < 1 μm high: finely punctate, microrugulate or microverrucate) (Fig. 1-3F)

Ecological and economic importance of *Ficus* subsect. *Urostigma*

All species of *Ficus* subsect. *Urostigma* occur mainly in tropical regions, though *F. subpisocarpa* Gagnep. can extend into the subtropics. The habitat of most species is generally a dry type of vegetation and/or there are seasonal conditions with a water deficit during a period of the year (Berg & Corner, 2005) such as found in savannah or on limestone. Only a few species live under everwet conditions, like *F. caulocarpa* (Miq.) Miq., which is commonly found in rain forests, and *F. verruculosa* Warb. that is abundant along streams or in swamps in Africa. *Ficus superba* (Miq.) Miq., though living under everwet conditions, is found along the coast in a saline habitat, which also causes physiological drought.

The species of the subsection are important food plants, not only in the wild, but also cultivated as the leaves are used as forage for cattle in Africa and Asia. Young shoots and young figs are eaten by humans. The shoots of at least five species in northern Thailand are eaten (Chantarasuwan & van Welzen, 2012), while some species are utilised in traditional medicine (de Padua et al., 1999) and/or they are sacred trees. Often species are used as ornamental plants and they can even be treated as bonsai, fetching high commercial prices.

The taxonomic history of *Ficus* subsect. *Urostigma*

The history of *Ficus* subsection *Urostigma* can be divided into five periods. Since Linneaus founded the genus *Ficus* in1753, his *F. religiosa* was the first species of the subsection that was described, thus forming the type of the subsection. In this period many species were described and an infrageneric classification was lacking. *Ficus virens* was described by Aiton (1789) from a cultivated plant growing in Kew gardens, but introduced from the West Indies by James Gordon around 1762. *Ficus tsjakela* Burm.f. was based on the vernacular name Tsjakela (Burman, 1768). Thunberg described the first African species, *F. cordata*, in 1786, the same year that Forster described *F. prolixa* from the Society Islands in the W Pacific. The first period ended with the publication of *F. saxophila* and *F. glabella* by Blume (1825).

The second period began when botanists (Gasparrini, 1844; Miquel, 1847) started to break up *Ficus* into several genera. Many species were first published under the generic name "Urostigma" in that time.

In the third period Miquel (1867) reversed the idea of breaking up *Ficus* and he re-united the genera again. Instead he introduced an infrageneric subdivision of six subgenera, *Urostigma* being one of them. Miquel further subdivided subgen. *Urostigma* according to distributions and morphological characters into series, whereby he recognised six series for Asia and Australia, three series for Africa, and five series for America. In 1887 King divided *Ficus* into seven sections based on the morphology of the flowers, which equalled the subgenera of Miquel. King divided his section *Urostigma* into series and subseries based on leaf characters. In 1960, Corner re-used the rank "subgenus". He recognized three subgenera, one of them subg. *Urostigma* with seven sections, among which sect. *Urostigma*, which contained four series. However, the species of subsect. *Urostigma*, as they are recognised today, were still spread over several sections or series and not yet members of a single taxon.

Berg started the fourth period with the recognition of subsection *Urostigma* in 2004. He united Corner's sections *Leucogyne*, *Urostigma*, and *Conosycea* into sect. *Urostigma*, which he subdivided into subsect. *Urostigma* (containing Corner's sect. *Leucogyne* and *Urostigma*) and subsect. *Conosycea* (containing Corner's sect. *Conosycea*). All African species were included in subsect. *Urostigma* in this period. The revision work of *Ficus* subsect. *Urostigma* by Chantarasuwan et al. (2013) was inspired by Berg's classification.

The fifth, the cladistic period, ran parallel with the fourth one. Classifications reflected monoplyletic groups based on phylogenies of large, mainly molecular data sets analysed with Bayesian and likelihood methods. For *Ficus* this period started when Weiblen (2000) published the first phylogeny based on DNA sequences and morphology. He was followed by Jousselin et al. (2003), who combined ITS and ETS data to construct the core phylogenetic relationships among 41 species of *Ficus*. For subsect. *Urostigma* real phylogenetic analyses began when Rønsted et al. (2005) combined ITS and ETS in their phylogenetic work, which included nine species of subsect. *Urostigma*. Rønsted et al. (2008) extended the phylogeny by adding the *G3pdh* marker for nearly half of the species of subsect. *Urostigma*. Most recently, Chantararasuwan et al. (2014) used four genes (ITS, ETS, *G3pdh*, and *ncpGS*) in combination with morphology and leaf anatomy to construct a phylogeny. The results showed subsect. *Urostigma* to be monophyletic and this new classification of *Ficus* subsect. *Urostigma* is presented here.

Problems

Morphologically, many species of subsect. *Urostigma* are very variable, which makes it difficult to distinguish species such as *F. virens*, which overlaps in some characters with *F. geniculata* Kurz (Berg, 2007). Another problem was caused by *Ficus rumphii* and *F. amplissima*, previously placed in section *Leucogyne* by Corner (1959), but transferred to subsect. *Urostigma* by Berg and Corner (2005). However, molecular phylogenetic research by Rønsted et al. (2005) showed that *F. rumphii* is embedded in subsect. *Conosycea*. Thus, the systematic position of both species is still doubtful. To resolve these problems, extra morphological studies (Chantarasuwan et al., 2013) and leaf anatomical studies (Chantarasuwan et al., 2014) were applied to find more characters. The combined results of both studies, elaborated with new phylogenetic analyses (Rønsted et al., 2005, 2008; Chantarasuwan et al., submitted) resolved the problem of the circumscription of the species and their classification. *Ficus amplissima* and *F. rumphii* will be part of subsect. *Conosycea* and no longer belong to subsect. *Urostigma*. This decision is corroborated by the pollinators. *Eupristina* wasps pollinate figs of subsect. *Conosycea* figs, while subsect. *Urostigma* is pollinated by species of *Platyscapa* (Wiebes, 1979; Berg and Wiebes 1992; Berg and Corner 2005; Cruaud et al. 2009). The leaf anatomy of *F. arnottiana* (subsect. *Urostigma*) presented yet another problem. *Ficus arnottiana* shows morphological similarity with species of subsect. *Conosycea*, but the molecular phylogeny of Chantarasuwan et al. (in press) shows *F. arnottiana* to be firmly embedded within subsect. *Urostigma*.

Research Questions

Based on the taxonomic problems encountered, the following research questions are addressed:

1) Which species can we morphologically distinguish in *Ficus* subsect. *Urostigma*? What are their diagnostic morphological characters? What is the extent of morphological overlap between the species?

2) Do the species of *Ficus* subsect. *Urostigma* differ in leaf anatomy? Does the leaf anatomy provide proper diagnostics for the recognition of species? Will leaf anatomy strengthen or improve morphological species circumscriptions?

3) Does pollen morphology show the same functionality as leaf anatomy in the characterisation of species?

4) What is the most likely phylogeny of *F.* subsect. *Urostigma*? How do the two species in section *Leucogyne*, *F. amplissima* and *F. rumphii*, fit in? How is *Ficus* subsect. *Urostigma* related to other subsections and sections within *Ficus* subgenus *Urostigma*?

5) How can the phylogenetic results be translated into a classification? Are clades recognisable with the aid of morphology, leaf anatomy, and/or pollen morphology? How can we explain the evolutionary trends in morphology, leaf anatomy, and pollen morphology?

6) Where and when did the major diversification events occur in the *Ficus* subsect. *Urostigma*? Which scenario results from the historical biogeography of the species? How can we explain the disjunction between the African and Asian-Australian species?

7) Which species of *Ficus* subsect. *Urostigma* are used by man and for which purposes?

Thesis goal and outline

The goal of this Ph.D. research is to focus on the systematics of *Ficus* subsect. *Urostigma* and related subsections or sections, as well as to resolve the phylogenetic relationships with other subsections or sections.

Chapter 2 contains a revision of *Ficus* subsect. *Urostigma* based on a morphological species concept. Vegetative and reproductive characters are carefully examined and used in species circumscriptions and descriptions and as characters in a data matrix for phylogenetic analyses. All data, including geography, uses, ecological data, are obtained from herbarium specimens and from field trips in Thailand. All literature related to the subsection is reviewed. Three new species and two new varieties are described. An identification key to the species is provided, together with descriptions and notes per taxon.

Chapter 3 deals with the leaf anatomy of *Ficus* subsect. *Urostigma*. Anatomical characters of the leaves are carefully examined and described per species.
A key to the species based on leaf anatomical characters is provided.

In **Chapter 4** the pollen morphology of *Ficus* subsect. *Urostigma* is studied. Pollen of the different species is described and compared.

Chapter 5 presents the integration of molecular, morphological and leaf anatomical data in a total evidence approach of the phylogenetic reconstruction of *Ficus* subsect. *Urostigma*. More insight is gained in the evolution of specific morphological and leaf anatomical traits. A new circumscription of the subsection is proposed, a taxonomic treatment is provided and nomenclatoral changes are made, even new entities are described.

In **Chapter 6** *Ficus cornelisiana* is described as a new species within *Ficus* subsect. *Urostigma* from the Sino-Himalayan region based on a new combination of morphological and anatomical characters.

Chapter 7 deals with the historical biogeography of *Ficus* subsect.*Urostigma*. Molecular dating was performed in a Bayesian framework with the program BEAST, and ancestral area reconstructions were made with S-DIVA in the program RASP.

Chapter 8 presents the utilization of *Ficus* subsect. *Urostigma* in Thailand. Species are used as food, ornamental plants or sacred trees.

Chapter 2

A revision of *Ficus* subsection *Urostigma* (Moraceae)

Bhanumas Chantarasuwan, Cornelis C. Berg, and Peter C. van Welzen

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Abstract

The present taxonomic revision of *Ficus* subsection *Urostigma* recognizes 27 species, of which three are new: *F. chiangraiensis*, *F. middletonii*, *F. pseudoconcinna*. Two new varieties are distinguished within *F. virens*, var. *dispersa* and var. *matthewii*. *Ficus lecardii* and *F. salicifolia*, formerly subspecies of *F. cordata*, are again reinstated to the species level. Typical characters for the subsection are monoecy, monostaminate flowers, red(brown) colored ovaries and cystoliths on only the abaxial leaf surface. *Ficus amplissima* and *F. rumphii* (section *Leucogyne*) were formerly part of subsection *Urostigma*, and they have been added here to the key and descriptions because of their morphological resemblance with the species in subsection *Urostigma*. Molecular–based phylogenetic analyses showed that at least *F. rumphii* is unrelated to subsection *Urostigma*. The two species only differ from subsect. *Urostigma* in their whitish ovaries and cystoliths at both sides of the leaf blade and they are pollinated by a different group of wasps, species of *Eupristina* subg. *Parapristina*.

Keywords–Monoecy, morphology, section *Leucogyne*.

Introduction

Presently, *Ficus* L. subsect. *Urostigma* (Gasp.) Berg contains 27 species, of which seven species are from continental Africa, Madagascar, and the Arabian Peninsula; and 20 species from Asia, Australia, and the Pacific. Typical are the tree habit, intermittent growth, often deciduous, leaves spirally arranged, often articulate or subarticulate, cystoliths only abaxially, figs axillary, more commonly just below the leaves, and/or ramiflorous on up to ca. 1 cm long spurs, staminate flowers near the ostiole or scattered among the pistillate ones, tepals red(dish), ovary red brown (or white).

This taxon started in a less elaborate circumscription as *Ficus* subgenus *Urostigma*, which was first described by Miquel in 1867. Miquel abandoned the idea of breaking up the genus *Ficus* into genera and he divided *Ficus* into six subgenera. *Urostigma* is one of the subgenera, then comprising ca. 270 species. *Urostigma* contains monoecious species with unistaminate or bistaminate flowers. However, Miquel subdivided subgen. *Urostigma* according to distribution, recognizing six series for Asia and Australia, three series for Africa, and five series for America. The species presently included in subsect. *Urostigma* were mainly placed in the series *Infectoriae* Miq. and *Religiosae* Miq. of Asia and Australia. The African representatives of the subsection were classified in the series *Grandiores* Miq., *Oblongifoliae* Miq., and *Ellipticifoliae* Miq. In 1887 King divided *Ficus* into seven sections of which sect. *Urostigma* was equivalent to Miquel's subgenus. King divided his section *Urostigma* into series and subseries based on leaf characters. The species of the present treatment occur in different subseries of King.

In 1960, Corner reused the rank "subgenus." He recognized three subgenera, one of them subg. *Urostigma* with seven sections, among which sect. *Urostigma* (with 15 species in Asia and six species in Africa) and sect. *Leucogyne* with two species in Asia (*F. amplissima* J. E. Sm. and *F. rumphii* Blume). These two groups contain the species treated here. The main difference between the two sections are the color of the ovary, the position of the staminate flowers and the position of the cystoliths: whitish ovaries, staminate flowers dispersed and cystoliths at both sides of the leaf blade in *Leucogyne*, and red(brown) ovaries, staminate flowers around the ostiole (not 100%) and cystoliths only abaxially in *Urostigma*.

Berg (1989) recognized two main groups in *Ficus* according to morphological and functional traits, in particular in connection to the unique pollination system by fig wasps. The first group comprises the subgenera *Pharmacosycea* and *Urostigma*, and the other contains the subgenera *Ficus*, *Sycidium*, and *Sycomorus*. Fourteen years later, Berg (2003) divided *Ficus* into six subgenera (*Pharmacosycea*, *Urostigma*, *Ficus*, *Synoecia*, *Sycidium*, and *Sycomorus*) based on major differentiating characters like monoecy–dioecy, adventitious roots, stipules, position of figs, bracts, stigmas, and waxy glands. This new classification did not completely correlate any longer with the pollination system; exceptions occurred. One exception was Berg's (2004) newly established subsection *Urostigma*. Berg (2004) united Corner's sections *Leucogyne*, *Urostigma*, and *Conosycea*, into sect. *Urostigma*, which he subdivided into subsect. *Urostigma* (containing Corner's sect. *Leucogyne* and *Urostigma*) and subsect. *Conosycea* (containing Corner's sect. *Conosycea*). Typical for subsect. *Urostigma* is the presence of intermittent growth. Berg did not recognize the series used by Corner. Berg also included African species in the otherwise Asian/Pacific subsection. The two species in former section *Leucogyne* are pollinated by different wasps than the rest of subsect. *Urostigma* (see paragraph on pollination below). Berg and Corner (2005) remarked that the differences between Corner's sect. *Leucogyne* and *Urostigma* are not good enough to justify recognition on a sectional or subsectional taxonomic level, and thus subsection *Urostigma* containing both taxa was maintained.

Recently, results of molecular phylogenetic studies by Rønsted et al. (2005, 2008) show that *F. rumphii* is not part of subsect. *Urostigma*, but that it is embedded in the not closely related subsect. *Conosycea*. Unfortunately, Rønsted et al. (2005, 2008) did not sample *F. amplissima*, the other species in former sect. *Leucogyne*, which is thus phylogenetically still incompletely known.

Transferring both species to subsection *Conosycea* complicates the morphological distinctiveness of the subsect. as the two species share major characters with subsect. *Urostigma*: (1) Both species show an intermittent growth like in subsect. *Urostigma*. (2) Staminate flowers of *F. amplissima* and *F. rumphii* are completely dispersed throughout the fig, which is also present in *F. densifolia* Miq., *F. hookeriana* Corner, *F. orthoneura* H. Lév. & Vaniot and *F. prolixa* G. Forst. of subsect. *Urostigma*, while *F. arnottiana* (Miq.) Miq. and *F. virens* Aiton var. *dispersa* Chantaras. show a transition with abundant staminate flowers around the ostiole and a few dispersed ones. (3) Leaf articulation is absent in subsect. *Conosycea*, section *Leucogyne* and in the African and Malagasy species of subsect. *Urostigma*, but mostly present in the Asian species of subsect. *Urostigma* (*F. orthoneura* and *F. hookeriana* excepted). (4) Color of the ovary is normally a good character to separate the two subsections, as ovaries in subsect. *Conosycea* are white (including the two *Leucogyne* species) and red(brown) in subsect. *Urostigma*. However, the ovary of *F. arnottiana* is white (or yellowish) and some samples of *F. religiosa* L. and *F. densifolia* also show partly white ovaries. In the first two characters, section *Leucogyne* corresponds with subsect. *Urostigma*, in the last one it resembles subsect. *Conosycea*. We will treat the taxa conforming to the phylogenetic analyses by Rønsted et al. (2005, 2008), with subsect. *Urostigma* as a monophyletic group by treating *F. amplissima* and *F. rumphii* separately.

The aim of this paper is to revise the complete *Ficus* subsect. *Urostigma*. The two species in Corner's section *Leucogyne* are added to the key, so that all species with intermittent growth can be keyed out, which will prevent confusion in the future. We will not formally reclassify section *Leucogyne* yet,

because the phylogenetic status of *F. amplissima* is unknown. In comparison with Berg and Corner (2005), this paper treats all species together, not only the Malesian ones. Descriptions and nomenclature are more complete and based on more specimens, and the latest species delimitations are presented.

Results

Habit—All species are essentially hemi–epiphytic, but without abundant aerial roots. Some species are often terrestrial. Most of the species remain medium–sized trees, rarely taller than 25 m, but some Asian species, like *F. caulocarpa* (Miq.) Miq., *F. superba* (Miq.) Miq., and *F. virens* Aiton often become 30–35 m tall (Berg and Corner 2005). The African species *F. verruculosa* Warb. is a shrub or a treelet, and the Malagasy species *F. madagascariensis* C. C. Berg is sometimes a shrub (Berg and Wiebes 1992). The trees show intermittent growth, for which morphological indications are different colors of parts of twigs of current or recent growth and of the previous season's growth. The transition is marked by a section with short internodes, which in some species bear persistent coriaceous stipules, forming terminal buds.

Indumentum—The indumentum consists of unicellular hairs of whitish, yellowish or brown colors which usually occur on leafy twigs, petioles, stipules, peduncles, and sometimes on the upper ostiolar bracts. Many species have translucent hairs on the inner surface of the fig (receptacle) among the flowers; these are called "internal hairs."

Leaves—The leaves are always spirally arranged. The lamina varies from broadest below the middle to broadest above the middle. The lamina is always symmetrical and ranges from small (up to 10 cm long) to medium–sized (10–20 cm long), but those of *F. hookeriana* Corner can be up to 25 cm long. The lamina is subcoriaceous to coriaceous and lacks a hypodermis except for *F. hookeriana* Corner and *F. orthoneura* H. Lév. & Vaniot, which have a well–developed hypodermis on both sides. The lamina is mostly glabrous on both sides, but the young leaves of *F. cupulata* Haines are sometimes puberulous. The margin is always entire. The venation is basically pinnate and brochidodromous. The basal lateral veins are distinct by the narrower angle of departure from the midrib. Some species, e.g. *F. rumphii*, *F. ingens* (Miq.) Miq., and *F. cupulata*, have branched basal veins. The tertiary venation varies from clearly scalariform to reticulate and/or partly parallel to the lateral veins. The leaves are articulate in most species, therefore the lamina is often detached from the petiole in dry material; the African and Malagasy species are not articulate.

Stipules—Stipules are often conspicuous as part of the terminal bud cover. They show differences in length on the same plant, usually quite long (more than 2 cm long), thin and caducous on the open shoots and shorter, usually not longer than 2 cm long, thicker and more persistent on the closed shoots. In many species the stipules form ovoid terminal buds at the shoot apex.

Figs—They are often borne below the leaves, sometimes only in the leaf axils, and in some species on spurs on the older wood. They occur solitary or in pairs, to up to eight together on the spurs. They are sessile or pedunculate. The number of basal bracts is usually three, in *F. rumphii* sometimes two. These bracts are persistent or caducous. The receptacle is subglobose to subpyriform and varies in size from 0.3–0.4 cm diam. when dry in *F. concinna* (Miq.) Miq. to 1.9–2.2 cm diam. when dry in *F. hookeriana*. They are mostly glabrous and in some species wrinkled when dry; in *F. rumphii*, *F. virens* var. *matthewii* Chantaras. they are maculate. The ostiole is circular and the upper two or three visible bracts are imbricate, usually glabrous but in some species hairy, e.g. in *F. cupulata*, *F. virens* var. *virens* and var. *matthewii*. The change of color during maturation of the syconium is from whitish to pinkish to purplish to blackish.

Flowers—The number of tepals varies from one to five. They are free or connate, mostly glabrous, and red to brown.

Staminate Flowers—They occur near the ostiole (Fig. 2-1A, D, E) or are dispersed regularly among the pistillate flowers (Fig. 2-1C, G), but in *F. arnottiana* and *F. virens* var. *dispersa* they are abundant around the ostiole and a few dispersed (Fig. 2-1B, F). The staminate flowers are mostly sessile, rarely shortly pedicellate, but in *F. rumphii* and *F. amplissima* (section *Leucogyne*) they are distinctly pedicellate. There is only one stamen with a 2-thecate anther.

Pistillate Flowers—They are sessile or pedicellate. The ovary is white or red brown. The styles differ in length; usually short- and long-styled flowers can be distinguished. Long-styled flowers are mostly sessile; short-styled ones are generally pedicellate and their ovaries tend to be longer than those of the long-styled flowers. However, the short-styled flowers of *F. religiosa* and *F. hookeriana* are mostly sessile and their ovaries are stipitate (Fig. 2-2A , B). There is only one stigma, which entangles with those of adjacent flowers, thus forming a syn-stigmatic layer (Berg 2004; Berg and Corner 2005). According to Kjellberg et al. (2001), usually 6–10% of the total number of flowers is staminate, and the anther/ovule ratio usually is 0.04–0.10, which is more or less related to the size of the receptacle. Exceptions are *F. densifolia*, *F. virens* var. *dispersa*, and *F. prolixa* for which the anther/ovule ratios are 0.27, 0.57, and 0.51, respectively, with a diameter of the receptacle when dry of (0.5–)0.7–1 cm, 0.6–0.8 cm, and 0.5–0.9 cm, respectively. In these three cases, the presence of at least some dispersed staminate flowers and a larger than usual anther/ovule ratio seems to be associated with passive pollen transport.

Pollination—The obligate pollination of figs by fig wasps is unique and a nice introduction is given by Weiblen (2004). The pollinators of subsection *Urostigma* belong to the Agaonidae (Hymenoptera: Chalcidoidea).

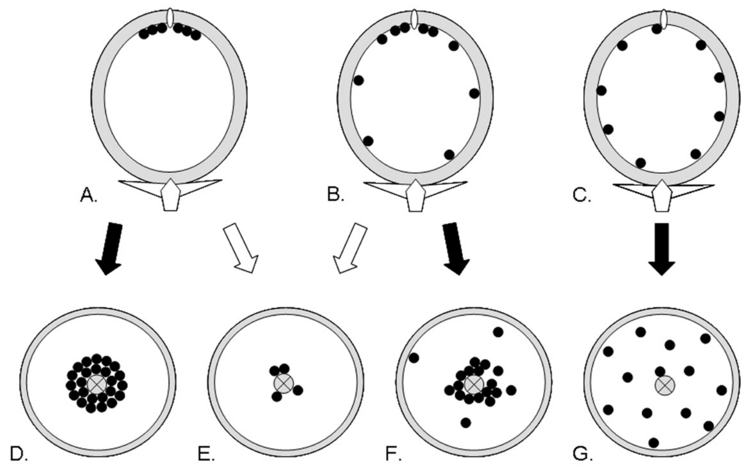

FIGURE 2-1. Diagram showing the various positions of the staminate flowers. A – C. longitudinal section. D – G. apical view of ostiole; patterns between both views indicated by arrows. A, D, E. only around the ostiole; B, F. concentrated around the ostiole but a few irregularly dispersed among the pistillate flowers; C, G. regularly dispersed among the pistillate flowers, few around the ostiole. E can be derived from A and B.

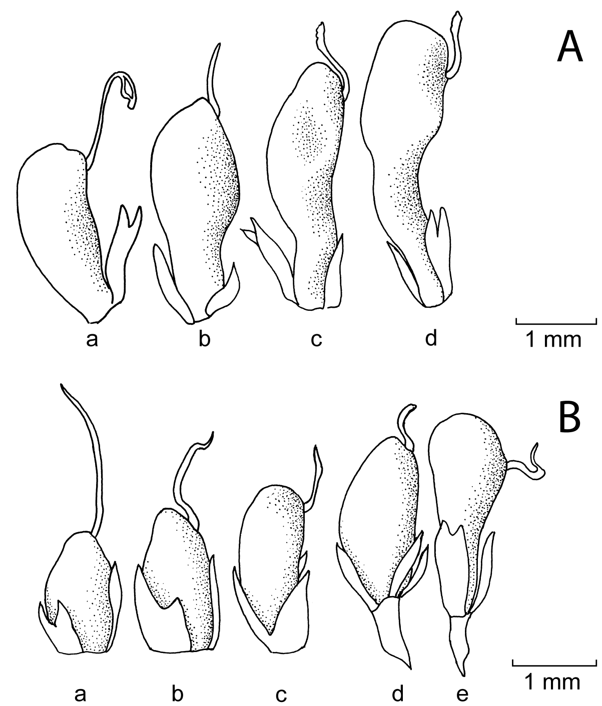

FIGURE 2-2. The pistillate flowers. A Short-styled flowers on a stipe. B. Long-styled flowers sessile, short-styled ones partly pedicellate with longer ovaries than the long-styled flowers. Drawing: Anita Walsmit Sachs, 2011.

The majority of species is pollinated by species of *Platyscapa*. However, *F. amplissima* and *F. rumphii* (section *Leucogyne*) are pollinated by species of *Eupristina* subgen. *Parapristina* (Berg and Wiebes 1992; Berg and Corner 2005; Cruaud et al. 2009).

Taxonomic treatment

FICUS L. subg. UROSTIGMA (Gasp.) Miq. sect. UROSTIGMA (Gasp.) Endl. subsect. UROSTIGMA (Gasp.) C. C. Berg, Blumea 49: 464. 2004. *Urostigma* Gasp. sect. *Religiosa* Miq., Fl. Ind. Bat. 1, 2: 332. 1859. *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. ser. *Religiosae* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867.—TYPE: *Ficus religiosa* L.

Urostigma Gasp. sect. *Caulobotrya* Miq., Fl. Ind. Bat. 1, 2: 334. 1859. *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. ser. *Caulobotryae* (Miq.) Corner, Gard. Bull. Singapore 17: 371. 1960.—LECTOTYPE (designated by Corner 1960): *Ficus caulocarpa* (Miq.) Miq.

Ficus L. subg. *Urostigma* (Gasp.) Miq. ser. *Infectoriae* Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867.—LECTOTYPE (designated here): *Ficus infectorea* Roxb. (= *Ficus virens* Aiton).

Ficus L. sect. *Gasparriniella* Sata, J. Soc. Trop. Agr. Taiwan 6: 18. 1934; Contr. Hort. Inst. Taihoku Imp. Univ. 32: 213, 377. 1944.—LECTOTYPE (designated here): *Ficus wightiana* (Wall. ex Miq.) Benth. (= *Ficus virens* Aiton).

Ficus L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. ser. Orthoneurae Corner, Gard. Bull. Singapore 17: 371. 1960.—TYPE: *Ficus orthoneura* H. Lév. & Vaniot.

Ficus L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. ser. *Superbae* Corner, Gard. Bull. Singapore 17: 371. 1960.—TYPE: *Ficus superba* (Miq.) Miq.

Trees, often deciduous, with intermittent growth, parts of twigs of recent growth different in color from those of the previous season, the transition being marked by a zone with short internodes. Leaves spirally arranged, often articulate or subarticulate; lamina often ovate to subovate to elliptic; cystoliths mostly only abaxially; venation reticulate to subscalariform or partly parallel to the lateral veins; petiole relatively long. Figs axillary, but more commonly just below the leaves, and/or on up to ca. 1 cm long spurs on the older wood; basal bracts small or sometimes large, persistent or caducous; internal hairs present and often ± chaffy or absent. Staminate flowers near the ostiole or scattered among the pistillate flowers, sessile or sometimes pedicellate, tepals (1–)2–4(–5), free or connate, red(dish) brown, stamen 1, the filament variable in length. Pistillate flowers sessile or pedicellate, tepals (1–)2–4(–5), free or

connate, red(dish) brown, ovary sometimes stipitate, red brown or white, style variable in length, long–styled flowers mostly sessile and short–styled ones pedicellate or stipitate, stigmas cohering and forming a synstigma.

Distribution—The subsection is distributed from West Africa and Madagascar through the Asian mainland to Japan and through (southern) Malesia to Australia and the Pacific. The distribution of some species is limited: *F. henneana* Miq. is confined to Australia, *F. cupulata* occurs only in India, and *F. madagascariensis* is endemic to Madagascar. The most widespread species is *F. virens*, ranging from Sri Lanka to N Australia and the Pacific.

Ecology—The subsection occurs mainly in tropical areas, but *F. subpisocarpa* extends to the subtropics. Most species are associated with relatively dry types of vegetation and/or seasonal conditions, often monsoon forest, savannah, or littoral vegetation, often on or near rocks, at low altitudes. In Africa, the species are mainly found in regions with savannah woodland, but *F. verruculosa* is often present in swamps. Species can be deciduous in the monsoon climate and may be evergreen in the rainforest climate. *Ficus rumphii* is common in villages, orchards, and town-gardens (Berg and Corner 2005). *Ficus religiosa* has been planted for a long time in Buddhist temple gardens. It often successfully establishes itself and migrates to natural vegetation, sometimes being invasive just like *F. rumphii*.

Key to the species, subspecies and varieties of *Ficus* subsect. *Urostigma*

(incl. *F. rumphii* and *F. amplissima* because of morphological similarity)

1. Leaves articulate (Asia, Australia, Pacific) 2
2. Ovary white, white with a red mark at the base or yellowish. Figs subsessile or up to 8 mm pedunculate . . . . 2. *F. arnottiana*
2. Ovary red brown, dark red, or brown. Figs sessile or pedunculate 3
3. Staminate flowers near ostiole 4
4. Fig lacking internal hairs or a few minute ones present 5
5. Basal bracts caducous 6
6. Figs (3–)4–6 mm diam. when dry . . . . 5. *F. concinna*
6. Figs (7–)8–25 mm diam. when dry 7
7. Figs solitary or in pairs in leaf axils; Australia . . . . 10. *F. henneana*
7. Figs 1–5 together on up to 1 cm long curved spurs (exceptionally solitary or in pairs axillary or just below the leaves); Asia 8
8. Stipules 0.5–1.6(–2.7) cm long, densely white woolly–tomentose; basal bracts 2–5 mm long, puberulous . . . . 24. *F. superba*
8. Stipules 0.3–1.1 cm long, puberulous; basal bracts 1–2.5 mm long, glabrous 9

9. Leafy twigs whitish puberulous, lateral veins 9–11 pairs, the basal pair up to 1/5–1/3 the length of the lamina; internal hairs minute ....23.2. *F. subpisocarpa* subsp. *pubipoda*
9. Leafy twigs (sub)glabrous, lateral veins (5–)7–10 pairs, the basal pair up to 1/10–1/4 the length of the lamina; internal hairs absent ....23.1. *F. subpisocarpa* subsp. *subpisocarpa*
5. Basal bracts persistent 10
10. Apex of the lamina caudate .... 20. *F. religiosa*
10. Apex of the lamina acute to acuminate, sometimes obtuse. 11
11. Figs sessile; basal bracts 2–4.5 mm long 12
12. Lateral veins 8–14 pairs, unbranched, basal pairs (1/7–)1/4–1/3 the length of the lamina; figs solitary or in pairs or up to 8 together on spurs .... 25. *F. tsjakela*
12. Lateral veins 4–9 pairs, usually branched, basal pair 1/5–1/3 the length of the lamina; figs solitary or in pairs 13
13. Receptacle 0.5–0.6 cm diam. Basal bracts 1.5–2 mm long ...... 22.2. *F. saxophila* var. *cardiophylla*
13. Receptacle 0.6–0.9 cm diam. Basal bracts (2.5–)3–4.5 mm long.......................... ....22.1. *F. saxophila* var. *saxophila*
11. Figs on up to 2 mm long peduncles, sometimes subsessile; basal bracts 1–2 mm long 14
14. Basal lateral veins 1/10–1/6 the length of the lamina, unbranched.....................19. *F. pseudoconcinna*
14. Basal lateral veins 1/5–1/3(–1/2) the length of the lamina, branched............................... 15
15. Figs axillary, just below the leaves or on the spurs on the older wood, solitary, in pairs or up to 4 together ....17. *F. prasinicarpa*
15. Figs axillary or just below the leaves, solitary or in pairs .... 1. *F. alongensis*
4. Fig with internal hairs present 16
16. Basal bracts 4–6 mm long, covering up to the middle of the receptacle 17
17. Lamina broadly ovate or elliptic to oblong, 16.3–22.5 by 9–15 cm; receptacle glabrous .... 4. *F. chiangraiensis*
17. Lamina (broadly) ovate, 8.2–12 by 7–9 cm; receptacle usually white tomentose .... 7. *F. cupulata*
16. Basal bracts 1–4 mm long, covering only the base of the receptacle 18
18. Epidermis of petiole flaking off 19
19. Figs 1–4 together on spurs, basal bracts 2–2.5 mm long, glabrous .... 9.1. *F. geniculata* var. *geniculata*
19. Figs 1–8 together on spurs, basal bracts 1.5–2 mm long, glabrous or puberulous 20
20. Receptacle 0.3–0.6(–0.7) cm diam. when dry, glabrous .... 3.1. *F. caulocarpa* var. *caulocarpa*
20. Receptacle 0.4–0.5 cm diam. when dry, white villous ....3.2. *F. caulocarpa* var. *dasycarpa*
18. Epidermis of petiole persistent 21
21. Basal lateral veins usually branched, the other lateral veins branched and often furcate away from the margin 22
22. Stipules white puberulous to tomentose; basal bracts 1–1.5 mm long, puberulous to tomentose or villose; upper ostiolar bracts glabrous (sometimes minutely puberulous), margin ciliate ....15. *F. middletonii*
22. Stipules glabrous or puberulous; basal bracts 1.5–3 mm long, minutely puberulous; upper ostiolar bracts puberulous, margin not ciliate ....27.1. *F. virens* var. *virens*
21. Basal lateral veins usually unbranched, or if branched then the other lateral veins unbranched 23
23. Stipules glabrous or puberulous; receptacle glabrous or puberulous 24
24. Receptacle 1.2–1.5 cm diam. when dry, ostiole 3.5–4 mm diam., upper ostiolar bracts puberulous ..... 27.4 *F. virens* var. *matthewii*
24. Receptacle 0.4–0.9(–1.2) cm diam. when dry, ostiole (1–)2–3 mm diam., upper ostiolar bracts glabrous 25
25. Lamina mostly obovate or elliptic; basal lateral veins up to 1/6–1/4 the length of the lamina ....27.3. *F. virens* var. *glabella*
25. Lamina mostly (broadly) ovate to lanceolate; basal lateral veins up to (1/10–)1/9–1/3 the length of the lamina 26
26. Epidermis of bud scales persistent .. .... 9.1 *F. geniculata* var. *geniculata*
26. Epidermis of bud scales flaking off ... .27.2 *F. virens* var. *dispersa*
23. Stipules white tomentose or villose, receptacle white tomentose or villose 27
27. Receptacle 0.4–1.2 cm diam. when dry, ostiole 1–2 mm diam., basal bracts 2–2.5 mm long ....9.2. *F. geniculata* var. *insignis*

27. Receptacle (1.1–)1.2–1.5 cm diam. when dry, ostiole 3.5–4 mm diam., basal bracts 3–4 mm long . . . . 27.4. *F. virens* var. *matthewii*
3. Staminate flowers dispersed but also near ostiole 28
28. Terminal bud ovoid, epidermis of bud scales flaking off . . . . 27.2. *F. virens* var. *dispersa*
28. Terminal bud (narrowly) ovate to lanceolate, epidermis of bud scales persistent . . . . 18. *F. prolixa*
1. Leaves not articulate (Africa, Madagascar, Mauritius, Réunion, Asia) 29
29. Ovary red brown (or white with a red dot) 30
30. Staminate flowers dispersed; Madagascar, Mauritius, Réunion and Asia 31
31. Figs subsessile or pedunculate up to 4 mm; basal bracts 1.5–2 mm long; Asia . . . . 16. *F. orthoneura*
31. Figs sessile; basal bracts 3–11 mm long 32
32. Receptacle 1.2–2.2 cm diam. when dry, ostiole 4–5 mm diam., basal bracts united into a cup; Asia . .11. *F. hookeriana*
32. Receptacle (0.5–)0.7–1 cm diam. when dry, ostiole 2.5–3 mm diam., basal bracts free; Madagascar, Mauritius and Réunion . . . . 8. *F. densifolia*
30. Staminate flowers near ostiole; Africa mainland, Arabia and Madagascar 33
33. Internal hairs present 34
33. Internal hairs absent 36
34. Lamina mostly (2.5–)3–5 times longer than wide . . . . 21. *F. salicifolia*
34. Lamina mostly 1.25–2.5 times longer than wide 35
35. Lateral veins usually branched, tertiary venation reticulate . . . . 12. *F. ingens*
35. Lateral veins usually unbranched, tertiary venation reticulate and partly parallel to primary lateral veins . . . . 13. *F. lecardii*
36. Figs pedunculate, (peduncle 2–5 mm long), axillary, just below the leaves or on the spurs on the older branches, solitary or in pairs or up to 4 together on the spurs . . . . 26. *F. verruculosa*
36. Figs sessile, sometimes subsessile, axillary or just below the leaves, solitary or in pairs 37
37. Lamina ovate to oblong to lanceolate, mostly 2.5–3 times longer than wide, lateral veins 7–12 pairs . . . . 14. *F. madagascariensis*
37. Lamina mostely cordiform, some ovate or elliptic, mostly 1.5–2(–2.25) times longer than wide, lateral veins 5–7 pairs . . . . 6. *F. cordata*
29. Ovary white (or pale yellow) (sect. *Leucogyne*) 38

38. Lamina elliptic to ovate, base attenuate to cuneate to obtuse to rounded, apex acute to acuminate; lateral veins 8–10 pairs. Basal bracts 3 . . . . 28. *F. amplissima*
38. Lamina ovate, base subcordate, subattenuate, broad cuneate or truncate, apex acute, acuminate or cuspidate, lateral veins 5–8 pairs. Basal bracts (2 or) 3 . . . . 29. *F. rumphii*

1. *Ficus alongensis* Gagnep., Notul. Syst. (Paris) 4: 84. 1927; C. C. Berg, Blumea 52: 599. 2007. *Ficus superba* (Miq.) Miq. var. *alongensis* (Gagnep.) Corner, Gard. Bull. Singapore 17: 376. 1960.—TYPE: INDOCHINA. Baie d'along île aux Biches, 8 Sep 1911, Lecomte & Finet 847 (holotype: P; isotype: P).

Ficus concinna (Miq.) Miq. var. *subsessilis* Corner, Gard. Bull. Singapore 17: 376. 1960.—TYPE: CHINA. Chekiang, South of Ping Yang, 21 Jun 1924, R. C. Ching 1917 (holotype: K; isotype: P).

Shrub or tree up to 12(–30) m tall. Branches brown or dark brown. Leafy twigs 2–3.5 mm thick, puberulous, periderm persistent. Leaves articulate; lamina ovate to oblong to elliptic, 3.8–12 by 2.8–5.3 cm, coriaceous, apex shortly acuminate, the acumen blunt, base subattenuate or obtuse, both surfaces glabrous; lateral veins 6–9 pairs, usually furcate away from the margin, the basal pair up to 1/5–1/3 the length of the lamina, usually branched, tertiary venation largely parallel to the lateral veins, partly reticulate; petiole 1–3.1 cm long, glabrous, epidermis persistent; stipules 0.5–0.8 cm long, glabrous, caducous or sometimes persistent at the shoot apex and forming a terminal bud. Figs axillary or just below the leaves, solitary or in pairs, subsessile or peduncle up to 1.5 mm long; basal bracts ca. 1.5 mm long, glabrous, mostly persistent; receptacle subglobose or depressed globose, 0.4–0.5 cm diam. when dry, glabrous or minutely puberulous, colors at maturity unknown, apex convex; ostiole ca. 2 mm diam., upper ostiolar bracts glabrous; internal hairs absent or minute and sparse. Staminate flowers near the ostiole, sessile or with a short pedicel; tepals 2–3, ovate or oval, free or connate at base to 3/4 the length of tepals, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3, ovate to lanceolate to oblong, free, sometimes connate at the base, reddish brown; ovary red brown.

Distribution and Habitat—This species is distributed in China (Prov. Shaanxi, Guangxi, Guangdong, Macau), Thailand, Cambodia, and Vietnam. It is found in wet primary forest at low altitudes but in China also at altitudes between 1,100 and 1,600 m.

Representative Specimens Examined—CAMBODIA. Stung Treng: Thala Barevat, Kalay Isl., 27 Jul 2000, *Meng 215* (K). CHINA. Guangdong (Kwangtung): Chekiang, 1920, Hee 232 (K); Yang Shan, S of Linchow, Jul–Sep 1932, *Tsui 524* (K, L). Shaanxi: Chang'an (Chang An), Yung Hsien, 23 Oct 1933, *Steward & Cheo 1187* (A, P, SING). Guangxi (Kwangsi): N of

Guangxi, Kwei–lin, San–min, P'an–ku–shan & Ch'ao–t'ien–shan, 5–23 Aug 1937, *Tsang 28020* (A). Macao: Bishop Hill, 19 Apr 1969, *Hu 7018* (K). THAILAND. Kanchanaburi: Sai Yok, 30 Dec 1961, *Larsen 9052* (SING). VIETNAM. Kon Tum: Dak Gley, ca. 7 km S of Dak Gley, near Dak Pet, Dak Poko R., 12 Nov 1995, *Averyanov et al. VH 1572* (AAU, P). Tonkin occidental: *Bon 2114* (P). Tonkin méridional, 1883–1891, *Bon s. n.* (P).

Note—Berg (2007a) and Berg et al. (2011) described the figs as devoid of internal hairs. However, many figs show sparse, minute internal hairs.

2. *Ficus arnottiana* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867; King, Ann. Roy. Bot. Gard. (Calcutta) 1: 56, t. 68A. 1887; Cooke, Fl. Bombay 2: 649. 1908; Corner, Gard. Bull. Singapore 21: 11. 1965; C. C. Berg, Thai Forest Bull., Bot. 35: 8. 2007. *Urostigma arnottianum* Miq., London J. Bot. 6: 564. 1847.—TYPE: INDIA. Probably Tamil Nadu, *Wight KD 4575* (holotype: K).

Urostigma courtallense Miq., London J. Bot. 6: 564. 1847. *Ficus arnottiana* (Miq.) Miq. var. *courtallensis* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867; King, Ann. Roy. Bot. Gard. (Calcutta) 1: 56, t. 68B. 1887. —TYPE: INDIA. Probably Tamil Nadu, Courtallum, 1836, *Wight KD 942*(= 2628) (holotype: K ?; isotype: E).

Ficus arnottiana (Miq.) Miq. var. *subcostata* Corner, Gard. Bull. Singapore 17: 379. 1960; C. C. Berg, Thai Forest Bull. Bot. 35: 18. 2007.—TYPE: NEPAL. Melcham, 21 May 1952, *O. Polunin*, *W. R. Sykes & L. H. J. Williams 4145* (holotype: BM; isotype: E).

Ficus glaberrima Blume subsp. *siamensis* auct. non (Corner) C. C. Berg: C. C. Berg, Thai Forest Bull., Bot. 35: 18. 2007, pro *F. arnottiana* var. *subcostata*.

Tree up to 15 m tall. Branches drying pale to dark brown, periderm persistent or flaking off. Leafy twigs (1–)3–6 mm thick, slightly angular to subterete, glabrous or minutely puberulous. Leaves articulate; lamina cordiform to (broadly) ovate, (1.5–)3.3–13.5(–21) by (1–)2.9–10.5(–16) cm, (sub) coriaceous, apex obtuse to acute to acuminate to caudate, the acumen sharp or blunt, base cordate to subattenuate to rounded to cuneate, both surfaces glabrous or sometimes the upper surface minutely puberulous on the midrib; lateral veins 5–8(–10) pairs, sometimes furcate away from the margin, the basal pair up to 2/5–3/5 the length of the lamina, branched or unbranched, tertiary venation reticulate to subscalariform; petiole (1.5–)3–13(–16.5) cm long, glabrous or minutely puberulous, epidermis persistent; stipules 0.3–1 cm long, glabrous or puberulous, usually caducous. Figs axillary and just below the leaves or on minute spurs on the older wood, in pairs or solitary or up to 4 together, subsessile or with a peduncle up to 8 mm long, glabrous; basal bracts 1–1.5 mm long, glabrous, persistent; receptacle subglobose, 0.4–1 cm diam. when dry, glabrous, apex convex; ostiole ca. 2 mm diam., the upper

ostiolar bracts glabrous; internal hairs absent. Staminate flowers abundant around the ostiole and a few dispersed or if few then only near the ostiole, sessile or pedicellate; tepals 3, connate, dark red. Pistillate flowers sessile or pedicellate; tepals 3, connate, dark red; ovary white or yellowish white with red mark at base.

Distribution and Habitat—This species is distributed in India, Nepal, and Sri Lanka; in deciduous forest, at altitudes up to 1,400 m.

Representative Specimens Examined—INDIA. Kanataka: North Kanara, Apr 1885, *Talbot 1207* (K). Andhra Pradesh: Cuddapha (Kadapa), Jul 1884, Gamble 15032 (K). Tamil Nadu (Madras): Pulney Mt., 1837, *Wight KD 2628* (= *KD 3009*) (E, U). Odisha (Orissa): Ganjam, Feb 1884, *Gamble 13822* (K). West Bengal: hill N of Bagodhar, 29 May 1905, Haines 789 (K). NEPAL. Far–Western: Seti zone, Bajura, between 81° 44′ 26′′E, 29° 19′ 16′′N– 81° 43′ 02′′E, 29° 24′ 11′′N, 9 Aug 1991, *Suzuki et al.* 9194138 (E). Mid–Western: Kanali zone, Humla, Melchham, 21 May 1952, *Polunin et al. 4145* (E). Eastern: Koshi zone, between Dhankuta–Sankhuwa Sabha, between 87°15′ E, 27° 05′ N– 87°15′ E, 27° 10′ N, 25 Jul 1990, *Minaki et al. 9070029* (E). SRI LANKA. North Central: Anuradhapura, Ritigala Strict Natural Reserve, 9 Aug 1973, *Jayasuriya 1293* (K, L). Sabaragamuwa: Balangorda, Uggalkaltota Rd., 10 miles SW of Balangorda, *Worthington 3754* (K). Uva: Monaragala, Savannah Park Country, 5 miles N of Bibile, 26 Oct 1973, *Jayasuriya 1361* (K).

Notes—King (1887) described the staminate flowers as few and near the mouth of the receptacle. Corner (1981) reported staminate flowers around the ostiole and sparsely scattered in the interior of the fig. However, we found both characters, thus the staminate flowers of *F. arnottiana* are present around the ostiole with a few dispersed (Fig. 2-1B, F) or only near the ostiole if there are few staminate flowers (Fig. 2-1E).

Berg (2007b) and Berg et al. (2011) reported the species to be present in Thailand also, but the Thai specimens have distinctly different flowers and they are here described as the new species *F. middletonii* (see there).

3. *Ficus caulocarpa* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 268, 287. 1867; Corner, Gard. Bull. Singapore 10: 283. 1939; 21: 10. 1965; Sasidh. & Augustine, Rheedea 9: 77. 1999; C. C. Berg and Corner, Fl. Males. Ser. 1, 17 (2): 604. 2005. *Urostigma caulocarpum* Miq., London J. Bot. 6: 568. 1847; Fl. Ind. Bat. 1, 2: 334. 1859. *Ficus infectoria* Roxb. var. *caulocarpa* (Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: 63, t. 79. 1887.—TYPE: PHILIPPINES. *Cuming 1930* (holotype: U; isotypes: BM, L, K).

Urostigma stipulosum Miq., London J. Bot. 6: 568. 1847; Fl. Ind. Bat. 1, 2: 334. 1859. *Ficus stipulosa* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867.—TYPE: PHILIPPINES. *Cuming 1978* (holotype: K; isotypes: BM, K).

Ficus weinlandii K. Schum., Fl. Schutzeb. Südsee Nachtr.: 248, 1905.—LECTOTYPE(designated by Berg and Corner, 2005): PAPUA NEW GUINEA. *Weinland 180* (lectotype: B; isolectotype: K).

Tree up to 30(–35) m tall. Branches drying brown or gray brown. Leafy twigs 3–6(–8) mm thick, glabrous or puberulous. Leaves articulate; lamina ovate, oblong, elliptic, or obovate, 5.5–19(–26.5) by 2–7.5(–9.8) cm, (sub) coriaceous, apex acute or (sub)acuminate, the acumen sharp or blunt, base cuneate, obtuse, rounded, or truncate (or cordate), both surfaces glabrous; lateral veins 9–16 pairs, the basal pair up to 1/10–1/5(–1/3) the length of the lamina, unbranched, tertiary venation reticulate; petiole 1.3–6.5(–8) cm long, glabrous or minutely puberulous at base, epidermis flaking off; stipules 0.3–1.1 cm long, glabrous or puberulous, persistent at the shoot apex or sometimes caducous, usually forming an ovoid terminal bud. Figs axillary, just below the leaves or on up to 0.5 cm long spurs on the older wood, solitary, in pairs, or up to 8 together on spurs, peduncle 0.1–0.5 cm long, glabrous or puberulous (or white villous), basal bracts 1.5–2 mm long, covering only the base of the receptacle, glabrous or puberulous, apex usually lobed, persistent; receptacle subglobose, 0.3–0.6(–0.7) cm diam. when dry, glabrous (or white villous), white to pink to purple to blackish at maturity, apex convex or flat, sometimes concave; ostiole 1–2 mm diam., the upper ostiolar bracts glabrous; internal hairs present. Staminate flowers near ostiole, sessile; tepals 2–3, broadly elliptic–ovate or lanceolate, free or connate, reddish brown. Pistillate flowers sessile or pedicellate; tepals (2–)3–4, lanceolate, spathulate, or ovate, free or sometimes connate, reddish brown; ovary dark red.

3.1 ***Ficus caulocarpa*** (Miq.) Miq. var. ***caulocarpa:*** Corner, Gard. Bull. Singapore 21: 10. 1965.

Peduncle 0.1–0.5 cm long, glabrous to puberulous, receptacle subglobose, 0.3–0.6(–0.7) cm diam. when dry, glabrous.

Distribution and Habitat**—**This variety is distributed in India, Sri Lanka, Myanmar, Thailand, Malaysia (Peninsula and Borneo), Indonesia (Borneo, Sulawesi, Lesser Sunda Islands, Moluccas), Timor Este, Taiwan, Japan (Ryukyu Isl.), Philippines, and Papua New Guinea; in evergreen forest, in coastal vegetation, on limestone outcrops or in lowland forest, in swamps and river plains, at low altitudes, but in rain forest up to 1,500 m.

Representative Specimens Examined**—**INDIA. Kerala: Shornur, 24 Feb 1990, *Dept. of Zoology 1* (L). INDONESIA. Kalimantan Barat: Ketapang, Gunung Palung National Park, Cabang Panti Research Site, 110° 06´ E, 1° 13´ S, 16 Mar 1997, *Weiblen et al. GW 905* (E, K, L). Kalimantan Timur: East Kutai Reserve, near Sengata and Mentoko R., 1977–1979, *Leighton 414* (L). Maluku: Morotai, 3 Jun 1949, *Politon 15* (L, SING), 17 (L). Nusa Tenggara Barat: Lombok, Rindjani–Vulkangebirge, Sembaluntal, N slope of Pussuk Mt.,

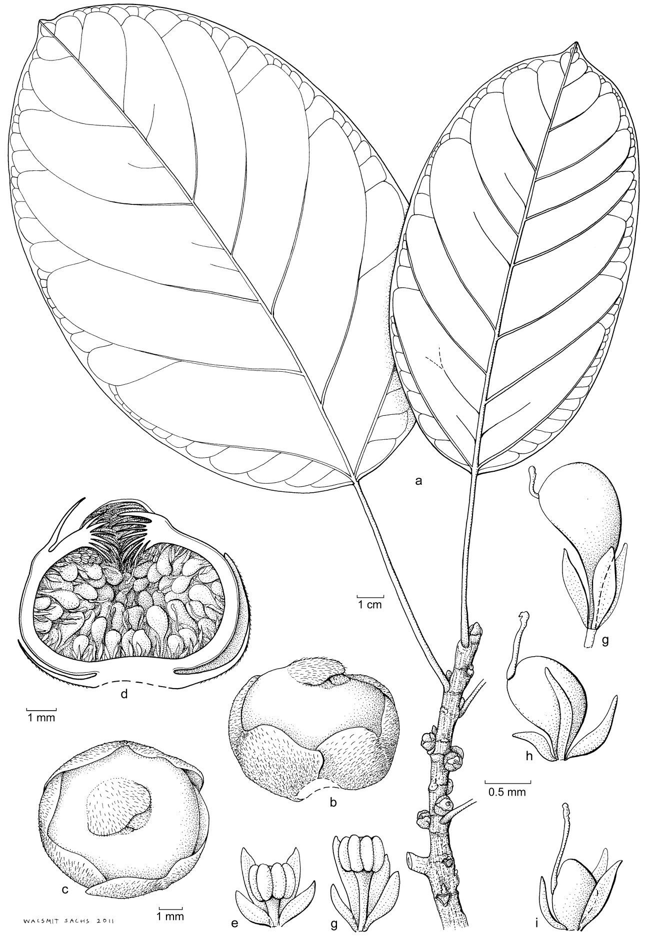

FIGURE 2-3. *Ficus chiangraiensis* Chantaras. (Moraceae). A. Twigs with leaves and figs. B. Fig with basal bracts. C. Ostiole. D. Fig in longitudinal section. E, F. Staminate flowers with free tepals. G. Pistillate flower with pedicel. H, I. Sessile pistillate flowers with free tepals.[*J. F. Maxwell 06-517* (L)]. Drawing: Anita Walsmit Sachs, 2011.

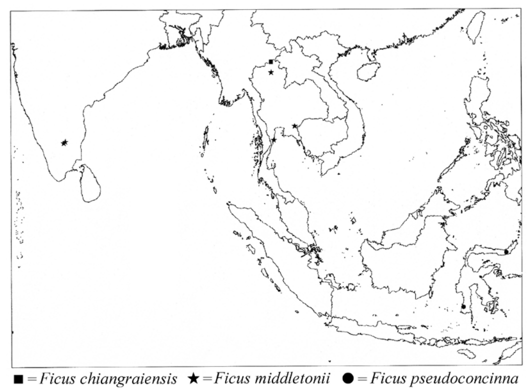

FIGURE 2-4. Distribution map of *Ficus chiangraiensis* Chantaras. (square), *F. pseudoconcinna* Chantaras. (dot), and *F. middletomii* Chantaras. (stars).

2 Jun 1909, *Elbert 1685* (L). Nusa Tenggara Timur: Flores, W Endeh, 4 Feb 1910, *Elbert 4228* (L). Papua: Manokwari, Warnapi, 30 Sep 1948, *Kostermans 484* (bb. 33.635) (L, SING); Jayawijaya, Angguruk, 6 Jun 1975, *Sinke 63* (L). Sulawesi Selatan: S shore of Laka Matano, W of Soroako, 21 Nov 1979, *de Vogel 5907* (L). JAPAN. Okinawa: Yaeyama, Yonaguni. 28 Aug 1951, *Walker & Tawada 6847* (L); Ishigaki, foot of Mt. Omoto, 16 Oct 1972, *Furuse 1498* (K). MYANMAR. Shan: Shan hill, 1892, *Huk 104* (K, U). MALAYSIA. Johore: Telvau, 4 Nov 1934, *Corner s. n.* (SING). Pahang: Bentang, 6 Dec 1922, *Burkill 9998* (K, SING). Sabah: 13 Feb 1985, *Dewol & Mansus SAN 68010* (L). Sarawak: Serian, Bukit Selabor, Lobang Mawang, Tebakang Rd., 30 Sep 1968, *Paie S 28113* (K, L, SING). Trengganu: Dungun–Masong Rd. 37 ½ –38 miles, 16 Jul 1953, *Sinclair SFN 39982* (SING). PAPUA NEW GUINEA. Madang: Morox, near Yoro, Bogia, 31 Mar 2005, *Weiblen GW 2384* (L). Morobe: *NGF 2972* (K, L). Oro: Tufi, between Naukwate and Koreaf, 21 Jun 1954, *Hoogland 4160* (L). PHILIPPINES. Cagayan: E Cagayan, Bagio cave, 31 Mar 1981, *Allen PNH 150015* (L). Palawan: May 1906, *Foxworthy BS 908* (K). Quezon: Quezon National Park, Atimonan, Lat 14° 00.4′ N, Long 121° 55.2′ E, 18 Mar 1996, *Castro et al. PPI 22299* (L). Romblon: Magdiwang, Tampayan, along Pawala R., 25 May 1992, *Stone et al. PPI 6682* (L). Zambales: Masinloc, Coto Mines, 2 Feb 1992, *Reynoso et al. PPI 4154* (L). Zamboanga del Norte: 25 Dec 1957, *Frake PNH 37976* (L). SINGAPORE. Alexandra Rd., 12 Apr 1932, *Corner s. n.* (SING). Pulau Ubin, 1997, *Lai LJ 168* (SING). SRI LANKA. Central: Kandy, 1854, *Thwaites C.P. 2931* (P, K); Matale, Matale East, 17 Aug 1953, *Wortington 6367* (K). TAIWAN. Tomita–cho, Taihoku–shi, 7 Jul 1932, *Tanaka & Shimada 11159* (L, SING); Heng Chun Branch, 1 Apr 1966, *Liao 10436* (L). THAILAND. Nakhon Si Thammarat: Thung Song, Yong falls, 6 Oct 1972, *Smithinand 11734* (BKF). Narathiwat: Waeng, Ban Kreusor, 14 Feb 2003, *Chantarasuwan 140203–7* (BKF, THNHM). Ranong: Kuw Chang, 6 Jan 1929, *Kerr 16568* (BK, K). Yala: Khaw Pee Saad, 28 Apr 1998, *Niyomtham & Puudjaa 5443* (BKF). TIMOR ESTE. Dili: Port Timor, 29 Dec 1953, *van Steenis 18343* (L).

Note—Based on the width of the leaf laminas two forms can be distinguished. Broad leaves (5–9.8 cm wide) are found in India, Sri Lanka, Myanmar, the northern part of Thailand, Philippines, Taiwan, and Japan; this form may be confused with *F. subpisocarpa*, but the basal bracts of the figs are persistent and the epidermis of the petiole is flaking off (caducous bracts and non flaking epidermis in *F. subpisocarpa*). The narrow leaves (2–5.5 cm wide) are present in Philippines, southern part of Thailand, Malaysia, Singapore, Indonesia, Timor Este, and Papua New Guinea.

3.2 *Ficus caulocarpa* (Miq.) Miq. var. ***dasycarpa*** Corner, Gard. Bull. Singapore 17: 378. 1960.—TYPE: PHILIPPINES. Luzon, Zambales Province, Moutain Pinatubo, *PNH 4788* (holotype: PNH, lost; isotype: US?).

Peduncle 0.3–0.5 cm long, white villous, receptacle subglobose, 0.4–0.5 cm diam. when dry, white villous.

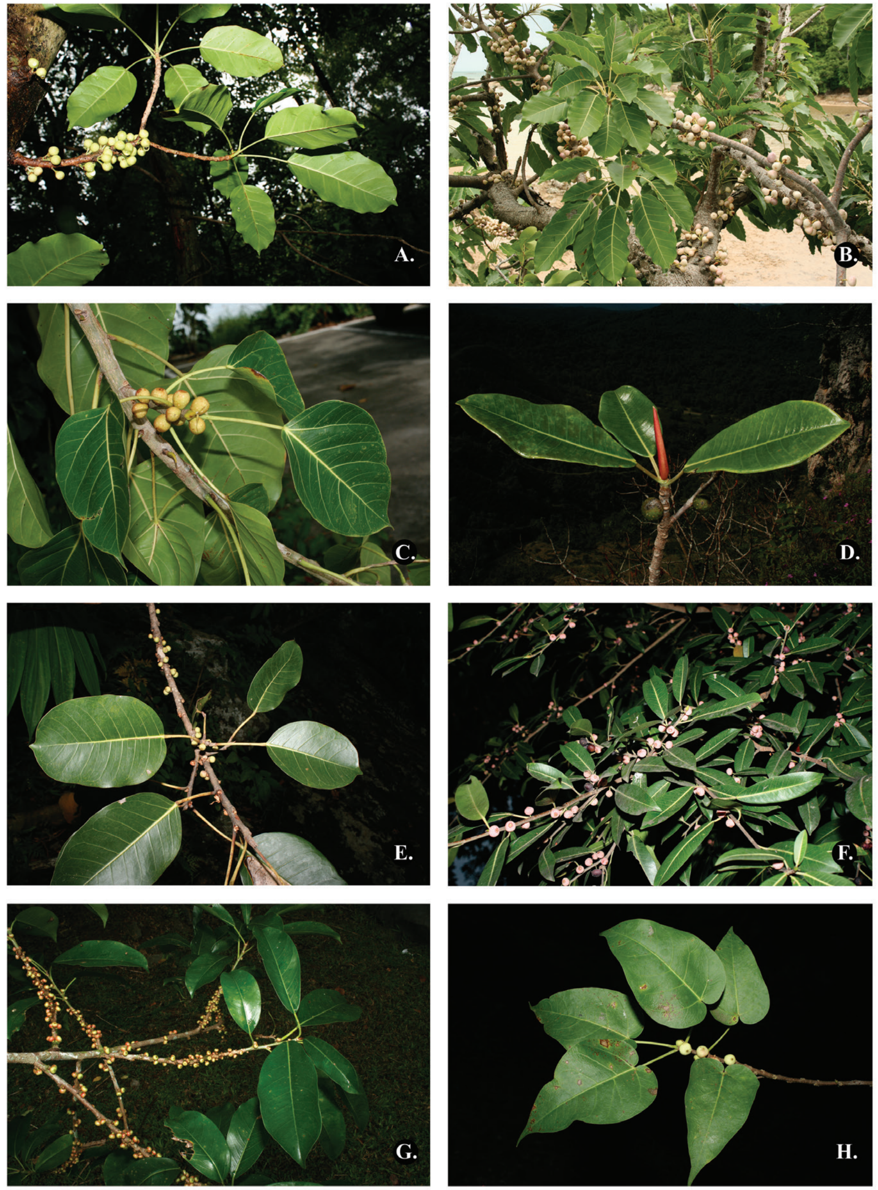

FIGURE 2-5. A. *Ficus subpisocarpa* Gagnep. subsp. *pubipoda* C. C. Berg; B. *Ficus superba* (Miq.) Miq.; C. *Ficus rumphii* Blume; D. *Ficus orthoneura* H. Lév. & Vaniot; E. *Ficus geniculata* Kurz; F. *Ficus concinna* (Miq.) Miq.; G. *Ficus virens* Aiton var. *glabella* (Blume) Corner; H. *Ficus saxophila* Blume subsp. *cardiophylla* (Merr.) C. C. Berg. All photographs by B. Chantarasuwan.

***Distribution and Habitat*—**This variety is endemic in the Philippines.
***Representative Specimens Examined*—**PHILIPPINES: Mindoro, Paluan, Apr 1921, *Ramos BS 39732* (K).

4. *Ficus chiangraiensis* Chantaras., sp. nov.—TYPE: THAILAND. Chiang Rai, Mae Fa Luang, Teut Tai subdistrict, Doi Bahng Ngoon, south slope, below the summit, above Banhg Mah Hahn (Akha hilltribe) village, *J. F. Maxwell 06–517* (holotype: L; isotype: CMU).

Petiolus glaber epidermis non desquamarans vel basi minute albe epidermis desquamarans; stipulae gemmas terminals ovoideas dense lanate tomentosas formantes. Fici axillares admodum infra folia vel 1–7(vel 8) in calcaribus curvatis ad 3mm longis in ligno vetiore (sub)sessiles, bracteae basales 4–6 mm longae albe strigosae persistentes receptaculo ad medio tegentes.

Tree, up to 18 m tall. Branches drying brown or gray brown. Leafy twigs 0.9–1 cm thick, glabrous, periderm flaking off. Leaves articulate; lamina broadly ovate to elliptic to oblong, 16.3–22.5 by 9–15 cm, coriaceous, apex (sub)acute or obtuse, base rounded or subattenuate, both surfaces glabrous; lateral veins 8–10 pairs, usually furcate away from the margin, the basal pairs up to 1/4–1/3 the length of the lamina, mostly branched and departing from the midrib at different distances from the base, tertiary venation reticulate; petiole 6.5–8.8 cm long, glabrous and epidermis persistent or minutely white hairy at the base and epidermis flaking off; stipules 0.9–1 cm long, densely woolly–tomentose, persistent and forming an ovoid terminal bud. Figs axillary, just below the leaves or on up to 3 mm long curved spurs on the older wood, solitary, in pairs, or up to 7(–8) together on the spurs, (sub)sessile; basal bracts 4–6 mm long, covering up to the middle of receptacle, white strigose, apex usually lobed, persistent; receptacle subglobose, 0.6–0.8 cm diam. when dry, outside surface wrinkled, glabrous, color at maturity unknown, apex convex; ostiole 2–3 mm diam., upper ostiolar bracts white hairy; internal hairs present. Staminate flowers near ostiole, sessile or sometimes with a short pedicel; tepals 3, connate, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3, ovate to lanceolate, free or sometimes connate at base, reddish brown; ovary red–brown. Figure 2-3.

***Distribution and Habitat*—**This species is distributed in Thailand; in primary evergreen forest and degraded hardwood forest with bamboo, at ca. 1,450 m. Figure 2-4.

***Representative Specimen Examined*—**THAILAND. Chiang Rai, Mae Fa Luang, Teut Tai, Doi Bahng Ngoon, above Banhg Mah Hahn (Akha hilltribe) village, 23 Jul 2006, *Maxwell 06–517* (CMU, L).

***Note*—**This new species has a typical combination of characters (articulate leaf, red brown ovaries, staminate flowers around ostiole, hairs inside the fig and relatively large bracts). Morphologically, it is closest to *F. cupulata*, a rare

and local endemic species of India, from which it differs in the completely glabrous receptacle (usually white tomentose in *F. cupulata*) and the distinctly larger leaves(16.3–22.5 by 9–15 cm versus 8.2–12 by 7–9 cm).

5. *Ficus concinna* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867; Merr., Fl. Manila: 176. 1912; Enum. Philipp. Flow. Pl. 2: 49. 1923; Corner, Gard. Bull. Singapore 21: 8. 1965; Kochummen, Tree Fl. Malaya 3: 144. 1978; Tree Fl. Sabah Sarawak 3: 234. 2000; C. C. Berg and Corner, Fl. Males. ser. 1, 17 (2): 605. 2005. *Urostigma concinnum* Miq., London J. Bot. 6: 570. 1847; Fl. Ind. Bat. 1, 2: 343. 1859. *Ficus glabella* Blume var. *concinna* (Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: 50. 1887.—TYPE: PHILIPPINES. *Cuming 1940* (holotype: U; isotypes: BM, E, L, K).

Urostigma parvifolium Miq., London J. Bot. 6: 568. 1847; Fl. Ind. Bat. 1, 2: 343. 1859. *Ficus parvifolia* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867., non Oken 1841.—TYPE: PHILIPPINES. *Cuming 1935* (holotype: U; isotypes: BM, E, L, K).

Ficus subpedunculata Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 217, 286. 1867.—TYPE: BHUTAN. 1802–03, *W. Griffith KD 4590* (holotype: K; isotype: U).

Ficus affinis Wall. ex Kurz, J. Asiat. Soc. Bengal 42, 2: 105. 1873; Forest Fl. Burma 2: 444. 1877. *Ficus glabella* Blume var. *affinis* (Wall. ex Kurz) King, Ann. Roy. Bot. Gard. (Culcutta) 1: 50. 1887.—TYPE: INDIA. Sillet, *Wallich Cat. 4524* (holotype: K–WALL; isotype: L?).

Ficus arayatensis Warb. in Perkins, Fragm. Fl. Philipp. 3: 196. 1905.—SYNTYPES: PHILIPPINES. Luzon, Prov. Pampanga, Mt. Arayat, Warburg 14035 (syntypes: B, K?); idem, Warburg 14036 (syntypes: B, K?); idem, *Warburg 14037* (syntypes: B, K?).

Ficus fecundissima H. Lév. & Vaniot, Feddes Repert. Spec. Nov. Regni Veg. 9: 19. 1911.—TYPE: CHINA. Kouy–Tchéou, Lo–Fou, *Cavalerie 3588* (holotype: E; isotypes: P, K).

Ficus pseudoreligiosa H. Lév., Fl. Kouy–Tchéou: 432. 1915.—TYPE: CHINA. Kouy–Tchéou, Lo Hou, roches derrièrele fort, *J. Esquirol 3518* (holotype: E; isotype: P).

Tree up to 10(–30) m tall. Branches drying pale to dark brown. Leafy twigs 1–2.5 mm thick, glabrous, periderm persistent or flaking off. Leaves articulate; lamina ovate, elliptic, oblong, lanceolate, obovate, or oblanceolate, 4–13.5 by 1–5.2 cm, (sub)coriaceous, apex acute to acuminate, the acumen sharp or blunt, base cuneate, obtuse, or rounded, both surfaces glabrous; lateral veins 8–14 pairs, the basal pair up to (1/10–)1/9–1/6 the length of the lamina, unbranched, tertiary venation reticulate to partly parallel to lateral veins;

petiole 0.8–3.5(–5) cm long, glabrous, epidermis persistent, sulcate above; stipules 0.3–0.6 cm long, puberulous, usually ciliate, caducous. Figs axillary, just below the leaves, or on minute spurs on the older wood, solitary, in pairs, or up to 4 on spurs; peduncle 1–5(–6) mm long, glabrous or puberulous; basal bracts ca. 0.5–1.5 mm long, glabrous or puberulous in the middle, caducous; receptacle subglobose, (0.3–)0.4–0.6 cm diam. when dry, glabrous, pink to purple or black at maturity, apex convex; ostiole 1–1.5 mm diam., upper ostiolar bracts glabrous; internal hairs absent or sometimes present, minute and sparse. Staminate flowers near ostiole, sessile or with a short pedicel; tepals 2–3, ovate, usually connate, red brown. Pistillate flowers sessile or pedicellate; tepals 2–3(–4), ovate or lanceolate, free, red brown; ovary dark red. Figure 2-5F.

Distribution and Habitat—This species is distributed in India, Bhutan, China (Prov. Yunnan, Guizhou, Guangxi, Guangdong), Myanmar, Thailand, Vietnam, Malaysia (Borneo), Indonesia (Sumatra), and the Philippines; in primary evergreen forest, mixed evergreen–deciduous scrub, on rocky seashores, on limestone hills, from low altitudes up to 1,900 m.

Representative Specimens Examined—BHUTAN. Wangdue Phodrang: Samtengang,11 Apr 1967, *Hara et al. 3600* (E, L). CHINA. Guizhou (Kweichow): 1936, *Teng 90789* (L). Guangxi (Kwangsi): Guilin (Kweilin), 1979, *Wan & Ghow 79050* (K).Guangdong, Qingyuan, Yang Shan, S of Linchow, July–Sept 1932, *Tsui 524* (L). Yunnan: 1933–4, *Tsiang 12286* (K). INDIA. Tamil Nadu (Madras): Khasia, *Hook fil. & T. Thomson 113* (K). Bihar: Singbhum, 2 May 1902, *Haines 373* (K). Odisha (Orissa): Kalahandi, Kalapat, 5 Apr 1941, *Mooney 1705* (K). Assam: Kamrup, Rangiya, 24 Feb 1952, *Chand 5271* (K, L). Manipur: Karong, 20 Oct 1950, *Chand 3872* (L). Andaman Islands: South Andaman, Kala Pahar, 20 Oct 1894, *King s. n.* (P). MALAYSIA. Sabah: Bod Goya isl, 15 Mar 1934, *Orolfo 3800* (K). INDONESIA. Sumatra: Danau Ranau, 19 Feb 1983, *Afriastini 837A* (L). MYANMAR. Bago (Pegu): Bago Yomah, 15 Jan 1871, *Kurz 3133* (K). PHILIPPINES. Batangas: Apr–May 1915, *Ramos & Deroy BS 22638* (K). Benguet: Dec 1908, *Bacani 15921* (K). Marinduque: Matalim, Dampulan, 121°00.5´ E, 13°47.5´ N, 30 Oct 1965, *Romero & Chavez PPI 29148* (K, L). Nueva Ecija: Dec1910, *Alvarez FB 22116* (K). Palawan: Busuanga, Coron, 1 May 1950, *Sulit PNH 12275* (L, SING). Rizal: Montalban, Mar 1906, *Merrill 5041* (L, K). THAILAND. Chiang Rai: Doi Tung Cha (Prachao Luang), 18 Nov 1920, *Kerr 4597* (BK, K, L). Chon Buri: Siracha, Si Chang Isl., Laem Tahm Pang, 8 Nov 1992, *Maxwell 92–704* (L). Kanchanaburi: Sai Yoke, 99°60´ E, 19°09´ N, 26 Nov 1971, *van Beusekom et al. 3990* (BKF, L, P). Nakhon Si Thammarat: Lansagah, Gahrome falls, Khao Luang National Park, 17 May 1985, *Ramsri 50* (BKF, L). Prachuap Khiri Khan: Sam Roy Yot, 99°55´ E, 12°15´ N, 5 May 1974, *K. Larsen & S. S. Larsen 33630* (BKF, K). Narathiwat: Waeng, 13 Jun 1970, *Smitinand 47574* (BKF). VIETNAM. Hanoi: Yen–Lang, Oct 1887, *Balansa 2947* (K, P). Can Tho: 26 Jan 1914, *Chevalier 30322* (P). Ho Chi Minh (Saigon): Botanical Garden, 27 Mar 1914, *Chevalier 31376* (K, L).

Note—Corner (1965) published a new variety, *Ficus concinna* (Miq.) Miq. var. *dasycarpa* Corner, from India with as typical character a white villose peduncle. Chaudhary et al. (2012) report this variety to be endemic. Probably the variety is rare, because we could not find any matching Indian material. Therefore, we cannot decide anything about the status of this variety.

6. *Ficus cordata* Thunb., Diss. Acad., Fic.: 8, with plate. 1786; Rees, Cycl. 14: n. 6. 1810; Hutch., Fl. Trop. Afr. 6, 2: 119. 1916; C. C. Berg et al., Fl. Cameroun 28: 125, t. 50. 1985; C. C. Berg, Kew Bull. 43: 81. 1988; Fl. Trop. E. Africa, Morac.: 60. 1989; Fl. Zambes. 9 (6): 55. 1991; C. C. Berg and Wiebes, African fig trees and fig wasps: 90. 1992. *Urostigma cordatum* (Thunb.) Gasp., Ricerche Caprifico: 82. 1845. *Urostigma thunbergii* Miq., London J. Bot. 6: 556. 1847, nom. superfl. *Ficus cordata* Thunb. subsp. *cordata*: C. C. Berg, Kew Bull. 43: 81. 1988; Fl. Zambes. 9, 6: 55. 1991; C. C. Berg and Wiebes, Africa fig trees and fig wasps: 92. 1992.—TYPE: SOUTH AFRICA. *Thunberg 24343* (holotype: UPS, microfiche seen).

Ficus tristis Kunth & C. D. Bouché, Ind. Sem. Hort. Berol.: 19. 1846. *Ficus cordata* var. *tristis* (Kunth & C. D. Bouché) Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 137. 1906.—TYPE: Cultivated specimen from Berlin Botanical Garden (holotype: B).

Ficus welwitschii Warb., Bot. Jahrb. 20: 160. 1894; Hutch., Fl. Trop. Afr. 6, 2: 118. 1916.— LECTOTYPE (designated by Berg et al. 1985): ANGOLA. Zenza do Galungo, *Welwitsch 6356* (lectotype: K; isolectotypes: B, P).

Ficus welwitschii Warb. var. *beroensis* Hiern, Cat. Afr. Pl. 1, 4: 999. 1900.—LECTOTYPE (designated by Berg et al. 1985): ANGOLA. Mossamedes, Bero R., *Welwitsch 6379* (lectotype: BM; isolectotypes: B, K).

Ficus cordata Thunb. var. *marlothii* Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 137. 1906.—LECTOTYPE (designated by Berg et al. 1985): NAMIBIA. *Fleck 395* (lectotype: Z).

Ficus cordata Thunb. var. *fleckii* Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 138. 1906.—LECTOTYPE (designated by Berg et al. 1985): NAMIBIA. *Fleck 387a* (lectotype: Z).

Shrub or tree up to 15 m tall. Branches drying grey to brown. Leafy twigs 2–4 mm thick, grey brown, glabrous or white puberulous or white pubescent, periderm persistent. Leaves not articulate; lamina cordiform, ovate or elliptic, 2–12 by 1.1–6.5 cm, apex acuminate to caudate, base (sub)cordate, truncate or rounded, both surfaces glabrous; lateral veins 5–7 pairs, usually furcate away from the margin, the basal pair up to (1/6–)1/4–1/2 the length of the lamina, usually branched, tertiary venation reticulate; petiole 0.8–2.5(–5.5) cm long, glabrous or minutely puberulous at base, epidermis persistent; stipules 0.25–0.8(–1) cm long, glabrous or puberulous, usually caducous. Figs axillary or below the leaves or on short spurs on the older wood, (sub)sessile, solitary or in pairs; basal bracts 2–3 mm long, sometimes the apex lobed, glabrous or white puberulous, persistent; receptacle subglobose, 0.5–0.9 cm diam. when dry, glabrous or puberulous, turning from green to whitish to orange to dark purple or dark red at maturity, apex convex; ostiole 1.5–2.5 mm diam., upper ostiolar bracts glabrous or minutely puberulous; internal hairs absent. Staminate flowers near ostiole, sessile; tepals 3–4(–5), spathulate, ovate, or lanceolate, free, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3–4(–5), ovate, lanceolate, or oblong, free, reddish brown; ovary red brown

***Distribution and Habitat*—**This species is distributed in Congo, Angola, Namibia, Botswana, and South Africa; in semi-desert, in rocky places, at altitudes up to 1,500 m.

***Representative Specimens Examined*—**ANGOLA. Luanda: Malanga, May–Aug 1903, *Gossweiler 1004* (K, P). BOTSWANA. Ngamiland: Aha hill, 21° 04.15′ W, 19° 41.60′ S, 27 Apr 1980, *P.A. Smith 3462* (K, U). CONGO. Without locality, 24 Sep 1921, *Dawe 75* (K). NAMIBIA. Erongo: Karibib, Namibrand, Okongawa, 9 May 1958, *Seydel 1555* (WAG). Otjozondjupa: Grootfontein, Rd. Tsumeb–Namutoni, 15 km from Tsumeb, by Otjikotosee, 29 Mar 1968, H. and *H. E. Wanntorp 488* (K). SOUTH AFRICA. Northern Cape: *Drege 9566* (P, WAG); Orange R., NW of Cape, 12 Jan 1909, *Pearson 3103* (WAG).

***Notes*—**Berg and Wiebes (1992) only mentioned the distribution to be W Angola, NW Botswana, Namibia, and SW South Africa. Here we add Congo. Formerly, three subspecies were distinguished (Berg and Wiebes 1992). All are recognized here as species (*F. cordata*, *F. lecardii*, and *F. salicifolia*), because the differences between the species are constant. The two easiest characters to separate the three species are the absence of internal hairs in the figs of *F. cordata* (present in the other two species) and the narrow (2.5–5 times longer than wide) leaves of *F. salicifolia* (1.25–2.5 longer than wide in the other two species).

7. *Ficus cupulata* Haines, Bull. Misc. Inform. Kew: 154. 1914; Khanna and Kumar, Bull. Bot. Surv. India 44: 145. 2002.—TYPE: INDIA. Central province, Pachmarhi, *Haines 3556* (holotype: K).

Shrub or small tree, 2–6 m tall. Branches drying gray brown to dark brown. Leafy twigs 6–8 mm thick, puberulous to tomentose, gray brown to dark brown, periderm persistent. Leaves articulate; lamina (broadly) ovate, 8.2–12 by 7–9 cm, apex subacuminate to obtuse, the acumen blunt, base cordate, both surfaces glabrous or sometimes puberulous; lateral veins 6–7 pairs, usually furcate away from the margin, basal pair up to 1/4–1/3 the length of the lamina, branched, tertiary venation reticulate; petiole 2.2–4 cm long, velutinous, epidermis persistent; stipules 0.4–0.8 cm long, white tomentose or villose, persistent at the shoot apex and forming an ovoid terminal bud. Figs axillary, just below the leaves or on up to 2–4 mm long spurs on the older wood, solitary or in pairs, sessile; basal bracts 5–6 mm long, covering up to the middle of the receptacle, tomentose or villose, apex usually lobed, persistent; receptacle subglobose, 0.8–1.1 cm diam. when dry, white puberulous or tomentose, apex convex; ostiole 3.5–4 mm diam., upper ostiolar bracts tomentose or villose; internal hairs present. Staminate flowers near the ostiole, sessile; tepals 3–4, usually connate, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3–4, ovate or lanceolate, free, reddish brown; ovary red brown.

***Distribution and Habitat*—**This species is distributed in Central India; in xerophytic vegetation, resembling tropical dry deciduous forest.

***Representative Specimens Examined*—**INDIA. Madhya Pradesh: Pachmarhi, Jun 1910, Haines 4 (K), Oct 1911, *Haines 3556* (K).

***Notes*—** This is an endemic and rare species only known from three specimens; two were collected by Haines in 1910–1911, and the last one was recently collected by Khanna and Kumar in 2000 (Khanna and Kumar, 2002). Thus seemingly, the species is not extinct.
See also note under *F. chiangraiensis*.

8. *Ficus densifolia* Miq., Ann. Mus Bot. Lugduno–Batavi 3: 218. 1867; C. C. Berg et al., Fl. Mascareignes, Moracées: 9. 1985.—TYPE: LA RÉUNION. Herb. *Mus. Paris 703* (holotype: P; isotype: L).

Ficus lucens Cordem., Fl. Réunion: 273. 1895.—TYPE: LA RÉUNION, *Cordemoy s.n.* (holotype: MARS).

Tree up to 6 m tall. Branches drying (dark) brown, periderm persistent. Leafy twigs (1.5–)2–5 mm thick, glabrous or minutely puberulous, periderm persistent. Leaves not articulate; lamina (broadly) ovate to elliptic, (3.5–)6–12.5 by (1.5–)3.8–8.8 cm, coriaceous, apex acute to (sub)acuminate, the acumen sharp or blunt, base rounded to truncate to cuneate to (sub)attenuate to subcordate, both surfaces glabrous; lateral veins 8–13 pairs, usually furcate away from the margin, the basal pair up to 1/6–1/3 the length of the lamina, usually branched, tertiary venation reticulate or partly parallel to lateral veins; petiole 1–4.7 cm long, glabrous, epidermis persistent; stipules (0.5–)0.9–1.9 cm long, glabrous, persistent. Figs axillary or below the leaves, solitary or in pairs, sessile; basal bract broadly ovate, 3–6 mm long, usually lobed at apex, glabrous, persistent; receptacle ovate or subglobose, (0.5–)0.7–1 cm diam. when dry, glabrous, apex convex; ostiole 2.5–3 mm diam.; upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers dispersed, sessile or pedicellate, tepals 2–3, broadly ovate to spathulate, sometimes connate at base or up to 2/3 the length of the tepals, red(dish) brown. Pistillate flowers sessile or pedicellate; tepals 2–3, ovate or lanceolate, sometimes connate at base or up to 3/4 the length of the tepals, reddish brown to dark red, ovary red brown or sometimes white with a red dot.

***Distribution and Habitat*—**This species is distributed in Madagascar, Réunion, and Mauritius; at altitudes up to 1,200 m.

***Representative Specimens Examined*—**MADAGASCAR. Ambanja: Ambodimanga, 12 Jun 1905, *d'Alleizette s.n.* (L). MAURITIUS. Near Petria Jafrail, Mar 1934, *Rav(?) 906* (K). RÉUNION. Bourbon, Oct 1875, *Balfour s.n.* (K); Mt. St. Denis, La Grande Chaloupe, 23 Oct 1973, *Bernardi 14565* (K); Without locality, 11 Nov 1970, *Cadet 2837* (P); Petite Plaine, Palmistes, 4 Mar 1971, *Friedmann 1092* (K, P, U).

***Note*—**We have only seen one specimen from Madagascar (seemingly collected in 1905). If the label information is correct, then this species is very rare on Madagascar and perhaps already extinct.

9. *Ficus geniculata* Kurz , J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 42: 105. 1873; Forest Fl. Burma 2: 447. 1877; King, Ann. Roy. Bot. Gard. (Culcutta) 1: 64, t. 80, t. 84X2. 1887; C. C. Berg, Thai Forest Bull. Bot. 35: 16. 2007.—TYPE: MYANMAR. Bago (Pegu), *Kurz 1537* (holotype: K).

Tree up to 30(–40) m tall. Branches drying brown. Leafy twigs (1.5–)2–6 mm thick, glabrous, puberulous or densely whitish tomentose, periderm persistent or sometimes flaking off. Leaves articulate, lamina (broadly) ovate to elliptic to oblong, (5–)10–15.7(–20) by (2.8 –)6–11 cm, coriaceous, apex acute to subacuminate, the acumen blunt or sharp, base cuneate to obtuse to rounded to subattenuate to (sub)cordate, both surfaces glabrous; lateral veins 8–14 pairs, the basal pair up to (1/10–)1/8–1/4(–1/3) the length of the lamina, sometimes branched, tertiary venation reticulate to partly parallel to the lateral veins; petiole (2.5–)3.5–8.5(–15) cm long, glabrous or whitish puberulous, epidermis persistent, sometimes flaking off at the apex or the base; stipules 0.5–0.9 cm long, glabrous or densely whitish puberulous to tomentose, persistent at the shoot apex and forming a terminal bud, epidermis of bud scales persistent. Figs axillary or below the leaves or on up to 0.5–1 cm long spurs on the older wood, solitary or in pairs or up to 4 on spurs, sessile or peduncle up to 2(–10) mm long, puberulous or tomentose; basal bracts 2–2.5 mm long, covering only the base of the receptacle, minutely puberulous, persistent; receptacle subglobose, 0.4–0.7(–1.2) cm diam. when dry, glabrous or puberulous or densely white tomentose to villose, white to pink to purple to black at maturity, apex convex or flat; ostiole 1–2 mm diam., upper ostiolar bracts glabrous; internal hairs present. Staminate flowers near the ostiole, sessile; tepals 3, usually connate, red brown. Pistillate flowers sessile or with a short pedicel; tepals 2–3(–4), lanceolate or ovate, sometimes connate, red brown; ovary red brown.

9.1 *Ficus geniculata* Kurz var. ***geniculata***: Kurz, Forest Fl. Burma 2: 447. 1877; C. C. Berg, Thai Forest Bull., Bot. 35: 17. 2007.

Ficus geniculata Kurz var. *abnormalis* Kurz, Forest Fl. Burma 2: 447. 1877.—LECTOTYPE(designated here): MYANMAR. Bago (Pegu), *Kurz 3134b* (lectotype: L).

Leafy twigs glabrous or puberulous. Lamina mostly (broadly) ovate, the basal lateral veins up to (1/10–)1/9–1/3 the length of the lamina; petiole glabrous, epidermis usually flaking off at the apex or the base; stipules glabrous or puberulous; basal bracts glabrous; receptacle glabrous. Figure 2-5E.

***Distribution and Habitat*—**This variety is distributed in India, Bangladesh, China (Prov. Sichuan), Myanmar, Thailand, Laos, and Vietnam; in primary evergreen forest or partly open areas in mixed deciduous forest, on granite, sandstone or limestone bedrock, at altitudes up to 1,450 m.

***Representative Specimens Examined*—**BANGLADESH. Chittagong: Kodala hill, 30 miles from Chittagong, Sep 1885, *King 136* (K). CHINA. Sichuan: Kientschang, Tetschang, between Cungmuying–Loyao, 2 Apr 1914, Handel–*Mazzetti 1094* (E). INDIA. Assam: Goalpara, Khasia hill, Jan 1886, *Man 9* (K). Jharkhand: Ranchi, Sep 1917, *Haines 4199* (K). Sikkim: *Hooker f. & Thomson s.n.* (K). LAOS. Xiangkhouang: 3 Nov 1920, *Poilane 2253* (P). MYANMAR. Bago (Pegu): Sep 1878, *Kurz 1537* (K). Mandalay: Maymyo Plateau, 5 Oct 1912, *Lace 5977* (K). THAILAND. Chiang Mai: Chiengdao, Mar 1957, *Bunchuai 337* (BKF, L). Chon Buri: Satthahip, Koh Khram, 4 Aug 1999, *Phengklai 11910* (BKF). Kanchanaburi: Thong Phaphum, Kroeng Kauvia, 4 Feb 1962, *Larsen & Smitinand 9543* (BKF). Prachuap Khiri Khan: Hua Hin, Dec 1960, *Champion s.n.* (BKF). Surat Thani: Kaw Tao, 14 Apr 1927, Kerr 12741 (BK). Utai Thani: Ban Rai, Huai Ka Kaeng Game Reserve, ca. 99° 14' E 15° 00' N, 27 Feb 1970, *van Beusekom & Santisuk 2954* (BKF). VIETNAM. Ho Chi Minh (Saigon): Botanical Garden, 27 Mar 1914, *Chevalier 31375* (K).

9.2 *Ficus geniculata* Kurz var. ***insignis*** (Kurz) C. C. Berg, Thai Forest Bull., Bot. 35: 17. 2007.–*Ficus insignis* Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 42(2): 105. 1873; For. Fl. Burma 2: 447. 1877.—TYPE: MYANMAR. Bago (Pegu), 15 Aug 1872, *Kurz 3151* (holotype: K).

Ficus avium Gagnep., Notul. Syst. (Paris) 4: 85. 1927.—TYPE: VIETNAM. Near Nhatrang, *Poilane 4559* (holotype: P).

Ficus virens Aiton var. *dasycarpa* Corner, Blumea 22: 299. 1975; Chew, Fl. Australia 3: 35. 1989.—TYPE: AUSTRALIA. Western Australia, Dale Gorge, Hamersley Range, Sep–Oct 1964, *J. Thomson s.n.* (holotype: PERTH).

Leafy twigs densely whitish puberulous or tomentose. Lamina ovate or elliptic to oblong; the basal lateral veins up to 1/6–1/3 the length of the lamina; petiole glabrous or whitish puberulous, epidermis persistent; stipules usually densely whitish puberulous to tomentose; basal bracts glabrous or minutely puberulous; receptacle densely white tomentose to villose.

Distribution and Habitat—This variety is distributed in India, Myanmar, Thailand, Cambodia, Vietnam, and Australia; in primary evergreen forest or partly open area in mixed deciduous forest, on granite, sandstone or limestone bedrock.

Representative Specimens Examined—AUSTRALIA. Northern Territory: between Bing Bong Station and Coast Mill, 45 km N of Borroloola, 15° 38' S, 136° 22' E, 14 Sep 1978, *Farrell TF 888* (BRI); Katherine, 16 miles Caves Reserve, 28 Oct 1977, *Parker 1144* (K, L). Western Australia: West Kimberley, Eastern Walcott Inlet, 16° 16' S, 124° 59' E, 22 May 1983, *Milewski 145* (PERTH); Dale Gorge, Hamersley Range, 25 Aug 1960, *George 1053* (PERTH). CAMBODIA. Phnom Penh: 10 Jul 1933, *Bèjaud 197* (K, P). INDIA. Tamil Nadu (Madras): Nilgiris, Oct 1883, *Gamble 13072* (K). Uttar Pradesh: Saharanpur, 6 Feb 1901, *Kanjilal 1045* (K). MYANMAR. Bago (Pegu): 15 Aug 1872, *Kurz 3151* (K). Magwe: 3 miles E of Natmauk, 12 Mar 1915, *Rogers 959* (E). VIETNAM. Khánh Hòa: Mt. Cô–Inh, near Nhatrang, 16 Sep 1922, *Poilane 4559* (P).

Notes—Corner (1975) identified some of the Australian figs as *Ficus virens* Aiton var. *dasycarpa*. These specimens show as dominant characters white tomentose to villose stipules and receptacles. However, all other characters are more in line with *Ficus geniculata* Kurz var. *insignis* (Kurz) C. C. Berg, thus we identified the specimens as *Ficus geniculata* var. *insignis*.
The subspecies has once been photographed in Thailand, no herbarium collections have been made so far.

10. *Ficus henneana* Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 216. 1867; Benth., Fl. Austral. 6: 165. 1967; F. M. Bailey, Queensl. Fl. 5: 1468. 1902.–*Ficus superba* Miq. var. *henneana* (Miq.) Corner, Gard. Bull. Singapore 17: 376. 1960; Chew, Fl. Australia 3: 32. 1989.—TYPE: AUSTRALIA. Queensland, Booby Is., *Henne s.n.* (holotype: L; isotype: NSW).

Ficus gracilipes F. M. Bailey, Queensland Bot. Bull. 3: 16. 1891.—TYPE: AUSTRALIA. Queensland, Brook field, *Exley* (holotype: BRI).

Ficus parkinsonii Hiern, J. Bot. 39: 1–2, tab. 417. 1901.—TYPE: AUSTRALIA. Queensland, Booby Is., *Banks* (holotype: BM).

Ficus pritzelii Warb., Repert. Spec. Nov. Regni Veg. 1: 74. 1905.—TYPE: AUSTRALIA. Queensland, Barron, *Diels 8371* (not seen).
Tree up to 20(–45) m tall. Branches drying (dark) brown. Leafy twigs 2–5 mm thick, glabrous or puberulous, periderm persistent or sometimes slightly flaking off. Leaves articulate; lamina ovate to elliptic to oblong, 3.2–13.5 by (1.2–)2–7.5 cm, (sub)coriaceous, apex acute to subacuminate, the acumen blunt, base cuneate to obtuse to rounded to (sub)cordate, both surfaces glabrous; lateral veins 8–12 pairs, often furcate away from the margin, the basal pair up to 1/10–1/5 the length of the lamina, unbranched, tertiary venation reticulate to partly parallel to the lateral veins; petiole 1.2–5.5 cm long, glabrous or puberulous, epidermis persistent; stipules 0.3–0.8 cm long, glabrous or puberulous, caducous or sometimes persistent at the shoot apex and forming a terminal bud. Figs axillary, solitary or in pairs; peduncle 0.4–0.8 cm long, glabrous or minutely puberulous; basal bracts ca. 1.5 mm long, caducous; receptacle subglobose, 1–2.1 cm diam. when dry, sometimes with a stipe up to 2 mm long, glabrous, surface usually wrinkled when dry, yellow to reddish purple or red at maturity, apex convex; ostiole 4–5 mm diam., upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers near the ostiole, sessile or on a short pedicel; tepals 3(–4), oblong or ovate, free, reddish brown. Pistillate flowers sessile or pedicellate; tepals (2–)3(–4), ovate, oblong, or lanceolate, free, reddish brown; ovary dark red.

Distribution and Habitat—This species is distributed in northeast and east Australia; in rain forest, monsoon forest, limestone outcrops, deciduous vine thickets, or coastal dunes, at altitudes up to 1,000 m.

Representative Specimens Examined—AUSTRALIA. New South Wales: New South Wales National Park, Jan 1902, *Boorman s.n.* (K); Whispering Gallery, 5 km SE of Albion Park, 8 Nov 1977, *Coveny 9750* (K, L). Northern Territory: Arnhem Land, Little Lagoon, Groote Eylandt, Arnhem Land Aboriginal Reserve, 30 May 1948, *Specht 446* (K, L); Arnhem Land, Elcho Isl., 135°33' E, 12°00' S, 14 Jul 1975, *Maconochie 2208* (K, L). Queensland: Atherton, State Forest Res 652, Cauley, 148° 30'E, 20° 50' S, 31 Jul 1974, *Hyland 4050* (R.F.K.) (K); Brisbane, Moreton, Mt. Tamborine, Mar 1947, *Clemens s.n.* (K); Cape York, Tolga Scrub, 13 May 1974, *Irvine 8484* (L).

11. *Ficus hookeriana* Corner, Gard. Bull. Singapore 17: 378. 1960, substitute name; 21: 10. 1965; Grierson & Long, Fl. Bhutan 1(1): 97. 1983; Zhekun and Gilbert, Fl. China 5: 41. 2003.–*Ficus hookeri* Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 215. 1867, non Sweet 1826.—TYPE: INDIA. Sikkim, *Hooker f.* (*Ficus n. 120*) (holotype: K; isotypes: BM, E, L, P).

Tree, up to 28 m tall. Branches drying brown, glabrous, periderm persistent. Leafy twigs 4–9 mm thick, glabrous or sometimes brownish villose, periderm persistent or sometimes flaking off. Leaves not articulate; lamina obovate or elliptic–oblong, 10–25.5 by 5–17 cm, coriaceous, apex acute to subacuminate, the acumen blunt or sometimes lobed, base (sub)cuneate, subattenuate, or rounded, both surfaces glabrous; lateral veins 8–11 pairs, usually furcate away from the margin, the basal pair up to 1/5–1/3 the length of the lamina, sometimes branched, tertiary venation reticulate; petiole 2.1–8.1 cm long, glabrous, epidermis persistent; stipules 0.4–0.8 cm long, glabrous, persistent at the shoot apex and usually forming an ovoid terminal bud. Figs axillary or below the leaves, solitary or in pairs, sessile; basal bracts 4.5–11 mm long, united into a cup, glabrous, persistent; receptacle subglobose, 1.2–2.2 cm diam. when dry, wrinkled, glabrous, maculate, apex flat; ostiole 4–5 mm diam., upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers dispersed, sessile; tepals 4, elliptic, free, (dark) red brown. Pistillate flowers sessile; tepals 3–5, lanceolate, (dark) red brown; ovary sessile or stipitate, dark red to brown.

Distribution and Habitat—This species is distributed in North India, Nepal, China (Prov. Guizhou), and Vietnam; usually in forest on limestone, altitude between 500 and 2,000 m.

Representative Specimens Examined—CHINA. Guizhou: Lipo country, Jan 1988, *Xianghou 684* (K). INDIA. Meghalaya: Mt. Khasia, 1859, *Hooker f. & T.Thomson* (*Ficus no 120*) (P, L). Munipur: 1886, *Vatt 5877* (P). Sikkim: without locality, *Hooker f.* (*Ficus n. 120*) (E, L). NEPAL. Eastern: Koshi zone, Sankhuwasabha, 87° 22'00" E, 27° 46' 00" N– 87° 20' 30" E, 27° 44' 00" N, 25 Aug 1998, *Noshiro et al. 9840182* (E). VIETNAM. Hoa Binh: Mai Choue, Pâw, Apr 1996, *Hiep NTH 2107* (P).

Note—This is one of the Asian species without an articulated petiole and the only species in this subsection with large basal bracts (4.5–11 mm long) that are united into a cup. The large, united bracts makes it distinct from *F. orthoneura*.

12. *Ficus ingens* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 288. 1867; Hutch., Fl. Trop. Afr. 6, 2. 121. 1916; C. C. Berg et al., Fl. Cameroun 28: 146, t. 48. 1985; C. C. Berg, Fl. Trop. E. Afr. Moraceae: 60, t. 20. 1989; Kirkia 13: 259. 1990; Fl. Zambes. 9, 6: 54. 1991; C. C. Berg and Wiebes, African fig trees and fig wasps: 90. 1992; Friis, Fl. Somalia 2: 100. 1999.–*Urostigma ingens* Miq., London J. Bot. 6: 554. 1847.–*Ficus schimperiana* A. Rich., Tent. Fl. Abyss. 2: 266. 1851, nom. superfl.—TYPE: ETHIOPIA. Djeladjeranne, *Schimper 1771* (holotype: K; isotypes: B, BR, L, K, P).

Urostigma caffrum Miq., Nieuwe Verh. Eerste Kl. Kon. –Ned. Inst. Wetensch. Amsterdam, ser. 3, 1: 141. 1849.–*Ficus caffra* (Miq.) Miq., Ann.Mus. Bot. Lugduno–Batavi 3: 288. 1867; Hutch., Fl. Trop. Afr. 6, 2: 121. 1916.—TYPE: SOUTH AFRICA. Macalesbery, *Burke s.n.* (holotype: B; isotypes: K, U).

Urostigma xanthophyllum Miq., London J. Bot. 6: 554. 1847; Hutch., Fl. Trop. Afr. 6, 2: 121. 1916.—TYPE: ETHIOPIA. *Schimper 943* (holotype: B; isotypes: K, L, P).

Urostigma xanthophyllum Miq. var. *ovatocordatum* Sonder, Linnaea 23: 136. 1850; Mildbread and Burret, Bot. Jahrb. 46: 209. 1911.—TYPE: SOUTH AFRICA. *Zeyher 1548* (holotype: B, not found yet).

Ficus stuhlmannii Warb. var. *glabrifolia* Warb., Bot. Jahrb. 20: 162. 1895; Mildbr. and Burret, Bot. Jahrb. 46: 209. 1911.—LECTOTYPE (designated by Berg et al. 1984): TANZANIA. Victoria Nyanza, Busisi, *Stuhlmann 750*

(lectotype: B).

Ficus pondoensis Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 140. 1906; Hutch., Fl. Trop. Afr. 6, 2: 121. 1916.—TYPE: SOUTH AFRICA. Pondoland, 1887–88, *F. Bachman 425* (holotype: B).

Ficus caffra (Miq.) Miq. var. *sambesiaca* Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 140. 1906; Mildbr. and Burret, Bot. Jahrb. 46: 209. 1911.—TYPE: ZIMBABWE. Boruma, *Menyhart 770* (holotype: Z).

Ficus caffra (Miq.) Miq. var. *longipes* Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 140. 1906; Mildbr. and Burret, Bot. Jahrb. 46: 209. 1911.—TYPE: SOUTH AFRICA. Transvaal, Pretoria, Wonderboompoort, *Rehmann 4435* (holotype: Z; isotype: BM).

Ficus caffra (Miq.) Miq. var. *natalensis* Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 140. 1906; Mildbr. and Burret, Bot. Jahrb. 46: 209. 1911.—TYPE: SOUTH AFRICA. KwaZulu–Natal, Camperdown, *Rehmann 7798* (holotype: Z).

Ficus caffra (Miq.) Miq. var. *pubicarpa* Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 140. 1906; Mildbr. and Burret, Bot Jahrb. 46: 209. 1911.—TYPE: SOUTH AFRICA. Cape province, *Drege s.n.* (holotype: B).

Ficus magenjensis Sim, Forest Fl. Port. E. Afr.: 99, t. 93B 1909; Hutch., Fl. Trop. Afr. 6, 2: 121. 1916.—TYPE: MOZAMBIQUE. Maganja da Costa, *Sim 5653* (holotype: K).

Ficus katagumica Hutch., Kew Bull. 7: 317. 1915.—TYPE: NIGERIA. Katagum, *Dalziel 305* (holotype: K).

Ficus kawuri Hutch., Kew Bull. 7: 319. 1915.—LECTOTYPE (designated by Berg et al. 1984): NIGERIA. *Dalziel 910* (lectotype: K).

Ficus ingentoides Hutch., Kew Bull. 7: 319. 1915; Fl. Trop. Afr. 6, 2: 123. 1916; Lebrun and Boutique, Fl. Congo Belge 1: 124. 1948.—LECTOTYPE (designated by Berg et al. 1984): ERITREA. near Acrur, *Schweinfurth & Riva 1687* (lectotype: K).

Ficus ovato-cordata De Wild, Ann. Soc. Sci. Brux. 40: 281. 1921; Lebrun and Boutique, Fl. Congo Belge 1: 121. 1948.—TYPE: DEMOCRATIC REPUBLIC OF CONGO (Zaire). 21 Sep 1914, *Bequaert 5821* (holotype: BR).

Ficus ingens (Miq.) Miq. var. *tomentosa* Hutch., Fl. Cap. 5, 2: 530. 1925; Troupin, Fl. Rwanda 1: 146. 1978; Fl. Plant Ligneuses Rwanda: 445. 1982.—

TYPE: SOUTH AFRICA. Cape prov., Queenstown Distr., Zwart Valley, *Galpin 8173* (holotype: K).

Tree up to 15(–20) m tall. Branches drying yellow brown to brown. Leafy twigs 2.5–6 mm thick, white or brown pubescent to tomentose to velutinous, periderm persistent or sometimes flaking off. Leaves not articulate; lamina ovate to lanceolate or elliptic to oblong, (2.5–)5.5–13(–20) by (2–)3.3–8(–11) cm, coriaceous, apex acute to acuminate, the acumen sharp or blunt, base obtuse, rounded, (sub)cordate, or truncate, both surfaces glabrous; lateral veins 7–11 pairs, usually furcate away from the margin, basal pair up to 1/6–1/3 the length of the lamina, branched, tertiary venation reticulate; petiole (0.5–)1–4.2 cm long, glabrous, puberulous, or velutinous, epidermis persistent or sometimes flaking off; stipules 0.4–1.2 cm long, glabrous, puberulous or tomentose to velutinous, usually caducous. Figs axillary or just below the leaves, solitary or in pairs, subsessile or with a peduncle up to 5 mm long, puberulous; basal bracts 1.5–2 mm long, puberulous, persistent, sometimes the apex lobed; receptacle subglobose, 0.5–1.2 cm diam. when dry, glabrous, minutely puberulous, tomentose, or white to brown velutinous, whitish to pink to yellow or pale red to purple at maturity, apex flat or convex; ostiole 2–3 mm diam., upper ostiolar bracts glabrous or minutely puberulous; internal hairs present. Staminate flowers near the ostiole, sessile or shortly pedicellate; tepals 2–3(–4), free or connate, reddish brown. Pistillate flowers usually sessile; tepals 3–4, ovate or broad lanceolate, free, reddish brown; ovary red brown.

Distribution and Habitat—This species is distributed in Senegal, Mali, Ivory Coast, Ghana, Benin, Niger, Nigeria, Cameroon, Gabon, Chad, Central African Republic, Congo, Sudan, Uganda, Rwanda, Burundi, Zambia, South Africa, Zimbabwe, Swaziland, Eritrea, Ethiopia, Kenya, Tanzania, Malawi, Mozambique, Djibouti, Somalia, Saudi Arabia, and Yemen; in grassland with scattered small trees or woodland remnants of evergreen forest, often in rocky places or in lowland (riverine) forest, at altitudes up to 1,700 m.

Representative Specimens Examined—BENIN. Atakora: Tanguieta, Tanougou waterfalls, 1° 26.63' E, 10° 48.17' N, 15 Apr 2001, *van der Maesen et al. 7601* (WAG). Borgou: Ndali, 30 Apr 1999, *Houngnon et al. 6616* (WAG). Zou: Djidja, Setto, 2° 04' E, 7° 30' N, 25 Aug 2001, *Akoegninou 5294* (WAG). BURUNDI. Bubanza: 29°23' E, 3°06' S, 2 Oct 1976, *Reekmans 5400* (K, WAG). CAMEROON. Adamava: Nganha Mt. near Ndigou, about 60 km E of Ngaoundéré, 3 Dec 1964, *de Wilde & de Wilde–Duyfjes 4486A* (WAG). North: 2 km E of Garoua, 13°25' E, 9°22' N, 23 May 1974, *Geerling & Néné 4881* (WAG). CENTRAL AFRICAN REPUBLIC. Matakil falls, 21°11' E, 8°26' N, 9 Dec 1982, *Fay 4068* (K). CHAD. Upper Outbangui: Nana, 21 Nov 1902, *Chevalier 6320* (K). DEMOCRATIC REPUBLIC OF CONGO (Zaire). Katanga: Dilolo, Jan 1950, *Schmitz 2673* (K). Kivu: Uvira, Kamanyola escarpment, 29 May 1959, *Léonard 4456* (K, L). DJIBOUTI. Randa: May 1959, *Chedeville 1290* (K). ERITREA. Anseba: Keren, Mt. Zeban, S of Keren, 30°27' E, 16°17' N, 17 Aug 1973, *Aweke & Gilbert 693* (WAG). Central: Asmara, 18 km SW of Asmara, on Adwa Rd., 39°13' E, 15°22' N, 20 Aug 1973, *Aweke & Gilbert 701* (WAG). ETHIOPIA. Oromia: about 50 km W of Lekemti, near bridge crossing Didessa R., 12 Apr 1966, *de Wilde & de Wilde–Duyfjes 10730* (WAG). Tigray: 23 km W of Makalle, 39°33' E, 13°31' N, 13 Aug 1973, *Aweke & Gilbert 637 A* (WAG). GABON. Without locality, 1984, *Williamson 38* (K). GHANA. Brong–Ahafo: near Jema–Nkwanta, 1°47.0' W, 7°53.1' N, *Jongkind & Nieuwenhuis 2558* (WAG). Northern: Gambaga, 5 Apr 1953, *Morton 159* (WAG). IVORY COAST. Marahoue: Bouaflé, Marahoue National Park, 5°55' W, 7°04' N,9 Feb 1998, *Jongkind & Musah 4317* (WAG). Vallée du Bandama: Katiola, Tiengala Rd., ca. 25 km N of Katiola, ca. 5°08' W, 8°19' N, 14 Sep 1978, *Dekker 144* (WAG). KENYA. Coast: Taita–Taveta, Voi, Nov 1955, *Ossent 119* (K). Eastern: Makueni, Kibwezi, Dwa rock, Jul 1943, *Bally 2576* (K). Rift Valley: Naivasha, Oilongonot Estate, Feb 1963, *Okerfoot 4729* (WAG). MALI. Kayes: Sebekoro, 30 Oct 1978, *Geerling & Coulibaly 5876* (WAG). Koulikoro: above Koronga, 3 Jun 1982, *Klug & Hamburg BFT 113* (K). MOZAMBIQUE. Maputo: Namaacha, 26 Jun 1948, *Torre 7994* (WAG). Niassa: Maniamba, Metangula, 11 Oct 1942, *Mendonca 764* (WAG). Tete: Angónia, Ulongue, NE of Dómue Mt., 19 Dec 1980, *Macuácua 1487* (WAG). NIGER. Bani kou beye, 2 Dec 1968, *Kawara 5620* (WAG). NIGERIA. Bauchi: Yankari Game Reserve, Kwa Rd., 10°00' E, 10°00' N, 30 Mar 1971, *Geerling 3522* (WAG). Niger (State): Minna, Gurara falls, Bank of Gurara R., 17 May 1973, *Eimunjeze et al. 66417* (WAG). RWANDA. Western: Kibuye, Lake Kivu, Iwawu Isl., 26 May 1978, *Troupin 15967*, *15968* (K). SAUDI ARABIA. Dalaghan National Park: 5 Mar 1981, *Hillcoat 97* (BM). SENEGAL. Niokolo–Koba National Park, Mount Assirik, 23 Mar 1976, *Tutin 8* (K). SOMALIA. Awdal: Borama, 13 Jan 1945, *Glover & Gilliland 586* (K). Somaliland: Auboba, 21 Nov 1933, *Gillett 4626* (K). SOUTH AFRICA. Eastern Cape: Pondoland, 1887–88, *Bachmann 425* (B). Gauteng: Wonderboompoort, *Rehmann 4435*(Z). KwaZulu–Natal: Alfred, Horseshoefarm, 17 Dec 1965, *Strey 6154* (K). SUDAN. Northern state: West Darfur, about 120 km E of Zalingei, 20 Jan 1965, d*e Wilde & de Wilde–Duyfjes 5432* (K, WAG). Southern Sudan: East Equatoria, Lower slopes of Mt. Konoro, towards Gilo, ca. 32°53' E, 4°03' N, 24 Nov 1980, *Friis & Vollesen 443* (K). TANZANIA. Arusha: Engari Nanyuki R., Arusha National Park, 11 Apr 1968, *Greenway & Kanuri 13454* (K). Kigoma: Mahali Mt., Lumbye R., 21 Sep 1958, *Newbould & Jefford 2491*(K). Morogoro: Ulanga, 10 km N of Itete, 2 Nov 1998, *Gereau et al. 6175* (L). UGANDA. Central: Lake Victoria, Lolui Isl., 14 May 1964, *Jackson 82* (K). Eastern: Mbale, Budama, E side of Sukulu hill, close to Busai–Tororo road, 5 miles S of Tororo, 10 Mar 1951, *Wood 392* (K). Northern: Kitgum, Chua, Paimol, *Eggeling 2350* (K). SWAZILAND. Manzini: Timbutini, 13 Aug 1958, *Compton 27936* (K). YEMEN. Jebelain: near Al Udayn, 8 Jun 1875, *Wood 299* (BM). Jebel Raymah: 7 Oct 1976, *Wood 1379* (BM). ZAMBIA. Copperbelt: Rd. Mpongwe (St. Anthony's Mission)–Lake Kashiba, NW of Mpongwe, 23 Nov 1982, *Berg & Bingham 1395* (U). Lusaka: 1 km N of Kafue bridge, 17 Nov 1982, *Berg & Bingham 1368* (K, U, WAG). Northwestern: Solwesi, Mutanda R. bridge, Solwezi–Mwinilunga miles 23, 15 Sept 1952, *Angus 455* (K). ZIMBABWE. Mashonaland Central: Mazowe, Mazoe dam, 31 Jan 1982, *Berg & Drummond 1335* (U, WAG). Mashonaland East: Mutoko, near Mutoko, 9 Feb 1982, *Berg & Campbell 1350* (U, WAG).

13. ***Ficus lecardii*** Warb., Ann. Mus. Congo, Bot. ser. 6, 1: 24, tab. 11. 1904; Hutch., Fl. Trop. Afr. 6, 2: 117. 1916.–*Ficus cordata* Thunb. subsp. *lecardii* (Warb.) C. C. Berg, Kew Bull. 43: 81. 1988; C. C. Berg and Wiebes, African fig trees and fig wasps: 92. 1992.—TYPE: SENEGAL. *Lecard 197* (holotype: BR; isotype: K).

Ficus salicifolia Vahl var. *latifolia* Hutch., Fl. Trop. Afr. 6, 2: 116. 1916.—TYPE: CHAD. Dar Banda Ndelli, *Chevalier 6767* (holotype: K; isotype: B).

Shrub or tree up to 8 m tall. Branches drying grey to brown. Leafy twigs 1.5–3 mm thick, brown, glabrous or puberulous, periderm persistent. Leaves not articulate; lamina (broadly) ovate, subovate, or oblong, 2–9(–12) by 1.5–6(–8) cm, apex subacute to acuminate, base cuneate to rounded to obtuse or subcordate, both surfaces glabrous; lateral veins 7–11 pairs, unbranched, the basal pair up to 1/5–1/4 the length of the lamina, tertiary venation reticulate and partly parallel to lateral veins; petiole 1–4.5 cm long, glabrous or minutely puberulous at the base, epidermis persistent; stipules 0.5–1 cm long, glabrous or puberulous, caducous. Figs axillary or just below the leaves, solitary or in pairs, subsessile or with a peduncle up to 3 mm long, glabrous or white puberulous; basal bracts 1.5–2 mm long, puberulous, persistent; receptacle subglobose, 0.6–0.8 cm diam. when dry, glabrous or puberulous, apex convex; ostiole 1.5–2 mm diam., upper ostiolar bracts glabrous; internal hairs present, minute and sparse. Staminate flowers near ostiole, sessile; tepals 3(–4), spathulate or ovate, usually free or sometimes connate at base, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3(–4), ovate, lanceolate, or oblong, free, reddish brown; ovary red brown.

***Distribution and Habitat*—**This species is distributed in Senegal, Guinea–Bissau, Mali, Ivory Coast, Burkina Faso, Nigeria, and Cameroon; in savannas, often near rocks, at altitudes up to 1,500 m.

***Representative Specimens Examined*—**BURKINA FASO (Upper Volta). Cascades, Comoe, 18 km N of Banfora, 5 Jun 1962, *Leeuwenberg 4360* (P, K, WAG). Hauts–Bassins: Houet, Bobo Dioulasso, 10 Dec 1973, *Ausru 5523* (P, WAG). CAMEROON. North: Garoua, Tinguelin, 13˚ 23' E, 9˚ 23' N, 31 Dec 1975, *Geerling 5552* (P). Far North: Bourha, 65 km south–eastern of Mokolo, 13 Oct 1964, *Letouzey 6949* (P, K). GUINEA–BISSAU (GUINÉ PORTUGUESA). Bafata: Contubo El, 18 Nov 1955, *Santo 3600* (WAG). Gabu: Canjadúdi, 10 Jun 1949, *Santo 2501* (K). Quinara: Buba Saltinho, 30 May 1948, *Santo 2485* (WAG). IVORY COAST. Denguélé: Odianné, Tiémé, 22 Oct 1974, *de Koning 4310* (WAG). Savanes: Korhoko, ca. 16 km N of Korhoko, Guine zone, Lataha, ca. 5˚35' W, 9˚35' N, 2 Nov 1978, *Dekker 318*

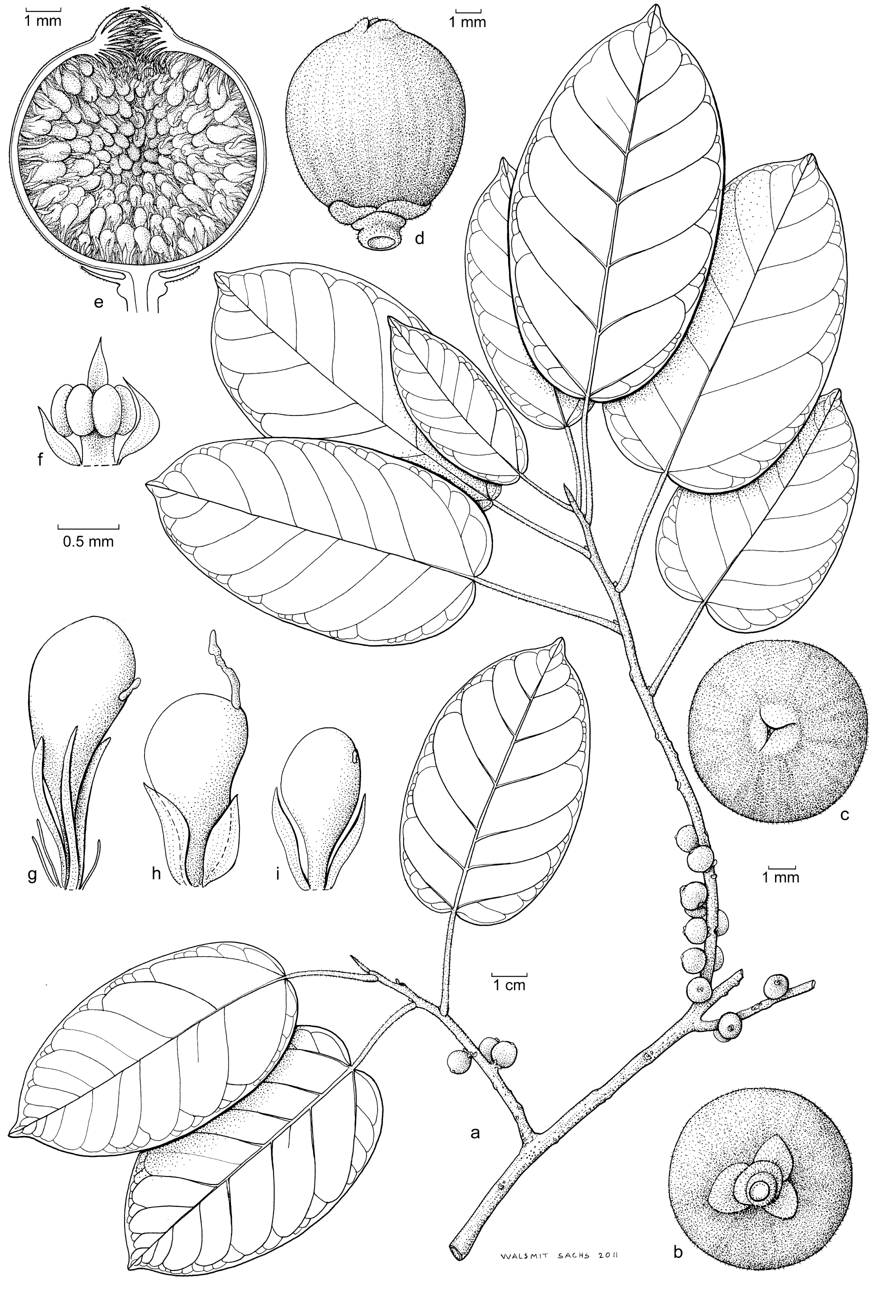

FIGURE 2-6. *Ficus middletonii* Chantaras. (Moraceae).–a. Twigs with leaves and figs; b. Basal bracts; c. Ostiole; d. Fig; e. Fig in longitudinal section; f. Staminate flower; g, h, i. Pistillate flowers. [*D. J. Middleton, S. Suddee, S. J. Davies & C. Hemrat 1178* (L)]. Drawing: Anita Walsmit Sachs, 2011.

(WAG). MALI. Kayes. Sebekoro, 30 Oct 1978, *Geerling & Coulibaly 5896* (K, P, WAG). Mopti. Sangna, 29 Oct 1969, *Hepper 3783* (K). Sikasso. 5° 40' W, 11° 19' N, 8 Nov 1984, *Hiemstra 776* (WAG). NIGERIA. Kaduna, Zaria, Kufena rock, 4 May 1950, *Keay FHI 25722* (K). Sokoto: Guaau, Kura village, 9 Jan 1968, *Daramola FHI 62543* (K). SENEGAL. Niokolo Koba National Park, 15 Apr 1976, *Tutin 12* (WAG). CHAD. Dar Banda Ndelli, 20 Dec 1902, *Chevalier 6767* (K), 31 Jan 1903, *Chevalier 7417* (K).

***Notes*—**Berg and Wiebes(1992) treated *F. lecardii* as a subspecies of *F. cordata*. Here we reinstate its species status, because of constant differences with *F. cordata* and *F. salicifolia*. For differences see the second note under *F. cordata*.

We already know that staminate flowers of some species of subg. *Sycidium* sect. *Palaeomorphe* contain pistillodes as large as the pistillate flowers. Here, we found some staminate flowers (*Letouzey 6949*) that also contained a pistillode, a very uncommon feature in subsect. *Urostigma*.

14. *Ficus madagascariensis* C. C. Berg, Bull. Mus. Natl. Hist. Nat., B, Adansonia Sér. 4, 8: 34. 1986; C. C. Berg and Wiebes, African fig trees and fig wasps: 93. 1992.—TYPE: MADAGASCAR. Menamaty, Oct. 1911, *Perrier de la Bathie 10045* (holotype: P).

Shrub or (large tree. Branches drying brown. Leafy twigs 1–3 mm thick, glabrous or minutely puberulous, periderm persistent or sometimes flaking off. Leaves not articulate; lamina ovate to oblong to lanceolate, 6.1–15 by 2.1–5.5 cm, subcoriaceous, apex acuminate to cuspidate, the acumen sharp, base obtuse or rounded, both surfaces glabrous; lateral veins 7–12 pairs, sometimes furcate away from the margin, the basal pair up to 2/7–1/4 the length of the lamina, tertiary venation reticulate; petiole 0.5–3.5(–5) cm long, glabrous, epidermis persistent; stipules 0.3–0.7 cm long, glabrous or white puberulous, persistent at the shoot apex and forming a terminal bud. Figs axillary or just below the leaves, solitary or in pairs, sessile; basal bracts 1–2 mm long, glabrous, persistent, apex usually lobed; receptacle subglobose or depressed–globose, 0.4–0.6 cm diam. when dry, glabrous or minutely puberulous, apex convex; ostiole ca. 1.5 mm diam., upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers near the ostiole, sessile; tepals 3, ovate, lanceolate, or oblong, free, reddish brown. Pistillate flowers sessile or pedicellate; tepals 2–3, ovate, lanceolate, or oblong, free, reddish brown; ovary red brown.

***Distribution and Habitat*—**This species is distributed in Madagascar; in dry forest or xerophytic bush but may perhaps also occur in rainforest (unidentified photo seen).

***Representative Specimens Examined*—**MADAGASCAR. Without locality, 1932–1933, *Perrier de la Bathie 19239* (P); without locality, *Montagnac 72* (WAG). Valley of Fiherenana: 2–3 Aug 1928, *Humbert & Swingle 5122* (K); 12 Aug 1928, *Humbert & Swingle 5229* (K). Mahajanga (Majunga): Tsingy de Bemaraha S of the Manambolo R., 44° 49' E, 19° 09' S, 11 Dec 1996, *Jongkind 3506* (WAG).

15. *Ficus middletonii* Chantaras., sp. nov.—TYPE: THAILAND. Prachuap Khiri Khan, Pran Buri, Khao Sam Roi Yot National Park, Trail from Tham Sai to Tham Phra Yanakhon, 18 Aug 2002, *Middleton, Suddee, Davies & Hemrat 1178* (holotype: L, isotypes: BKF, E, L).

Folii basis (sub)cordata ad rotundata, stipulae gemmam anguste ovatam terminalem formantes albe puberulae ad tomentosae. Fici subsessiles vel pedunculo ad 1.5 mm longo, cum pilis interioribus. Flores staminati prope ostiliolum, tepala 3–4 libera.

Tree 10–20 m tall. Branches drying brown, periderm persistent. Leafy twigs 1.5–3(–5) mm thick, glabrous to puberulous. Leaves articulate; lamina ovate, 5–10(–4) by 2.5–6.5(–11) cm, (sub)coriaceous, apex acute to acuminate, the acumen blunt, base subcordate or obtuse to rounded, both surfaces glabrous; lateral veins 7–9 pairs, branched and often furcate away from the margin, the basal pair up to 1/5–1/3 the length of the lamina, usually branched, tertiary venation reticulate; petiole 1.5–5(–9.5) cm long, glabrous or puberulous, epidermis persistent; stipules 0.6–1 cm long, white puberulous to tomentose, persistent at the shoot apex and forming a terminal bud. Figs axillary, just below the leaves, or on up to 4 mm long spurs on the older wood, in pairs or solitary, subsessile or with a peduncle up to 1.5 mm long, puberulous to tomentose; basal bracts 1–1.5 mm long, covering only the base of the receptacle, puberulous to tomentose or villose, margin usually ciliate, persistent; receptacle subglobose, 0.5–0.8 cm diam. when dry, glabrous or minutely puberulous, cream to orange at maturity, apex convex; ostiole ca. 2 mm diam., the upper ostiolar bracts glabrous, sometimes minutely puberulous, margin ciliate, internal hairs present. Staminate flowers near the ostiole, sessile or pedicellate; tepals 3–4, ovate or lanceolate, free or sometimes connate at base, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3–4, ovate or lanceolate, free, reddish brown; ovary red brown. Figure 2-6.

***Distribution and Habitat*—**This species is distributed in South India and Thailand; in scrub forest on limestone rocks, at altitudes up to 1,050 m. Figure 2-4.

***Representative Specimens Examined*—**INDIA. Tamil Nadu (Madras): Dharmapuri, Harur, Chitteri hill, Nochikkottai, 8 Aug 1978, *Matthew RHT 16107* (K); Salem, Yercad, Servarayans, Yercad Ghat Rd., Hair Pin Bend 10, 2 Jul 1979, *Matthew RHT 23476* (L). THAILAND. Lampang: Wahng Nua, Doi Luang National Park, Wahng Gayo falls, 11 Jul 1997, *Maxwell 97–729*(A). Prachuap Khiri Khan: Pran Buri, Khao Sam Roi Yot National Park, 18 Aug 2002, *Middleton et al. 1178* (A, BKF, E, L). Sa Kaeo: Khao Cha Kan temple, 27 Mar 2005, *Tanming 69* (L).

***Note*—**This species was always referred to *F. arnottiana*. However, we found many characters that are distinctively different, such as the position of the staminate flowers (only near ostiole), tepals mostly free, ovary of pistillate flowers red brown, and internal hairs present in the figs.

16. *Ficus orthoneura* H. Lév. & Vaniot, Repert. Spec. Nov. Regni Veg. 4: 66. 1907; Corner, Gard. Bull. Singapore 21: 10. 1965; Zhekun and Gilbert, Fl. China 5: 41. 2003.—TYPE: CHINA. Guizhou: Kouy–Tcheou, Houo Kiang, 6 Jun 1904, *J. Cavalerie 2050* (holotype: E; isotype: P).

Ficus hypoleucogramma H. Lév. & Vaniot, Repert. Spec. Nov. Regni Veg. 4: 65. 1907.—TYPE: CHINA. Guizhou: Kouy–Tcheou, *Esquirol 597* (holotype: E).

Ficus caesia Hand.–Maz., Anz. Akad. Wiss. Wien, Math.–Naturwiss. Kl: 59: 54. 1922.—TYPE: CHINA. Prov. Cuidschou austro–occid., 20 Jun 1917, *Handel–Mazzetti 10378* (not found yet).

Ficus fedorovii W. T. Wang, Acta Phytotax. Sin. 6: 268. 1957.—TYPE: CHINA. Yunnan, Ho–kou, Lao–fan–chai, *W. T. Wang 3226* (not found yet, photograph in Acta Phytotax. Sin. 6: t21. 1957.)

Shrub or tree to10 m tall. Branches drying brown or dark brown, periderm flaking off. Leafy twigs 3–6 mm thick, glabrous or sometimes puberulous, periderm persistent or sometimes flaking off. Leaves not articulate; lamina elliptic to oblong or obovate, 6.6–16 by 3.2–10 cm, coriaceous, apex acute to rounded, base obtuse to cuneate, both surfaces glabrous, the upper surface usually shining; lateral veins 11–14 pairs, the basal pair up to 1/9–1/6 the length of the lamina, unbranched; tertiary venation reticulate; petiole 1.5–4 cm long, glabrous or minutely puberulous, epidermis persistent; stipules (2–)3–9 mm long, glabrous or minutely puberulous, margin ciliate, persistent at the shoot apex, usually forming an ovoid terminal bud. Figs axillary or just below the leaves or on up to 6 mm long spurs on the older wood, in pairs or solitary, subsessile or with a peduncle 2.5–4 mm long, glabrous or minutely puberulous; basal bracts 1.5–2 mm long, free, covering only the base of the receptacle, minutely puberulous and ciliate, persistent; receptacle subglobose, 0.7–1.3 cm diam. when dry, wrinkled, minutely puberulous or glabrous, apex convex; ostiole 2.5–4 mm diam.; upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers dispersed, sessile or pedicellate; tepals 3–4(–5), lanceolate or oblong (or ovate), free, reddish brown. Pistillate flowers sessile or pedicellate; tepals (2–)3–4, ovate or lanceolate, free, red brown; ovary reddish brown. Figure 2-5D.

***Distribution and Habitat*—**This species is distributed in China (Prov. Yunnan), Myanmar, Thailand, and Vietnam; on limestone, at altitudes between 200 and 1,700 m.

***Representative Specimens Examined*—**CHINA. Yunnan: Yunnan–Sen, 1900–1920, *Cavalerie 7807* (K). MYANMAR. Mandalay: Maymyo Plateau, 14 Sep 1912, *Lace 5959* (K). THAILAND. Kanchanaburi: Sai Yoke, Erawan falls, 26 Jan 1962, *Larsen & Smitinand 9270* (BKF). Khon Kaen: Tham Pha Phuang, 18 Jul 1973, *Smitinand 11812* (BKF). VIETNAM. Ninh Binh: Cuc Phuong National Park, 105º 43.08' E, 20º 14.22' N, 20 Dec 1999, *Cuong et al. 765* (L); Thua valley, Mo village, Thanh Yen, Thanh Hoa, 105º 38.27' E, 20º 15.70' N, 6 Mar 2002, *Cuong NMC1577* (L).

***Note*—**See also note under *F. hookeriana*.

17. *Ficus prasinicarpa* Elmer [Leafl. Philipp. Bot. 9: 3451. 1937, nom. inval.; Corner, Gard. Bull. Singapore 21: 8. 1965; C. C. Berg and Corner, Fl. Males. Ser. 1, 17 (2): 606. 2005] ex C. C. Berg, Blumea 56: 164. 2011.—TYPE: PHILIPPINES. Luzon, Sorsogon Prov, Irosin (Mt. Bulusan), *Elmer 16129* (holotype: PNH, lost; isotype: L).

Ficus glabella Blume var. *papuana* King, Ann. Roy. Bot. Gard. (Culcutta) 1: 50. 1887; Diels, Bot. Jahrb. Syst. 67: 184. 1935.—TYPE: NEW GUINEA. *Beccari PN 157* (not seen).

Tree up to 15 m tall. Branches drying red brown to dark brown. Leafy twigs 1.5–3.5 mm thick, glabrous, periderm flaking off. Leaves articulate; lamina ovate to elliptic to oblong to obovate, 4.7–16.4(–18) by 2.1–9(–10) cm, subcoriaceous to coriaceous, apex acute to acuminate (or up to caudate), the acumen blunt or sometimes sharp, base cuneate to obtuse to rounded to cordate, both surfaces glabrous; lateral veins 6–11 pairs, the basal pair up to 1/5–1/3(–1/2) the length of the lamina, mostly branched, usually departing from the midrib at different distances from the base, tertiary venation reticulate, partly parallel to the lateral veins; petiole 1–3.9(–4.5) cm long, glabrous, epidermis persistent; stipules 0.3–0.6(–0.8) cm long, glabrous or puberulous, caducous or sometimes persistent at the shoot apex and forming a terminal bud. Figs axillary, just below the leaves or on short spurs on the older wood, solitary, in pairs, or up to 4 together on the spurs, subsessile or with a peduncle up to 2 mm long, glabrous; basal bracts 1–2 mm long, glabrous or minutely puberulous in the middle, persistent; receptacle subglobose or subpyriform, 0.4–0.8 cm diam. when dry, glabrous, turning to purplish at maturity, apex flat or convex; ostiole 1.5–2 mm diam., upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers near the ostiole, sessile, tepals 2, broadly ovate, usually connate, red brown. Pistillate flowers sessile or pedicellate; tepals 2–3, elliptic, ovate or oblong, free, red brown; ovary dark red.

***Distribution and Habitat*—**This species is distributed in Indonesia (Sulawesi, Moluccas, Papua), Philippines, Papua New Guinea, and Solomon Islands; in rain forest, secondary forest, littoral vegetation, savannahs, on limestone cliffs, at low altitudes to up to 1,100 m.

Representative Specimens Examined—INDONESIA. Maluku: Morotai, Ngele 2, 23 Jun 1949, *Kostermans 1593* (K). Papua: Radjah Ampat, Waigeo Isl., Majalibid bay, Lupiltol, 11 Feb 1955, *P. van Royen 5495* (K). Sulawesi Selatan: Maros, Leangleang prehistoric park, 8 Jun 1986, *Chin 3405* (L). PHILIPPINES. Bulacan: Mt. Biak na Bato, San Miguel, 121˚04.7' E, 15˚07.5' N, 12 Sep 1994, *Garcia et al. PPI 15069* (K, L). Bukidnon: vicinity of Tanculan, Jul 1916, *Fénix BS 26087* (K). Negros Occidental: Cauayan, 122˚22.6' E, 9˚52.5' N, 21 Aug 1995, *Madulid & Majaducon PPI 36089* (K, L). Palawan: Quezon, Tawa–tawa, 117˚32' 6"E, 8˚56' 4"N, 1 Feb 1994, *Gaerlan et al. PPI 13431* (K, L). Quezon: Real Watershed area, Kawatan, 121˚ 09.2' E, 14˚12.1' N, 19 Feb 1995, *Romero et al. PPI 15671* (K, L). Sorsogon: Rosin (Mt. Bulusan), May 1916, *Elmer 16129* (K, L). PAPUA NEW GUINEA. Milne Bay: Menapi, Cape Vogel Peninsula, 18 Apr 1953, *Brass 21972* (K). Morobe: Lae, Lasanga Isl., 147˚ 15' E, 7˚ 25' S, 6 Nov 1969, *Streimann NGF 44299* (K, L); Musi Isl., Buso, 147˚ 10' E, 7˚ 25' S, 20 Aug 1970, *Streimann NGF 45207* (K, L). West Sepik: Selio Isl., Aitape, 142˚ 30' E, 3˚ 10' S, 31 May 1969, *Millar & Vandenberg NGF 40898* (K, L, SING). SOLOMON ISLANDS. Malaita: Lilisiana–Fiu Rd., Auki area, 15 Aug 1968, *Gafui et al. BSIP 10490* (K). New Georgia, Rendova Isl., W coast, near Zaimane R., 15 May 1963, *Whitmore BSIP 1939* (K, SING). Rennell: 24 Aug 1962, *Dissing 2881* (SING). Santa Isabel: Regi–Tanabuli villages, 28 Sep 1967, *Hunt 2760* (K, SING).

Notes—Berg and Corner(2005) mentioned that this species closely resembles *F. saxophila* (*F. saxophila* subsp. *saxophila* here), from which it differs in the presence of short peduncles and absence of indumentum on the basal and ostiolar bracts. However, the basal bracts of this species are only 1–2 mm long, while those of *F. saxophila* are much longer (2.5–4.5mm).
The caudate leaf apex is rare and only known from two samples, *Ridsdale SMHI 434* from Malapakan Isl. (Philipppines) and *Schram BW 14995* from Job Isl. (New Guinea).

18. ***Ficus prolixa*** G. Forst., Fl. Ins. Austr.: 77. 1786; Endl., Ann. Wiener Mus. Naturgesch. 1: 165. 1836; Guillaumin, Ann. Sci. Nat. Bot. ser 2, 7: 185. 1837; Drake, Ill. Fl. Ins. Pacif.: 297. 1892; Fl. Polynésie Franç.: 194. 1893; S.Moore, J. Linn. Soc., Bot. 45: 411. 1921; F.Br., Bull. Bernice P. Bishop Mus. 130: 40, fig. 6a–d. 1935; J.Florence, Fl. Polynésie Franç. 1: 150. 1997.–*Urostigma prolixum* (G. Forst.) Miq., London J. Bot. 6: 560. 1847.–*Ficus prolixa* G. Forst. var. *prolixa*: J. Florence, Fl. Polynésie Franç. 1: 150. 1997.—LECTOTYPE (designated by Florence 1997): SOCIETY ISLANDS. Tahiti, *Forster s.n.*(=FP 3546) (lectotype: BM); *Forster 410* (isolectotype: BM)

Ficus umbilicata Bureau ex Drake, Fl. Polynésie Franç.: 195. 1893.—TYPE: GAMBIER ISLANDS. Mangareva, 1841, *J. B. Hombron s.n.* [= FP2447] (holotype: P).

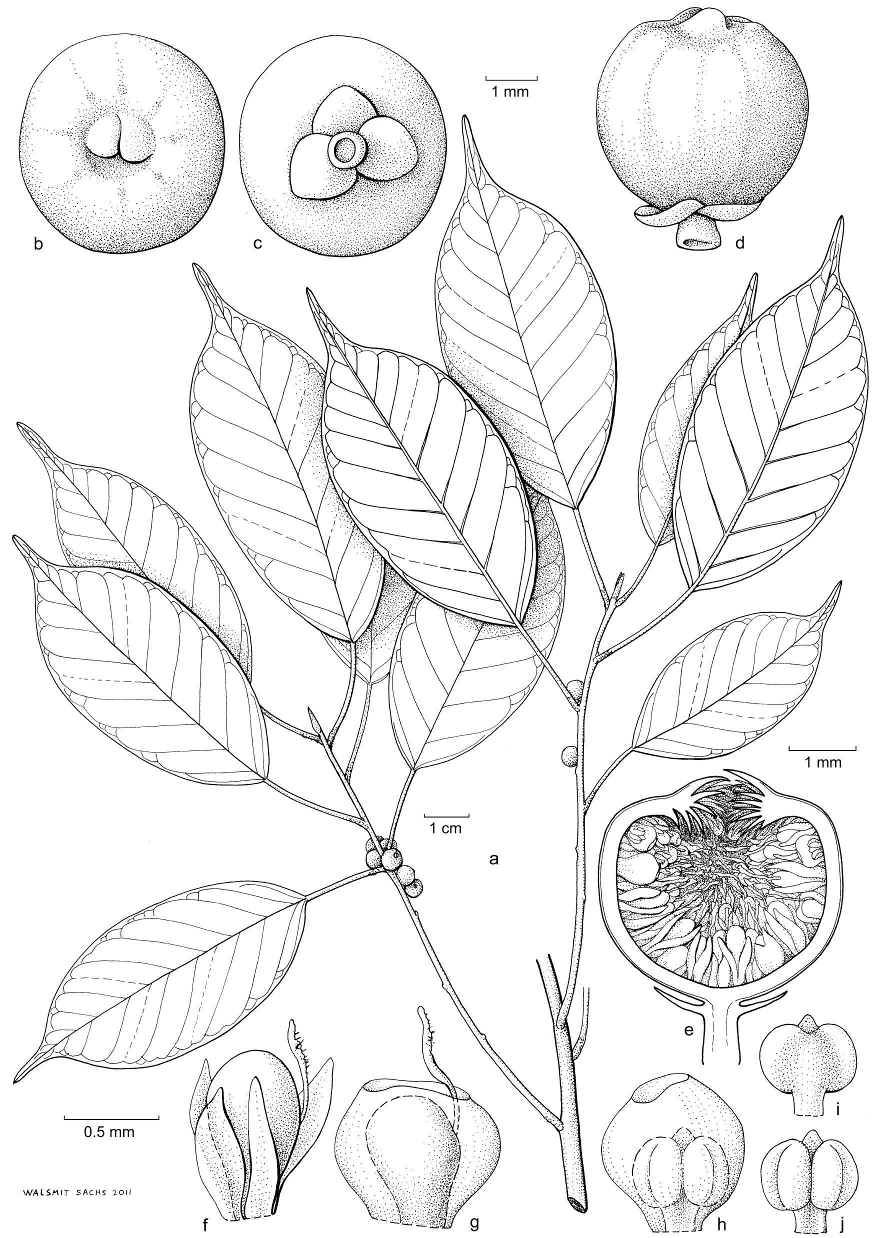

FIGURE 2-7. *Ficus pseudoconcinna* Chantaras. (Moraceae).–a. Twigs with leaves and figs; b. Ostiole; c. Basal bracts; d. Fig; e. Fig in longitudinal section; f. Pistillate flower with free tepals; g. Pistillate flower with connate tepals; h. Staminate flower with connate tepals; i. stamen (back side); stamen (front side). [*Whitmore & Sidiyasa TCW3429* (L)]. Drawing: Anita Walsmit Sachs, 2011.

Ficus aoa Warb., Bot. Jahrb. Syst. 25: 615. 1898.—SYNTYPES: SAMOA. Savaii, Centralgebiet, Warburg 504 (syntype: B, probably lost).; Upolu, Lanuto'o –Kamm, *Warburg 374* (syntype: B, probably lost).

Ficus inaequibractea Warb., Repert. Spec. Nov. Regni Veg. 1: 80. 1905.—TYPE: NEW CALEDONIA. 21 Sep 1902, *Schlechter 14730* (holotype: B, probably lost; isotypes: BM, E, L).

Ficus prolixoides Warb., Repert. Spec. Nov. Regni Veg. 1: 79. 1905.—TYPE: NEW CALEDONIA. *Balansa 3021* (ad 3026) (holotype: B, probably lost).

Ficus mariannensis Merr., Philipp. J. Sci., C 9: 73. 1914.—TYPE: GUAM. Nunu, *R. C. McGregor 384* (holotype: A; isotype: BM).

Ficus tenuistipula Merr., Philipp. J. Sci., C 9: 75. 1914.—TYPE: GUAM. Upi road, *R. C. McGregor 395* (holotype: A; isotype: L).

Ficus marquesensis F. Br., Bull. Bernice P. Bishop Mus. 130: 39. 1935.—TYPE: MAQUESAS. Nukuhiva, Mauu, 18 Jun 1921, *Brown 420* (isotype: P).

Ficus prolixa G. Forst. var. *subcordata* Corner, Gard. Bull. Singapore 17: 378. 1960.—TYPE: GUAM. *Fosberg 35333* (holotype: A; isotype: L).

Tree 15–20(–25) m tall. Branches drying dark brown. Leafy twigs 2–4 mm thick, glabrous or puberulous, drying brown, periderm persistent or sometimes flaking off. Leaves articulate; lamina ovate to elliptic to oblong, 5.5–13.5(–15.1) by 2.5–7.4 cm, (sub)coriaceous, apex acute to subacuminate, the acumen sharp or blunt, base cuneate, obtuse, rounded, truncate, or (sub)cordate, both surfaces glabrous; lateral veins 7–11 pairs, the basal pair up to 1/5–1/3 the length of the lamina, mostly branched, usually departing from the midrib at different distances from the base, tertiary venation reticulate, partly parallel to the lateral veins; petiole 0.9–2.5(–3.7) cm long, glabrous or puberulous, epidermis persistent or sometimes flaking off at base; stipules 0.4–1.2 cm long, glabrous or puberulous, usually persistent at the shoot apex and forming a (narrowly) ovate to lanceolate bud, epidermis of bud scales persistent. Figs axillary or just below the leaves, solitary or in pairs, (sub)sessile or peduncle up to 3 mm long, glabrous; basal bracts broadly ovate, 2.5–4 mm long, glabrous or puberulous, persistent; receptacle subglobose or subpyriform, 0.6–0.9 cm diam. when dry, reddish or purple to black at maturity, glabrous, apex convex or flat or concave; ostiole 2–3 mm diam., upper ostiolar bracts glabrous; internal hairs present. Staminate flowers dispersed, sessile or shortly pedicellate; tepals 2–3, elliptic, free or connate, reddish brown. Pistillate flowers sessile or pedicellate; tepals (1–)2–3, elliptic, broadly ovate, free or connate, reddish brown; ovary red brown.

***Distribution and Habitat*—**This species is distributed in Guam, Northern Mariana Isl., New Caledonia, Vanuatu, Nauru, Fiji, Niue, Cook Isl., and French Polynesia; in scrub forest, on rough limestone hill or on limestone cliffs, at low altitudes (up to 480 m).

***Representative Specimens Examined*—**COOK ISLAND. Mangaia: Oneroa–Tamarua Rd., 27 Jul 1974, *Sykes 287260* (L). Rarotonga Isl.: Tupapa valley: 28 Aug 1969, *Philipson 10144* (L). FIJI. Rotuma Isl.: Haua, 1 Aug 1938, *John 19396* (L, SING). FRENCH POLYNESIA. Marquesas Islands: Eiao, NW side, Vituha Bay and summit ridge, 1 Aug 1977, *Gagné 1289* (L); Nukuhiva, Baie Marquisienne, SW side, 5 Aug 1977, *Gagné 1281* (L); Hivaoa, between Eiaone and Puamau, NW of Puamau, 16 Nov 1963, *Decker 939* (L); Tahuata, Vaitahu, Mt. Amatea, 10 Apr 1975, *Schäfer 5497* (K). Society Islands: Raiatea, Uturoa, 10 Sep 1926, *Moore 29* (L); Tahiti, Mt. Hiurai, 10 May 1990, *Florence 10308* (L). GUAM. Asanite bay: 8 Jul 1965, *Fosberg 46274* (L). Rota: between Rota and Tataacho Point, 20 Jun 1946, *Fosberg 24972* (L). MARIANA ISLANDS. Pagan: without locality, 8 Aug 1954, *Bonham 17* (L). Saipan: Chalankanoa, W coast of Isl., 1 Feb 1950, *Fosberg 31278* (L). Tinian: Marpo valley, E of Tinian, 9–11 Jun 1946, *Fosberg 24731* (L). NAURU. Without locality, 11 Dec 1990, *McKee 45237* (L). Meneng, 29 Nov 1978, *Fosberg 58663* (L). NEW CALEDONIA. South: Paita, Tiaré, 11 Dec 1955, *McKee 3574* (L); Noumea, Yaouhe, 21 Sep 1902, *Schlechter 14730* (E, L). NIUE. Vinivini: Muitauliku Rd., 11 Nov 1965, *Sykes 170364* (L).VANUATU. Tanna: Lenakel, 21 Feb 1928, *Kajewski 29* (K); Eromanga, Dillon bay, 17 May 1928, *Kajewski 273* (K); Aneityum, Anelgauhat bay, 15 March 1929, *Kajewski 900* (K).

19. *Ficus pseudoconcinna* Chantaras., sp. nov.—TYPE: INDONESIA. North Sulawesi: Dumoga–Bone proposed National Park, Bank of Tumpa river, 17 Sep 1984, *T. C. Whitmore & K. Sidiyasa TCW 3429* (holotype: L; isotype: BO).

Laminae foliorum acuminatae acumen acutum, venae basales laterales ad 0.1–0.67 lamiae longitudino eramosae. Fici axillares admodum infra folia subsessiles vel pedunculo ad 0.2 cm longo, bracteae basales persistentes, receptaculum subglobosum 0.3–0.6 cm diam. i.s., sine pilis interioribus.

Tree, up to 20 m tall. Branches drying pale to dark brown. Leafy twigs 1–2 mm thick, glabrous. Leaves articulate; lamina oblong to elliptic to lanceolate, 5–11 by 1–4 cm, (sub)coriaceous, apex acuminate, the acumen sharp, base cuneate to rounded, both surfaces glabrous; lateral veins 8–10 pairs, the basal pair up to 1/10–1/6 the length of the lamina, unbranched, tertiary venation reticulate to partly parallel to the lateral veins; petiole 2–3 cm long, ca. 1 mm thick, glabrous, the epidermis persistent; stipules 0.2–0.5 cm long, glabrous, persistent at the shoot apex and forming a terminal bud or sometimes caducous. Figs axillary or just below the leaves, in pairs or solitary, subsessile or with a peduncle up to 0.2 cm long; basal bracts 1.5–2 mm long, glabrous, persistent; receptacle subglobose, 0.3–0.6 cm diam. when dry, glabrous, turning from white to pink to purple to black at maturity, apex convex; ostiole 1–1.5 mm diam., slightly prominent to flat, the upper ostiolar bracts glabrous; internal hairs absent.

Staminate flowers near the ostiole, sessile; tepals 2–3, connate, reddish brown. Pistillate flowers sessile or pedicellate; tepals 2–3, ovate or spathulate, free, reddish brown; ovary red brown. Figure 2-7.

***Distribution and Habitat*—**This species is distributed in Indonesia (endemic on Sulawesi); on limestone cliffs or rocks (and river banks). Figure 2-4.

***Representative Specimens Examined*—**INDONESIA. Sulawesi Selatan: Maros, Ulu Leang, Tompokbalang, 30 Sep 1975, *Soenarko 355* (L). Sulawesi Utara: Dumoga–Bone proposed National Park, Bank of Tumpa R., 17 Sep 1984, *Whitmore & Sidiyasa TCW 3429* (L).

***Note*—**This species differs from *F. concinna* by the distinctly persistent basal bracts.

20. ***Ficus religiosa*** L., Sp. Pl. 2: 1059. 1753; Burm.f., Fl. Ind.: 225. 1768; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867; King, Ann. Roy. Bot. Gard. (Culcutta) 1: 55, t. 67A. 1887; Hook.f., Fl. Brit. India 5: 513. 1888.; Gagnep. in Lecomte, Fl. Indo–Chine 5: 767. 1928; Corner, Wayside Trees 1: 683, t. 204, 206. 1940; Gard. Bull. Singapore 21: 6. 1965; C. C. Berg and Corner, Fl. Males. Ser. 1, 17(2): 608. 2005.–*Urostigma religiosum* (L.) Gasp., Giorn. Bot Ital. 2: 214. 1844; Ann. Sci. Nat. Bot., Sér. 3, 3: 343. 1845; Miq., London J. Bot. 6: 563. 1847; Fl. Ind. Bat. 1, 2: 333, t. 23. 1859.—TYPE: not indicated, *Hb. Linnaeus 1240.4 and 1240.5* (LINN) are representative specimens.

Ficus caudata Stokes, Bot. Mat. Med. 4: 358. 1812.–TYPE: Specimen gathered in Fothergill's garden, *Obs. 8388* (not found, LIV?, NMW).

Ficus superstitiosa Link, Enum. Hort. Berol. Alt. 2: 449. 1822.—TYPE: not indicated (synonymy based on Berg and Corner 2005).

Ficus rhynchophylla Wall. ex Steud., Nomencl. Bot. ed. 2, 1: 637. 1840, nom. inval., in synon.–*Ficus religiosa* L. var. *rhynchophylla* (Wall. ex Steud.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867.—TYPE: not indicated (synonymy based on Berg and Corner 2005).

Urostigma affine Miq., London J. Bot. 6: 564. 1847.—TYPE: INDIA. Assam, Bengali, *Hb. Hooker s.n.*, s.d. (holotype: K).
Ficus peepul Griff., Notul. 4: 393. 1854.—TYPE: INDIA. Assam, Tezpoor (not seen).

[*Ficus religiosa* L. var. *cordata* Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867, nom. nud.]

Tree up to 25(–35) m tall. Branches drying (dark) brown or yellow-brown. Leafy twigs 2–7 mm thick, glabrous or white puberulous. Leaves articulate;

lamina ovate to cordiform, (5–)10–21(–27) by (2.5–)7–13.5(–17) cm, coriaceous, apex caudate, the acumen sharp, base cordate to cuneate to truncate to subattenuate, both surfaces glabrous; lateral veins 7–11 pairs, the basal pair up to (1/8–)1/7–1/5(–1/4) the length of the lamina, usually branched, tertiary venation reticulate to subscalariform; petiole (2.5–)4–10(–12) cm long, glabrous; stipules 0.5–1 cm long, glabrous or ciliate, caducous or sometimes persistent at the shoot apex and forming a terminal bud. Figs axillary or below the leaves, solitary or in pairs, sessile; basal bracts 3, 3–5 mm long, puberulous or ciliate, apex usually lobed, persistent; receptacle subglobose, 0.5–0.8 cm diam. when dry, glabrous, turning from pink to purple to black at maturity, apex convex to flat; ostiole 2–2.5 mm diam.; upper ostiolar bracts glabrous and ciliate; internal hairs absent. Staminate flowers near the ostiole, sessile; tepals 3–4, ovate or oblong, free, reddish brown. Pistillate flowers sessile; tepals (2–)3–4, lanceolate or oblong, free, reddish brown; ovary sessile or stipitate, red brown, dark at apex to pale at base.

***Distribution and Habitat*—**This species is distributed in Pakistan, India, Nepal, Sri Lanka, Bhutan, Myanmar, Thailand (Northern), Laos, and Vietnam. Cultivated worldwide in tropical areas.

***Uses*—** Ornamental plants that are cultivated worldwide. They are sacred trees in Hinduism and Buddhism. In Sri Lanka people use the bark for dyeing, it contains tannin and fibers; leaves for silkworm (Corner 1981).

***Representative Specimens Examined*—**BHUTAN. Samdrup Jongkha, 26°48', 91°28' , 27 Jun 1979, *Grierson & Long 2115* (K). INDIA. Maharashtra: Mumbai (Bombay), Karjat, North Konkan, 29 Jan 1949, *Fernandes 65* (L). Tamil Nadu (Madras): Salem, Attur, Manmalai hill, Manmalai village, 7 Jul 1979, *Matthew 23664* (L). Uttar Pradesh: Lakhimpur Kheri, Kheri, Upper Gangetic Plain, 31 Mar 1898, *Duthie 22768* (K). West Bengal: N of Calcatta, 1863–4, *Griffith KD 4591* (K). NEPAL. Eastern: Kosi, Tumlingta, Arun valley, 8 Nov 1972, *Wraber 34784* (K). Central: Kaski, Pokhara, 18 Jun 1967, *Hara et al. 26070* (L). LAOS. Saravan. Eutu B. Zlang Phu et Zateng, 22 Oct 1928, *Poilane 16100* (P). PAKISTAN. Punjab: Rawanpindi, 29 Dec 1917, *Sprague 4* (K). SRI LANKA. Central: Kandy, Jan 1979, *Kostermans 27310* (K, L). Western: Colombo, 11 Feb 1937, *Coert 1461* (L). MYANMAR. Mandalay: Maymyo, 25 Aug 1912, *Lace 5925* (K). Sagaing: Shwebo, Jun 1891, *Huk 67* (K). THAILAND. Tak, Bhumipon dam, Jedeeluang temple, 12 Dec 2502, *Boonnak 561* (BKF). VIETNAM. Hanoi: Jun 1908, *d'Alleizette s.n.* (L); Giang, Chaudoc, Mt. Bai, Nov 1867, *Pierre 269* (SING).
***Note*—**Berg and Corner (2005) mention that *F. religiosa* occurs in the northern part of Thailand. However, the specimens from Thailand were mainly collected on temple grounds (thus cultivated plants). Even when found outside the temples, then it remains unsure whether they occur naturally, are escaped, or are cultivated.

21. ***Ficus salicifolia*** Vahl, Symb. Bot. 1: 28, t. 23. 1790; Willd., Sp. Pl., ed. 4, 4 (2): 1149. 1806; Hutch., Fl. Trop. Afr. 6 (2): 115. 1916.–*Ficus cordata* Thunb. subsp. *salicifolia* (Vahl) C. C. Berg, Kew Bull. 43: 82. 1988; Fl. Trop. E. Africa, Morac.: 63. 1989; C. C. Berg and Wiebes, African fig trees and fig wasps: 92. 1992.–*Urostigma salicifolium* (Vahl) Miq., London J. Bot. 6: 556. 1847.—TYPE: YEMEN. *Forsskål 780* (holotype: C; isotype: B).

Ficus indica Forssk., Fl. Aegypt.–Arab.: 179. 1775, non L., 1753.—TYPE: YEMEN. *Forsskål s.n.* (holotype: C)

Ficus religiosa Forssk., Fl. Aegypt.–Arab.: 170. 1775, non L., 1753.—TYPE: YEMEN. *Forsskål s.n.* (holotype: C; isotype: B).

Ficus salicifolia Vahl var. *australis* Warb., Vierteljahrsschr. Naturf. Ges. Zürich 51: 139. 1906.—TYPE: SOUTH AFRICA. Transvaal, *Rehmann s.n.* (holotype: Z).

Ficus pretoriae Burtt–Davy, Trans. Roy. Soc. S. Afr. 2: 365. 1912; Hutch., Fl. Trop. Afr. 6, 2: 116. 1916; F. White, Forest Fl. Northern Rhodesia: 32. 1962.–SYNTYPES: SOUTH AFRICA. Transvaal, Pretoria District, Magaliesberg, *Burtt–Davy 2750 & 2806* (K, PRE).

Shrub or tree up to 15 m tall. Branches drying grey to brown. Leafy twigs 1.5–4 mm thick, grey brown, glabrous or white puberulous or white pubescent, periderm persistent. Leaves not articulate; lamina subovate, oblong, lanceolate or elliptic, 3–21(–27) by 0.9–7.5 cm, apex acuminate or obtuse, base (sub)attenuate to cuneate to obtuse to rounded to (sub)cordate, both surfaces glabrous; lateral veins 8–16 pairs, sometimes furcate, the basal pairs up to (1/10–)1/8–1/3 the length of the lamina, tertiary venation reticulate to partly parallel to lateral veins; petiole 0.7–6 cm long, glabrous or minutely puberulous at the base, epidermis persistent; stipules 0.3–1.7 cm long, glabrous or white puberulous, persistent at the shoot apex and forming a terminal bud or sometimes caducous. Figs axillary, just below the leaves or on up to 2–3 mm long spurs on the older wood, solitary, in pairs, or up to 4(–6) on spurs, subsessile or with a peduncle up to 0.6 cm long, glabrous or white puberulous; basal bracts 1.5–3 mm long, glabrous or white puberulous, persistent or sometimes caducous; receptacle subglobose, 0.5–1.2 cm diam. when dry, glabrous or puberulous, apex convex; ostiole 2–2.5 mm diam., upper ostiolar bracts glabrous or puberulous; internal hairs present, minute and sparse. Staminate flowers near ostiole, sessile; tepals 3–4(–5), spathulate, ovate, or lanceolate, free, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3–4(–5), ovate, lanceolate, or oblong, free, reddish brown; ovary red brown.

Distribution and Habitat—This species is distributed in Algeria, Niger, Libya, Congo, South Africa, Botswana, Egypt, Sudan, Zimbabwe, Uganda, Eritrea, Ethiopia, Kenya, Tanzania, Djibouti, Somalia, Saudi Arabia, Yemen, United Arab Emirates, and Oman; in woodland, often in rocky places, at altitudes up to 2,700 m.

Representative Specimens Examined—ALGERIA. Massif du Hoggar, 16 km NE of Tamanrasset, 5°38' E, 22°50' N, 19 Mar 1981, *Podlech 34881* (L). BOTSWANA. Central: Serowe, 14 km E of Serowe to Palapye, 28 Nov 1994, *Cole 1055* (WAG). CONGO. Orientale: Ango, 7 Jul 1955, *Boutique 126* (K). DJIBOUTI. Tadjourah: between Tadjourah and Lake Assal, 5–6 Jan 1971, *Bavazzano & Lavranos s.n.* (K). EGYPT. Aswan: Gebel Elba, site 11, Mar 1997, *Sheded s.n.* (E). ERITREA. Southern (Debub): Lungo R., between Majo and Addi–Cajé (Adi Keyh), 11 May 1902, *Pappi 5205* (P). ETHIOPIA. Dire Dawa: 27 km NE of Dire Dawa on road to Djibouti, 42˚03' E, 9˚45' N, 10 Apr 1972, *Gilbert 2322* (K), Mountain between Alemaya and Dire Dawa, 3 Dec 1975, *Jansen 4813* (WAG), About 13 km on road Dire Dawa to Harrar, 41˚53'E, 9˚32'N, 22 Feb 1969, *De Wilde 4718* (WAG). Harari: near Harar, slopes of Dengego (escarpment S of Dire Dawa), 11 Mar 1975, *Bos & Jansen 9861* (WAG). KENYA. Central: Kiambu, ca. 18 miles from Kikuya, Ndeiya Grazing Scheme, 36˚32' E, 01˚11' S, 20 Jan 1963, *Verdcourt 3548* (K). Rift Valley: Nakuru, Kenya K3, Lake Nakuru National Park, 16 Nov 1973, *Kutilek 158* (K). Eastern: Isiolo, Uaso Nyiro, at Buffalo Springs, between Isiolo and Archer's Post, 25 Jan 1961, *Polhill 334* (K). LIBYA. Djebel Uweinat, 12 Dec 1968, *Léonard 4959* (E, P).NIGER. Italemen: 9˚20' E, 18˚42' N, 24 Mar 1979, *Newby ZP140* (K), 24 Mar 1979, *Newby ZP 152* (K). OMAN. Ash Shargiyah: Wadi Dawgah, 058˚ 12' E, 22˚ 31' N, 23 Apr 1993, *McLeish 1777* (E); Wadi Bani Habib, 057˚ 36' E, 23˚ 04' N, 15 Jun 1993, *McLeish 2152* (E). Dhofar: Leger Waterhole, 055˚ 05' E, 17˚ 06' N, 16 Sep 1993, *McLeish 2478* (E). SAUDI ARABIA. Makkah (Mecca): near market Mecca, 23 Aug 1949, *Nur s.n.* (SING). SOMALIA. Awdalland: Borama, 26 Jul 1957, *Hemming 1290* (K). Puntland: Bari, Galgalla, W of Karin, 6 Dec 1985, *Thulin 5628* (K). Somaliland: Upper Sheik, 12 Feb 1954, *Bally 9649* (K). SOUTH AFRICA. Gauteng: Wild part of Pretoria National Botanical Garden, 28˚16'52" E, 25˚44'13" S, 6 May 2005, *Nevhutalu & Nkuna 956* (K). KwaZulu–Natal: Ngotshe, Leuwsburg, Craigadam Forest, Ithala Nature Reserve, 24 Jan 1978, *Mc Donald 503* (K). SUDAN. Northern State: Dafur, Jebel Marra, Kelok Hing, 14 Feb 1964, *Wickens 1296* (K). TANZANIA. Arusha: Masai, 55 km N of Arusha, 10 Dec 1964, *Leippert 5337* (K). UGANDA. Karamoja, Dodoth, Kaabong, 17 Sep 1950, *Dawkins 645* (K). Northern: Kitgum, Chua, *Eggeling 2407* (K). UNITED ARAB EMIRATES. Ras Al Khaimah: 11 km E of Ras Al Khaimah town, Wadi Haqil 4065/28560, 4 Nov 1992, *Martin 105* (E). YEMEN. Socotra: Balfour 448, 410, *476* (E); Feb–Mar 1880, Balfour 354, 646, *647* (E). ZIMBABWE. Midlands: Kwe Kwe, Sable Park, 10 Sep 1975, S*tephens 271* (U).

Notes—This is the only species of the subsection that shows basal bracts persistent or sometimes caducous. Berg and Wiebes (1992) treated *F. salicifolia* as a subspecies of *F. cordata*. Here we reinstate its species status, because of constant differences with *F. cordata* and *F. lecardii*. For more differences see the second note under *F. cordata*.

The figs are usually solitary or in pairs when axillary or they are in groups of up to 4 on a spur. However, two samples from Ethiopia; De Wilde 4718 and Jansen 4813 show up to 4 axillary figs and up to 6 on a spur.

22. *Ficus saxophila* Blume, Bijdr. Fl. Ned. Ind. 9: 437. 1825; Decne., Ann. Mus. Hist. Nat. Paris 3: 493. 1834; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 260, 287. 1867; King, Ann. Roy. Bot. Gard. (Culcutta) 1: 17, t. 12, t. 81B. 1887; Koord. & Valeton, Bijdr. Boomsoort. Java 11: 56. 1906; Merr., Philipp. J. Sci. 1, Suppl.: 47. 1906; Elmer, Leafl. Philipp. Bot. 2: 537. 1908; Koord., Atlas 4: t. 702. 1916; Merr., Enum. Philipp. Flow. Pl. 2: 65. 1923; Elmer, Leafl. Philipp. Bot. 9: 3474. 1937; Backer, Blumea 6: 303. 1948; Corner, Gard. Bull. Singapore 21: 6. 1965; C. C. Berg and Corner, Fl. Males. Ser. 1, 17 (2): 610. 2005; C. C. Berg, Thai Forest Bull., Bot. 35: 22. 2007.–*Urostigma saxophilum* (Blume) Miq., Fl. Ind. Bat. 1, 2: 333. 1859.–*Ficus petrophila* Hassk., Cat. Hort. Bot. Bogor.: 75. 1844, nom. superfl.—TYPE: INDONESIA. Java, Bantam, *Reinwardt s.n.* (holotype: L).

Tree up to 35 m tall. Branches drying dark brown. Leafy twigs (1.5–)2–4.5 mm thick, glabrous or puberulous, periderm persistent. Leaves articulate; lamina ovate to elliptic, 3.5–22.5(–24) by 2–11.3(–15) cm, (sub)coriaceous, apex acuminate, the acumen sharp, base cordate to rounded, both surfaces glabrous; lateral veins 4–9 pairs, usually furcate away from the margin, the basal pair up to 1/5–1/3 the length of the lamina, usually branched, tertiary venation reticulate to subscalariform; petiole 2–7 cm long, glabrous or puberulous; stipules 0.3–1 cm long, glabrous, puberulous or tomentose, persistent at the shoot apex and forming a terminal bud or sometimes caducous. Figs axillary or just below the leaves, solitary or in pairs, sessile; basal bracts broad ovate, (1.5–)2–4.5 mm long, persistent, glabrous, puberulous or ciliate, apex usually lobed; receptacle subglobose or depressed–globose, 0.5–0.9 cm diam. when dry, glabrous or sometimes minutely puberulous, sometimes maculate, red at maturity, apex convex to flat; ostiole ca. 2.5 mm diam., prominent, upper ostiolar bracts glabrous, margin ciliate; internal hairs absent. Staminate flowers near ostiole, sessile; tepals 2 or 3, oblong or ovate, free, red brown or reddish. Pistillate flowers sessile or pedicellate; tepals (2–)3–4, ovate or lanceolate, free or sometimes connate at base, red brown; ovary dark red.

***Note*—**For difference with *F. prasinicarpa* see note under latter.

22.1 *Ficus saxophila* Blume subsp. ***saxophila***

Leafy twigs 2–4.5 mm thick. Lamina 7–24 by 4–15 cm; petiole 2–5. (–7) cm long, glabrous; stipules glabrous or puberulous. Basal bracts (2.5–)3–4.5 mm long, glabrous, puberulous or ciliate; receptacle 0.6–0.9 cm diam. when dry, glabrous or sometimes minutely puberulous.

***Distribution and Habitat*—**This subspecies is distributed in Vietnam, Thailand, Indonesia (Java, Lesser Sunda Islands, Sulawesi, Papua), Philippines, and Australia (Christmas Island, Indian Ocean); in coastal vegetation, often in rocky places, sometimes in forest, at low altitudes.

***Representative Specimens Examined*—**AUSTRALIA. Christmas Island: Audruo's Lookout, Oct 1904, *Ridley 113* (SING); Steep point, Oct 1904, *Ridley 110* (SING). INDONESIA. Java: 1859–1860, *Teijsmann 46* (L). Nusa Tenggara Timur: West Timor, Roti, Baa, Oct 1925, *Veearts s.n.* (L). Papua: Manokwari, Dessa Mami, 27 Aug 1948, *Kostermans 335* (bb. 33520) (K, L, SING). Sulawesi Selatan: Malili, Kawata, 10 Oct 1932, *Neth.Ind.For.Service CEL./V–188* (L, SING). PHILIPPINES. Bataan: Lamao R., Mt. Mariveles, Feb 1905, *Meijer 2588* (K, SING). Cebu: Mar 1912, *Ramos BS 11045* (K, L). Negros oriental: Dumaguete (Cuernos mts.), Mar 1908, *Elmer 9644* (K, L). Sorsogon: Irosin (Mt. Bulusan), Oct 1915, *Elmer 14427* (K, L). THAILAND. Saraburi, Phraputtabath, Phraputtabath temple, 18 Sep 2010, *Chantarasuwan 180910–1* (L, THNHM). VIETNAM. Ho Chi Minh City (Saigon): 20 May 1921, *Poilane 1990* (L).

22.2 *Ficus saxophila* Blume subsp. ***cardiophylla*** (Merr.) C. C. Berg, Thai Forest Bull., Bot. 35: 23. 2007.–*Ficus cardiophylla* Merr., Univ. Calif. Publ. Bot. 13: 129. 1926.—TYPE: VIETNAM. Cho Ganh, *Petelot 1291* (holotype: A; isotype: P).

Ficus bonii Gagnep. Notul. Syst. (Paris) 4: 86. 1927.—TYPE: VIETNAM. Lang–he, Ninh–binh region, *Bon 4045* (holotype: P).

Leafy twigs 1.5–2 mm thick. Lamina cordiform, 3.5–10.6(–11.3) by 2–4. (–7.5) cm; petiole 1–2.8 cm long; stipules puberulous. Basal bracts 1.5–2 mm long, puberulous; receptacle 0.5–0.6 cm diam. when dry, usually minutely puberulous. Figure 2-5H.

***Distribution and Habitat*—**This subspecies is distributed in China (Prov. Guangxi), Thailand, and Vietnam; on limestone hills, at altitudes up to 350 m.

***Representative Specimens Examined*—**CHINA. Guangxi: Lungchow, *Morse 144* (K). THAILAND. Chumphon: Muang, Krating, Wat Tham Khao Khun Krating, 12 Jun 2006, *Williams 1669* (L). Saraburi: Tap Kwang, 3 Oct 1963, *Smitinand & Sleumer 1342* (BKF, L, SING); Phraphutthabath, Khunkhol, Tham Makak, near Bo Phran Lang–nuea, 20 Nov 2005, *Pooma et al. 5716* (L). Satun: Tarutao Isl., on cliff along the beach, 17–22 May 2005, *Tunming & Gardner s.n.* (L). VIETNAM. Tankeuin: 25 Dec 1885, *Balansa 745* (L).

23. *Ficus subpisocarpa* Gagnep., Notul. Syst. (Paris) 4: 95. 1927; Gagnep. in Lecomte, Fl. Indo–China 5: 769. 1928; C. C. Berg and Corner, Fl. Males. Ser. 1, 17(2): 611. 2005; C. C. Berg, Thai Forest Bull., Bot. 35: 23. 2007.—TYPE: VIETNAM. Near Haipong, *Balansa 769* (holotype: P).

Shrub or tree up to 10(–15) m tall. Branches drying dark brown or gray brown. Leafy twigs (1.5–)2.5–8 mm thick, (sub)glabrous or white puberulous, periderm flaking off. Leaves articulate; lamina ovate to elliptic to oblong, 4–16(–24) by 2–9(–13) cm, (sub)coriaceous, apex acute to subacuminate, the acumen blunt, base rounded to obtuse to cuneate to subattenuate, rarely cordate, both surfaces glabrous; lateral veins (5–)7–11 pairs, the basal pair up to 1/10–1/4(–1/3) the length of the lamina, unbranched, tertiary venation reticulate to partly parallel to the lateral veins; petiole (1.5–)2.3–4.5(–7) cm long, glabrous or sometimes puberulous at the base, epidermis persistent or flaking off at the base of the glabrous petiole; stipules 0.3–1.1 cm long, puberulous, persistent at the shoot apex, usually forming an ovoid terminal bud. Figs usually on up to 0.5 cm long spurs on the older wood, sometimes also axillary or just below the leaves, 1–4 together but solitary or in pairs in the leaf axils; peduncle 0.1–0.8(–1.1) cm long, glabrous or minutely puberulous; basal bracts 1–2.5 mm long, glabrous, caducous; receptacle subglobose or subpyriform, 0.7–1.2(–1.4) cm diam. when dry, glabrous, surface wrinkled when dry, turning from whitish to pink to purple or black at maturity, apex flat or convex; ostiole (1.5–)2–3 mm diam., upper ostiolar bracts glabrous; internal hairs usually absent or sometimes minute and sparse. Staminate flowers near the ostiole, sessile; tepals 2–3, connate, red brown. Pistillate flowers sessile or with a short pedicel; tepals 2–3, usually connate, reddish brown; ovary red brown or dark red.

Note—See note under *F. caulocarpa* for differences. For differences with *F. superba* see note under latter.

23.1 ***Ficus subpisocarpa*** Gagnep. subsp. ***subpisocarpa*** C. C. Berg, Thai Forest Bull., Bot. 35: 24. 2007.–*Ficus superba* (Miq.) Miq. var. *japonica* Miq., Prolus. Fl. Jap.: 132. 1866/67; Ann. Mus. Bot. Lugduno–Batavi 2: 200. 1865; Corner, Gard. Bull. Singapore 21: 7. 1965.—TYPE: JAPAN. Distr. Kowara, *Siebold s.n.* (holotype: L).

Shrub or tree up to 7 m tall; leafy twigs (sub)glabrous. Lamina: lateral veins (5–)7–10 pairs, the basal pair up to 1/10–1/4 the length of the lamina; petiole glabrous or puberulous, epidermis persistent or sometimes flaking off at base; stipules 0.3–0.7(–1.1) cm long, (minutely) puberulous. Figs on spurs or axillary, up to 4 together; peduncle 0.1–0.7(–0.9) cm long, glabrous or whitish puberulous; basal bracts 1–2 mm long, glabrous; receptacle 0.7–1 cm diam. when dry; ostiole 1.5–2.5 mm diam.; internal hair absent.

Distribution and Habitat—This subspecies is distributed in China (Prov. Guangdong, Hainan, Hong Kong), Taiwan, Cambodia, Vietnam, Indonesia (Moluccas?, see note), and Japan; in evergreen or deciduous forest, on limestone rock, from low altitudes up to 1,300 m.

Representative Specimens Examined—CAMBODIA. Kampot: North Kampot, Srê–Krasang, 10 Feb 1928, *Poilane 14775* (L). CHINA. Guangdong (Kwangtung): Sin–fung, Wamei Tong, Sha Lo Shan, 1–31 Dec 1937, *Taam 237* (L). Hainan: Yaichow, Feb 1983, *How & Chun 70185* (K). Hong Kong: High Isl., 23 Feb 1970, *Hu 9525* (K); Dog Stomach village, Shatin, 28 Nov 1968, *Hu 6293* (K); Moyenne, 19 Dec 1894, *Bodinier 1003* (P). INDONESIA. Maluku: Seram, 1859–1861, *de Vriese s.n.* (L). JAPAN. Kyushu: Kagoshima, Mt. Kaimon, 17 Apr 1927, *Kondo 2210* (L). Okinawa: Yaeyama Gunto, Iriomote, between Shira–hama and Sonai, 17 Aug 1951, *Walker & Tawada 6523* (L); Ogami Jima, 25 Aug 1956, *Fosberg 38416* (L). Shikoku: Kochi, Okinoshima, Sukumo–shi, 24 Nov 1966, *Kitamura & Murata 2592* (L). TAIWAN (Formosa). Takuw plain, Apr 1895, *Henry 2030* (K); Savage, Matouan, 8 May 1912, *Price 437* (K). VIETNAM. Ninh Thuan: Phanrang, Cana, 24 Oct 1925, *Poilane 12425* (A, P).
Cultivated–AUSTRALIA. New South Wales: Grafton, 11 Nov 1934, *White 11158* (L).

Note—Only one specimen collected by de Vriese in the Moluccas (Seram). This is a strange gap in the distribution. However, the data on the labels of De Vriese are unreliable, but always collected in Indonesia, which means that there is always a disjunct distribution. On the other hand, the collected material may also be a cultivated specimen.

23.2 ***Ficus subpisocarpa*** Gagnep. subsp. ***pubipoda*** C. C. Berg, Thai Forest Bull., Bot. 35: 24. 2007.–TYPE: THAILAND. Chaiyaphum, Thungkamang, *van Beusekom et al. 4218* (holotype: BKF; isotypes: K, L, P).

Tree up to 15 m tall; leafy twigs whitish puberulous. Lamina: lateral veins 9–11 pairs, the basal pair up to 1/5–1/3 the length of the lamina; petiole puberulous at base and this part usually flaking off; stipules 0.6–1.1(–1.5) cm long, densely puberulous. Figs mainly on spurs, up to 3 together; peduncle 0.3–0.8(–1.1) cm long, whitish puberulous; basal bracts 1.5–2.5 mm long, glabrous or minutely puberulous; receptacle 0.8–1.2(–1.4) cm diam. when dry; ostiole 2–3 mm diam.; internal hairs present, minutely and sparse. Figure 2-5A.

Distribution and Habitat—This subspecies is distributed in Myanmar, Thailand, Cambodia, Vietnam, Peninsular Malaysia, and Singapore; in evergreen or deciduous forest, at altitudes up to 1,400 m.

Representative Specimens Examined—CAMBODIA. Kampong Speu: Chbar Mon, 10 km W of Phom Penh, 104° 30' E, 11° 40' N, 3 Apr 2001, *Huq et al. 10864* (L). MALAYSIA. Kedah: Pulau Adang, Apr 1894, *Anonymous 15727* (K). Penang: Balik Pulau, 24 Jan 1910, *Anonymous 14146* (K). Perak: Palau Pangkor, near Telok Ketapang, 18 Aug 1981, *Chin & Kusen 3123* (L). Selangor: Pulau Angsa, 21 Nov 1956, *Burkill & Shah HMB 998* (L, SING). MYANMAR. Bago (Pegu): 15 Aug 1872, *Kurz 3134* (K). Rangoon (Yangon): Jan 1908, *Meedold 8149* (K). Tanintharyi: Tenasserim and Andamans, 1862–3, *Helfer KD 4613* (K, L). SINGAPORE. Cathedral Compound, 14 Dec 1934, *Corner s.n.* (SING). THAILAND. Chiangmai: Hot, Rd. No. 108, Maesariang–

Hot, Mai Moeng Nao Arboretum, *Pooma et al. 5814* (L). Khon Kaen: Muang, Tha Pra, 10 Jun 1970, *Smitinand 11031* (BKF). Nakhon Ratchasima: Nong–ra–wieng, 26 Jan 1995, *Phengklai & Garcia 207* (BKF). Prachuap Khiri Khan: Hua Hin, Wat Khao Sanam–chai, Nong–kae, 99° 58' 02" E, 12° 31' 16" N, 8 Jan 2002, *Chayamarit et al. 3036* (BKF). Phangnga: Ko Surin Nua, 16 Apr 1976, *Chemsirivattana & Smitinand 2110* (BK). Trat: Lam Hob, Lam Takeam, Ko Chang, 11 Jul 1955, *Boonnak 479* (BKF). VIETNAM. Central Vietnam, without locality, 25 Nov 1941, *Poilane 30152* (L).

24. *Ficus superba* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 264, 287. 1867; King, Ann. Roy. Bot. Gard. (Culcutta) 1: 59, t. 72. 1887; Gagnep. in Lecomte, Fl. Indo–China 5: 773. 1928; Corner, Gard. Bull. Singapore 10: 287. 1939; Wayside Trees 1: 679. 1940; Gard. Bull. Singapore 21: 7. 1965; C. C. Berg and Corner, Fl. Males. Ser. 1, 17 (2): 612. 2005.–*Urostigma superbum* Miq., Pl. Jungh.: 46. 1851; Fl. Ind. Bat. 1, 2: 334. 1859.—TYPE: INDONESIA. Java, Koang, *Junghuhn 285* (holotype: L).

Ficus tenuipes S. Moore, J. Bot. 63, suppl.: 107. 1925.—TYPE: TIMOR. Kailakuk, *S. Moore 3771* (holotype: BM).

Ficus timorensis Decne., Nouv. Ann. Mus. Hist. Nat. Paris 3: 495. 1834; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867, p.p., in syn. sub *F. superba*; King, Ann. Roy. Bot. Gard. (Culcutta) 2: 185. 1887.—TYPE: TIMOR. *Herb. Mus. Paris no. 9* (holotype: P?, n.v.; isotype: L).

Urostigma accedens Miq., Fl. Ind. Bat. 1, 2: 347. 1859.—TYPE: INDONESIA. Timor (not found yet).

Tree up to 30 m tall. Branches drying brown to blackish. Leafy twigs (3–)4.5–12 mm thick, subglabrous or white puberulous. Leaves articulate; lamina ovate to oblong to elliptic to obovate, (6–)9–25(–27.8) by (3–)5.1–13.6 cm, subcoriaceous, apex (sub)acuminate, the acumen blunt, base rounded to cuneate or subcordate, both surfaces glabrous; lateral veins (6–)7–9(–11) pairs, usually furcate away from the margin, the basal pair up to 1/7–1/3 the length of the lamina, sometimes branched, tertiary venation reticulate to partly parallel to the lateral veins; petiole 4–14.5(–20) cm long, glabrous or sometimes puberulous at the base, epidermis persistent; stipules 0.5–1.6(–2.7) cm long, densely white woolly–tomentose, persistent and forming an ovoid terminal bud or sometimes all of them caducous. Figs on up to 0.6–1.2 cm long curved spurs on the older wood, up to 5 together; peduncle 0.6–1.6 cm long, densely puberulous; basal bracts 2–5 mm long, puberulous, caducous; receptacle subpyriform or subglobose, (0.8–)1.1–1.5 cm diam. when dry, glabrous or usually white tomentose, and the surface wrinkled, white to pink to purple to black at maturity, apex convex; ostiole 2–3 mm diam., upper ostiolar bract glabrous; internal hairs absent. Staminate flowers near the ostiole, sessile or pedicellate; tepals 2–3, connate, reddish brown. Pistillate flowers sessile

or pedicellate; tepals 2–3, ovate or lanceolate, sometimes connate, reddish brown; ovary dark red. Figure 2-5B.

***Distribution and Habitat*—**This species is distributed in Thailand, Cambodia, Malay Peninsula, Singapore, Indonesia (Sumatra, Java, Lesser Sunda Islands), Timor Este; in coastal forest and monsoon forest, often in rocky places, at low altitudes.

***Representative Specimens Examined*—**CAMBODIA. Without locality, Dec 1837, *Pierre 1330* (P). INDONESIA. Java: Jawa Tengah, Semarang, *Koorders 9191* (L); Pekalongan, *Koorders 13521* (L); Jawa Timur: Situbondo, Besuki (Besoeki), *Koorders 9345* (L). Nusa Tenggara Barat: Sumbawa, Sultanat Bima, 11 Dec 1909, *Elbert 3828* (L). Nusa Tenggara Timur: Flores, Wai buba, Makantarak, 19 Apr 1984, *Afriastini 1573a* (L); Sumba, J.A.J. Verheijen 4185; West Timor, 18 Jun 1926, *bb 9811* (L). Sumatra: Riau, Natuna, S of Ranai, Boengoeran, 13 Apr 1928, *van Steenis 1323* (L, SING). MALAYSIA. Kedah: Pulau Langkawi, Tanjung Burau, 17 Mar 1990, *Kamarudin FRI 31380* (K). Penang: Tanjong Tokong, 23 Jun 1937, *Henderson SFN 21413* (SING). Kelantan: Kota Bahru, 21 Apr 1937, *Corner s.n.* (SING). Pahang: Pulau Tioman, Pulau Tulai, 27 May 1927, *Nor 1855* (SING). Trengganu: Kuala Trengganu, 12 May 1892, *Holttum SFN 15234* (K, SING). SINGAPORE. Changi Rd., junction of Bedok, 22 Mar 1984, *Kiah & Leong 686* (SING). THAILAND. Chon Buri: Sattahip, Toong Brong, 9 Jun 1971, *Maxwell 71–404* (BK). Prachuap Khiri Khan: Pran Buri, Khao Sam Roi Yot National Park, 18 Aug 2002, *Middleton et al.* (BKF, L). Saraburi: Muang, Sahm Lahn forest, 17 Mar 1974, *Maxwell 74–189* (BK). Trang: Ko Kradan, 11 Feb 1966, *Hansen & Smitinand 12228* (BKF). TIMOR ESTE. Dili: Dom Aleixo, Bairro do Pité, 22 Feb 2005, *Paiva & Sousa T 625* (L).

***Notes*—**This species is usually confused with *F. subpisocarpa*, but can easily be distinguished by the densely, white woolly–tomentose stipules and the up to 5 figs on long curbed spurs (stipules puberulous, up to 4 figs on short spurs in *F. subpisocarpa*). Specimen *Verheijen 4185* from Sumba, Indonesia, shows a densely brown instead of white tomentum on the receptacle.

25. *Ficus tsjakela* Burm.f., Fl. Ind.: 227. 1768; Cooke, Fl. Bombay 2: 650. 1908; Worthington, Ceylon Trees: 417. 1959; Matthew, Fl. Tam. Carnatic 3: 1530. 1983; Manilal, Fl. Silent Valley: 260. 1988. *Tsjakela* Rheede, Hort. Malab. 3: 87, t.64. 1682, nom. inval.–*Urostigma tsjakela* (Burm.f.) Miq., London J. Bot. 6: 567. 1847.–*Ficus tjakela* (Burm.f.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867, nom. illig.; King, Ann. Roy. Bot. Gard. (Culcutta) 1: 57, t.70, t. 84X. 1887; King in Hook., Fl. Brit. India 5: 514. 1888; Fisher in Gamble, Fl. Pres. Madras: 1362. 1928.–*Ficus tsjahela* (Burm.f.) M. F. Barrett, Bull. Torry Bot. Club 37(1): 86. 1946, nom. illig.; Corner, Gard. Bull. Singapore 21: 7. 1965; Saldanha and Nicolson, Fl. Hassan Dist.: 83. 1976; Corner, Revis. Handb. Fl. Ceylon 3: 237. 1981; Nair and Nayar, Fl. Courtallum 1: 42. 1986.—TYPE: Rheede (1682) t. 64, based on *Tsjakela* Rheede.

Urostigma caulobotryum Miq., London J. Bot. 6: 568. 1847.—TYPE: INDIA. Peninsula Ind. Orientalis, Herb. *Wight KD 2638* (= no. 26) (holotype: E; isotypes: L, U).

Urostigma ceylonense Miq., London J. Bot. 6: 570. 1847.—TYPE: CEYLON. Columbo, Kiribella vel Kiripaella Cingal, 7 Apr. 1796, *Heyne* ? in herb. Arnott (holotype: K, not yet found).

Ficus infectoria Willd., Sp. Pl., ed. 4, 4 (2): 1137. 1806.—TYPE: Willdenow? (holotype: B, probably lost).

Tree up to 25 m tall. Branches drying dark brown. Leafy twigs (1.5–)3–5 mm thick, glabrous, brown, periderm persistent. Leaves articulate; lamina ovate to oblong or lanceolate 8.5–18.2 by 3.7–7.6 cm, coriaceous, apex caudate or acuminate, the acumen blunt, base cuneate, obtuse, or rounded, both surfaces glabrous and upper surface usually shining; lateral veins 8–14 pairs, the basal pair up to (1/7–)1/4–1/3 the length of the lamina, unbranched, tertiary venation reticulate; petiole 1.9–4.5 cm long, glabrous, epidermis persistent; stipules 0.5–1.5 cm long, glabrous, persistent at the shoot apex and forming a terminal bud. Figs just below the leaves or on 1–3 mm long spurs on the older wood, solitary, in pairs or up to 8 together on the spurs, sessile; basal bracts 2–2.5 mm long, glabrous, apex usually lobed, persistent; receptacle subglobose or depressed–globose, 4–7 mm diam. when dry, glabrous, apex convex or flat; ostiole 1.5–2 mm diam., upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers near the ostiole, sessile; tepals 2–3, ovate or broadly lanceolate, free, red brown. Pistillate flowers sessile or pedicellate; tepals 3–4, ovate or broadly lanceolate, free, red brown; ovary red brown.

***Distribution and Habitat*—**This species is distributed in India, Sri Lanka; in grassland, rocky hills, from sea level to ca. 1,475 m.

***Representative Specimens Examined*—**INDIA. Karnataka: Mysore, Hassan, Yettinahalla, Shiradi ghat, 5 Apr 1972, *Ramamoorthy & Gandhi HFP 2737* (K). Tamil Nadu (Madras): Nilgiris, Sep 1883, *Gamble 12915* (K); Dindigul, Kodaikanal, Shembaganur–Periakulam coolie path, 9 Feb 1985, *Matthew RHT 40999* (K); Dharmapuri, Harur, Thally, Devarbetta, 19 Mar 1980, *Matthew RHT 27128* (L); Salem, Yercad, Yercad, 26 Apr 1977, *Arockiasamy RHT 7437* (K). SRI LANKA. North Central: Anuradhapura, Ritigala Strict Natural Reserve, 9 Aug 1973, *Jayasuriya 1292* (L). Sabaragamuwa: Ratnapura, ca. 10 miles SE of Godakewela on the Pelmadulla–Hambantota Rd., 24 Nov 1974, *Davidse & Sumithraarachchi 8789* (K, L). Central: Kandy, Peradeniya, Ganoruwa hill, 6 Jun 1968, *Wirawan 615* (L, K). Western: Colombo, 12 Aug 1952, *Worthington 6000* (K).

***Note*—**There is much confusion regarding the epithet "tsjakela", "tjakela" and "tsjahela". Burman (1768), as the first author, used "tsjakela" and the name refers to Rheede's (1862) name *Tsjakela*. Therefore, King's (1887) name "*tjakela*", and Corner's (1965) "*tsjahela*" are considered to be incorrect spelling.

26. *Ficus verruculosa* Warb., Bot. Jahrb. 20: 166. 1894; Hutch., Fl. Trop. Afr. 6, 2: 114. 1916; C. C. Berg et al., Fl. Cameroun 28: 154, fig. 51. 1985; C. C. Berg, Fl. Trop. East Afr., Morac.: 63. 1989; Kirkia 13: 260. 1990; Fl. Zambes. 9, 6: 56. 1991; C. C. Berg and Wiebes, African fig trees and fig wasps: 93. 1992; F. White and Dows.–Lem., Evergreen Forest Fl. Malawi: 393. 2001.—TYPE: ANGOLA. Huila, between Monino and Eime, *Welwitsch 6375* (holotype: B; isotypes: K, P).

Ficus verruculosa Warb. var. *stipitata* Mildb. & Burret, Bot. Jahrb. 46: 206. 1911.—TYPE: CAMEROUN. Garua, *Ledermann 3417* (holotype: B).

Ficus praeruptorum Hiern, Cat. Afr. Pl. 1, 4: 1004. 1900.—TYPE: ANGOLA. *Welwitsch 6373* (holotype: BM; isotypes: B, K, P).

Shrub or small tree up to 5 m tall. Branches drying brown to dark brown. Leafy twigs 1.5–3.5(–5) mm thick, glabrous, puberulous or tomentose, periderm persistent. Leaves not articulate; lamina ovate, elliptic, oblong or lanceolate, 3.5–13.5(–20) by 1.4–5.3(–8.5) cm, coriaceous, apex (sub)acute to obtuse to rounded, base obtuse to rounded to subcordate; both surfaces glabrous, the upper surface usually shining; lateral veins 8–13(–16) pairs, the basal pair up to (1/10–)1/6–1/3 the length of the lamina, unbranched, tertiary venation reticulate, partly parallel to lateral veins; petiole 0.4–2(–3) cm long, glabrous or minutely puberulous, epidermis persistent; stipules 0.3–1.5 cm long, glabrous or puberulous, persistent at the shoot apex and forming a terminal bud or caducous. Figs axillary, just below the leaves or on short spurs on the older wood, solitary or in pairs or up to 4 together on the spurs; peduncle 0.2–0.5 cm long, glabrous or puberulous; basal bracts 1–1.5 mm long, glabrous or puberulous, persistent; receptacle subglobose, 0.5–1 cm diam. when dry, glabrous or minutely puberulous, surface wrinkled when dry, dark purple to dark red at maturity, apex flat or convex; ostiole ca. 2 mm diam., upper ostiolar bracts ciliate; internal hairs absent. Staminate flowers near the ostiole, sessile; tepals 2–3, ovate or spathulate, free, reddish brown. Pistillate flowers sessile or pedicellate; tepals 2–3(–4), ovate or lanceolate, sometimes connate at the base, reddish brown; ovary red brown.

***Distribution and Habitat*—**This species is distributed in Guinea, Benin, Nigeria, Cameroon, Chad, Congo, Angola, Namibia, South Africa, Botswana, Zambia, Zimbabwe, Uganda, Rwanda, Burundi, Kenya, Tanzania, Malawi, and Mozambique; in open grassland and areas with rocky woodland, along streams or in swamps as a low bush, altitudes up to 1,200 m.

Representative Specimens Examined—ANGOLA. Benguella, Bailundo, *Wellman 1906* (K). Huila, between Monino and Eime, *Welwitsch 6375* (B, K). Malange, 1905, *Gossweiler 1006* (K). BENIN. Atakora: Natitingou, Taneka–Koko, R. Taneka, 1° 30.95' E, 9° 52.48' N, 27 Jan 2006, *van der Maesen 7587* (WAG). BOTSWANA. Ngamiland: Moremi Wildlife Reserve, Gadikwe Isl., 30 Jul 1984, *Barker & Reid 35* (K). BURUNDI. Bururi: Buranga (Dunga), 29° 54' E, 4° 09' S, 20 Oct 1977, *Reekmans 6548* (K, WAG). Kirundo: Kanyinya, lake Oiseaux, 10 Dec 1967, *Lewalle 2494* (K). Ruyiki: Bukemba, Mosse, 30° 10' E, 3° 55' S, 11 Jun 1976, *Reekmans 5279* (WAG). CAMEROON. Northwest: Bamenda, 1958, *Hepper 2074* (K). North, ca. 10 km. S of Garoua, 18 Dec 1964, *de Wilde & de Wilde–Duyfjes 4987* (K, WAG). CHAD. Chari oriental: Ndelle, 17–20 Dec 1902, *Chevalier 6866* (K). CONGO. Katanga: Lubumbashi, 8 km de Lubumbashi, Sep 1951, *Schmitz 3655* (K). GUINEA. Faranah: Dinguiraye, Dec 1936, *Jacques–Félix 1485* (P). KENYA. Western: Kitale, 13 May 1953, *Bogdan 3733* (K). MALAWI. Central: Ntchisi, Ntchisi forest reserve, 14 Apr 1991, *Radcliffe–Smith 5982* (K, WAG). North: Mzimba, Mzuzu, Lunyangwa R., 11 Oct 1973, *Pawek 7369* (K, WAG). MOZAMBIQUE. Maputo: Zitrundo and Ponta do Ouro, 31 Jan 1979, *Schäfer 6680* (K, WAG). Tete: Fingee, Nhimbe, Camarira R., 19 Aug 1976, *Macuácua & Costa 213* (WAG). NAMIBIA. Okavango: Omurumba Omatago at Kapupahedi Camp, 17 Feb 1956, *de Winter & Marais 4750* (K). NIGERIA. Niger: Kontagora, 26 Nov 1905, *Barter 1317* (K). RWANDA. Northern: Byumba, Marais Kajumbura, Akagara National Park, 30 Mar 1973, *Troupin 14898* (K). SOUTH AFRICA. Near Kaukanje, 26 Sep 1959, *Kirk s.n.* (K). TANZANIA. Rukwa: Sumbawanga, ca. 2 km SW from the junction with the Sumbawanga–Mbala (Zambia) Rd., on the road to Safu, 31° 29' 27" E, 08° 34' 54" S, 14–15 Nov 1993, *Schmidt et al. 1173* (K). Ruvuma: Songea, 12 km E of Songea by Nonganonga stream, 28 Dec 1955, *Milne–Redhead & Taylor 7946* (K). UGANDA. Central: Masaka, SW side of lake Nabukabo, 7 Oct 1953, *Drummond & Hemsley 4669* (K). ZAMBIA. Lusaka, Kalundu, 16 Dec 1976, *Bingham 2124* (U). Northwestern: Solwezi, stream W of Inutanda bridge, 4 Jul 1930, *Milne–Redhead 668* (K). Western: Mongu, Namushakende, 23°13' E, 15°25' S, 19 Feb 1999, *Bingham & Luwiika 11907* (K). ZIMBABWE. Manicaland: Mutare (Umtali), farm on road to Hondi valley, 23 Feb 1949, *Chase 1380* (K). Mashonaland Central: Guruve(Sipolilo), 28 Sep 1978, *Nyariri 380* (K, U). Matabeleland North: Wankie (Hwange), Wankie special nature area A, Aug 1956, *Davies 2060* (K).

27. *Ficus virens* Aiton, Hort. Kew. 3: 451. 1789; Corner, Gard. Bull. Singapore 17: 376. 1960; 21: 9. 1965; Backer & Bakh.f., Fl. Java 2: 35. 1965; Corner, Rev. Handbook Fl. Ceyl. 1, 2: 128, t. 7. 1977; Kochummen, Tree Fl. Malaya 3: 161. 1978; Tree Fl. Sabah & Sarawak 3: 316. 2000; C. C. Berg and Corner, Fl. Males. Ser. 1, 17 (2): 614. 2005.—TYPE: Introduced to Kew about 1762 by James Gordon (holotype: BM).

Ficus pilasbi Sm. in Rees, Cycl. 14: n. 3. 1810.—TYPE: NEPAL. Narian Hetty, Dec 1802, *Buchanan s.n.*, .(holotype: K, photograph).

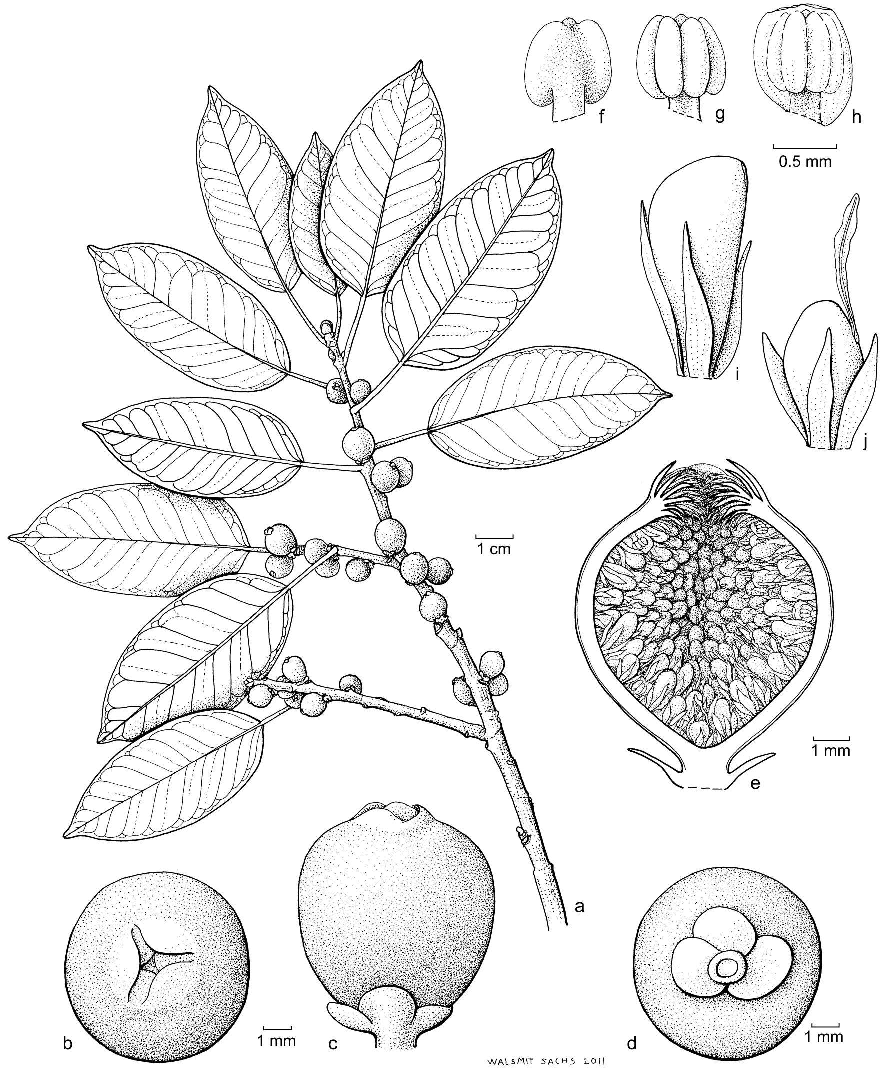

FIGURE 2-8. *Ficus virens* Aiton var. *dispersa* Chantaras. (Moraceae).–a. Twigs with leaves and figs; b. Ostiole; c. Fig; d. Basal bracts; e. Fig in longitudinal section; f. Stamen (back side); g. Stamen (front side); h. Staminate flower with connate tepals; i, j. Pistillate flowers. [*A. Floyd NGF 6457* (L)]. Drawing: Anita Walsmit Sachs, 2011.

Ficus infrafoliacea Sm. in Rees, Cycl. 14: n. 31. 1810.—TYPE: NEPAL, *Buchanan s.n.* (holotype: K, photograph).

Ficus infectoria Roxb., Hort. Bengal.: 66. 1814., excl. syn. Rheede t. 64, non Willd. 1806; Roxb., Fl. Ind., ed. Carey 3: 551. 1832; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 264. 1867; Kurz, Forest Fl. Burma 2: 446. 1877; King, Ann. Roy. Bot. Gard. (Culcutta) 1: 60, t. 75–78. 1887; F. M. Bailey, Queensl. Fl. 5. 1474. 1902; Ridl., Fl. Malay Penins. 3: 337. 1924; Gagnep. in Lecomte, Fl. Indo–Chine 5: 760. 1928.–*Urostigma infectorium* (Roxb.) Miq., London J. Bot. 6: 566. 1847; in Zoll., Syst. Verz. 2: 90. 1854; Fl. Ind. Bat 1, 2: 339. 1859.–TYPE: *Willdenow 1137* (holotype: K).

Ficus terminalis B. Heyne ex Roth in Roem. and Schult., Syst. Veg. 1: 513. 1817.—TYPE: INDIA. India orientali legio, *Heyne 1814* (isotype: L).

Ficus scandens Buch. –Ham., Trans. Linn. Soc. 15: 149. 1826., non Lam. 1788.—TYPE: ad Matsiae pagos; information based on Berg and Corner 2005 (not found yet).

Ficus lacor Buch. –Ham., Trans. Linn. Soc. London, Bot. 15: 150. 1827.—TYPE: Herb. F. (Buchanan) *Hamilton 2406* (holotype: E).

Urostigma cunninghamii Miq., London J. Bot. 6: 560. 1847.–*Ficus cunninghamii* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867; Benth., Fl. Austral. 6: 286. 1873; F. M. Bailey, Queensl. Fl. 5: 1468. 1902.–*Ficus infectoria* Roxb. var. *cunninghamii* (Miq.) Domin, Bibl. Bot 89: 562. 1921.–*Ficus lacor* Buch.–Ham. var. *cunninghamii* (Miq.) M. F. Barrett, Amer. Midl. Nat. 36: 422. 1946.—TYPE: AUSTRALIA. Queensland, Brisbane River, *Cunningham s.n.* (holotype: K).

Urostigma fraseri Miq., London J. Bot. 6: 561. 1847.–*Ficus caulobotrya* Miq. var. *fraseri* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867.–*Ficus fraseri* (Miq.) F. Muell., Fragm. Phyt. Austral. 6: 195. 1868, non Miq. 1848.–*Ficus infectoria* Roxb. var. *fraseri* (Miq.) Domin, Bibl. Bot. 89: 562. 1921.—TYPE: AUSTRALIA. Queensland, Bremer River, 1829, *Fraser 704* (holotype: K).

Urostigma psychotriifolium Miq., London J. Bot. 6: 561. 1847.–*Ficus psychotriifolia* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867.–*Ficus infectoria* Roxb. var. *psychotriifolia* (Miq.) Domin, Bibl. Bot. 89: 562. 1921.—TYPE: AUSTRALIA. Queensland, Brisbane River, 1829, *Fraser 73* (holotype: K).

Urostigma aegeirophyllum Miq., London J. Bot. 6: 565. 1847.–*Ficus infectoria* Roxb. var. *aegeirophylla* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867.—TYPE: INDIA. Bengal, *J. D. Hooker s.n.* (holotype: K).

Urostigma lambertianum Miq., London J. Bot. 6: 565. 1847.–*Ficus lambertiana* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867.–*Ficus infectoria* Roxb. var. *lambertiana* (Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: 60, t. 75–78. 1887.–*Ficus lacor* Buch. –Ham. var. *lambertiana* (Miq.) M. F. Barrett, Amer. Midl. Nat. 45: 153.1951.—TYPE: INDIA. Bombay, *Lambert in herb. Hooker* (holotype: K).

Urostigma wightianum Wall. ex Miq., London J. Bot. 6: 566. 1847.–*Ficus wightiana* (Wall. ex Miq.) Benth., Fl. Hongk.: 327. 1861; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867.–*Ficus infectoria* Roxb. var. *wightiana* (Wall. ex Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: 60, 63, t. 75–77. 1887.—TYPE: INDIA. Bongaloor, *Wallich 4540* (Herb. Wight.) (holotype: K; isotype: E).

Urostigma perseifolium Miq., London J. Bot. 6: 567. 1847.—SYNTYPES: Ind. Or., Pulney mountains, Wight KD 2635(syntype: E); 1836, *Wight KD 3060* (syntype: L).

Urostigma timorense Miq., London J. Bot. 6: 569. 1847, non *F. timorensis* Decne. 1834.; Miq., Fl. Ind. Bat. 1, 2: 343. 1859.–*Ficus timorensis* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867.—TYPE: TIMOR. *Herb. Hook.*, (holotype: K).

Urostigma apiculatum Miq., London J. Bot. 6: 570. 1847.–*Ficus apiculata* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867, non Miq. 1854.—TYPE: INDIA. *Wight 1916* (isotype: E).

Ficus terminalioides Griff., Post. Pap. 2: n. 101. 1848; Ic. Pl. Asiat. 4: t. 550. 1854.—TYPE: BHUTAN, no locality, not indicated. (holotype: K, not found yet).

Urostigma moritzianum Miq. in Zoll., Syst. Verz. 2: 91, 97. 1854; Fl. Ind. Bat. 1, 2: 342. 1859.—TYPE: INDONESIA. Java, Bandung, *H. Zollinger 851* (holotype: U).

Urostigma nesophilum Miq., J. Bot. Neerl. 1: 237. 1861.–*Ficus nesophila* (Miq.) F. Muell., Austral. Veg. (Intercol. Exhib. 1866/1867) 5: 26. 1866; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 268, 286. 1867.–*Ficus glabella* Blume var. *nesophila* (Miq.) K. Schum., Fl. Schutzgeb. Südsee: 273. 1900.—TYPE: AUSTRALIA. Quail Island, *Flood s.n.* (holotype: K).

Ficus monticola Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 216, 286. 1867.—TYPE: INDIA. Mont Khasia, *J. D. Hooker and T. Thomson* (*Ficus* no. 121) (holotype: P; isotype: L).

Ficus saxophila Blume var. *sublanceolata* Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 260. 1867.–*Ficus virens* Aiton var. *sublanceolata* (Miq.) Corner, Gard. Bull. Singapore 17: 377. 1960; Chew, Fl. Australia 3: 35. 1989.—TYPE: INDONESIA. Sumatra, 1859–1860, *W. H. de Vriese and J. E. Teijsman s.n.* (holotype: K; isotype: L).

Ficus glabella Blume forma *grandifolia* Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 267. 1867.—TYPE: INDONESIA. Sumatra, Mandheling, 1857–1861, *W. H. de Vriese s.n.* (isotype: L).

Ficus infectoria Roxb. var. *forbesii* King, Ann. Roy. Bot. Gard. (Culcutta) 1: 63, t. 78. 1887.—TYPE: INDONESIA. Sumatra, *H. O. Forbes 2701* (holotype: K; isotype: L).

Ficus syringifolia C. Fraser ex C. Moore, Handb. N.S.W.: 81. 1893, non Kunth and C. D. Bouché 1847.—TYPE: AUSTRALIA. Brisbane river, Jul 1855, *F. van Mueller s.n.* (holotype: K).

Ficus carolinensis Warb. in K. Schum. and Lauterb., Nachtr. Fl. Schutzgeb. Südsee: 242. 1905; Volkens, Bot. Jahrb. Syst. 31: 462. 1902.–*Ficus prolixa* G. Forst. var. *carolinensis* (Warb.) Fosberg, Phytologia 5: 289. 1955.—TYPE: CAROLINE ISLANDS. Yap, *Volkens 263* (holotype: B).

Ficus nitentifolia S. Moore, J. Bot 63, Suppl.: 107. 1925.—TYPE: INDONESIA. Timor, *S. Moore 3618* (holotype: BM; isotype: L).

Tree up to 35 m tall. Leafy twigs 1–5 mm thick, glabrous or puberulous, periderm persistent or sometimes flaking off. Leaves articulate; lamina ovate to elliptic to lanceolate to obovate, 5.2–18.5(–20) by 2.5–8.5(–9.5) cm, (sub) coriaceous, apex (sub)acuminate, acute, or obtuse, base cuneate, cordate, obtuse, or subattenuate, both surfaces glabrous; lateral veins 8–12(–15) pairs, sometimes furcate away from the margin, the basal pair up to 1/10–1/5(–1/2) the length of the lamina, unbranched or sometimes branched, tertiary venation reticulate to subscalariform; petiole 1.6–6.1 cm long, glabrous, epidermis persistent; stipules 0.25–1.5 cm long, glabrous, puberulous or white tomentose or villose, caducous or sometimes persistent at the shoot apex and forming an ovoid terminal bud. Figs axillary, just below the leaves, or on up to 0.5 cm long spurs on the older wood, solitary, in pairs, or up to 4 together on the spurs, sessile or with a peduncle up to 2.5(–10) mm long, glabrous or minutely puberulous; basal bracts 1.5–4 mm long, covering only the base of the receptacle, glabrous or (minutely) puberulous, persistent; receptacle subglobose (or depressed–globose), 0.4–1.5 cm diam. when dry, surface usually wrinkled, glabrous or minutely puberulous at the apex to white tomentose or villose, turning from white to pink, purple, or black at maturity, apex convex to flat; ostiole (1–)2–4 mm diam., the upper ostiolar bracts glabrous or puberulous; internal hairs present. Staminate flowers near the ostiole or dispersed, sessile or with a short pedicel; tepals 3–4(–5), ovate

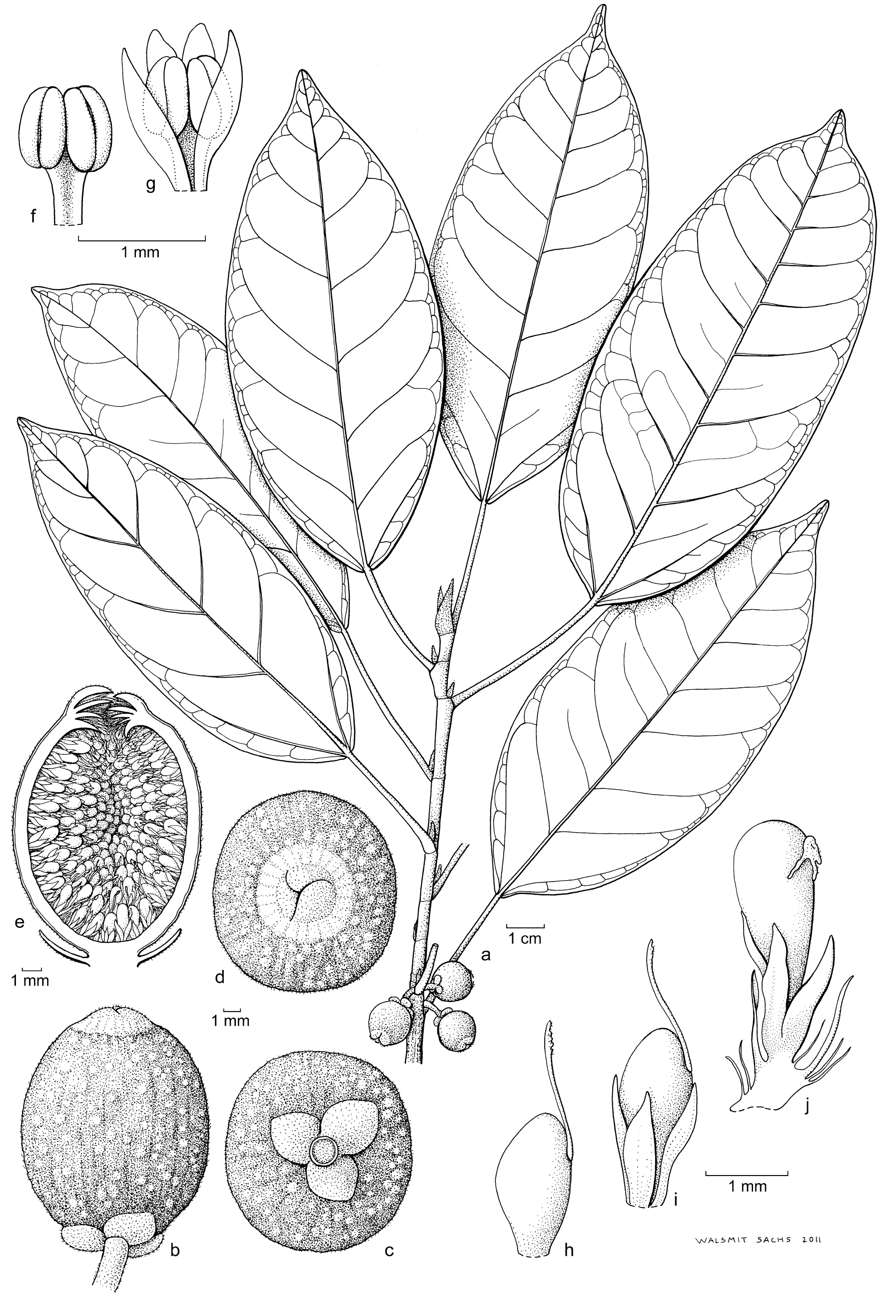

FIGURE 2-9. *Ficus virens* Aiton var. *matthewii* Chantaras. (Moraceae).–a. Twig with figs; b. Fig; c. Basal bracts; d. Ostiole; e. Fig in longitudinal section; f. Stamen; g. Staminate flower with free tepals; h. Ovary; i, j. Pistillate flowers. [*K. M. Matthew RHT 50937* (L)]. Drawing: Anita Walsmit Sachs, 2011.

or lanceolate, or sometimes connate, reddish brown. Pistillate flowers sessile or pedicellate; tepals 3–4(–5), lanceolate, free or sometimes connate, reddish brown; ovary red brown.

Note—Aiton (1789) thought that the type of *F. virens* was introduced from the West Indies in Kew about 1762 by James Gordon, but Corner (1959) believes that Aiton was erroneous. Up to now, the origin of the type is still unclear.

27.1 ***Ficus virens*** Aiton var. ***virens***: Corner, Gard. Bull. Singapore 21: 9. 1965; Chew, Fl. Australia 3: 35. 1989.

Lamina usually broadest below the middle; base (sub)cordate, cuneate, obtuse, or subattenuate; lateral veins usually furcate away from the margin, basal lateral veins up to 1/8–1/4(–1/2) the length of the lamina, usually branched; stipules 0.25–1.1 cm long, glabrous or puberulous. Figs axillary, just below the leaves, or on short spurs, solitary or in pairs; basal bracts 1.5–3 mm long, minutely puberulous, margin ciliate, apex usually lobed; receptacle 0.4–0.9(–1.2) cm diam. when dry, glabrous or puberulous; ostiole (1–)2–3 mm diam., upper ostiolar bracts puberulous. Staminate flowers near the ostiole, tepals free.

Distribution and Habitat—This variety is distributed in North India, Nepal, Sri Lanka, Bhutan, China (Prov. Yunnan, Hainan, Hong Kong), Myanmar, Thailand, Peninsular Malaysia, Indonesia (Sumatra, Java, Sulawei, Lesser Sunda Islands, Moluccas), Laos, Vietnam, Micronesia, Timor Este, Papua New Guinea, and Australia; in open secondary shrubbery on calcareous soil, in evergreen forest or deciduous forest.

Representative Specimens Examined—AUSTRALIA. New South Wales: Sydney, Rose Bay, 12 Nov 1975, *Marchant 12275* (L). Northern Territory: Sir Edward Pellew Group, 136˚ 49' E, 15˚ 43' S, 10 Feb 1976, *Craven 3812* (L). Queensland: Atherton, 143˚ 25' E, 13˚ 50' S, 10 Sep 1973, *Hyland 6850* (L). Western Australia: Buccaneer Archipelago, Long isl., 16˚ 33' 31" S, 123˚ 22' 30" E, 15 Jun 1982, *Hopkins BA0176* (PERTH); Dampier archipelago, Dampier isl., Dec 1986, *Glennon 307* (PERTH); Boiga falls, Drysdale River National Park, 15˚ 08' S, 127˚ 06' E, 3 Aug 1975, Kimberley & Kenneally 3006 (PERTH). BHUTAN. Without locality, 1838, *Griffith KD 4613* (K). CHINA. Hainan: Yaichow, March–July 1933, *How 70848* (L). Hong Kong: Fanling–Sheung Shui, 1 Oct 1973, *Chan 1236* (K). Yunnan: West Yunnan, Tali range, 25˚40' N, Jun 1906, *Bulley 4704* (K). INDIA. Andhra Pradesh: Kadapa (Cuddapah), Feb 1883, *Gamble 10784* (K). Jarkhand: Singbhum, 11 Jan 1903, *Haines 588* (K). Odisha (Orissa): Ganjam, Balirai, Feb 1884, *Gamble13843* (K). Rajastan: Tonk, Toda Rai Singh, 22 Sep 1974, *Shetty 1304* (L). West Bengal: Chota–Nagpore Plateau, Dec 1880, *Gamble 8829* (K). NEPAL. Upper Nepal, without locality, *Smith s.n.* (K). INDONESIA. Bali: near Singaraja, 21 Jun 1976, *Meijer 10575* (L). Jawa Barat: Preanger, *Koorders 9161* (L). Jawa Tengah: Semarang, *Koorders 9204* (L); Pekalongan, *Koorders*

22473 (L). Jawa Timur: Wana wisata Coban Rondo, Pujon Malang, 6 Sep 1980, *Wiriadinata 2037* (L). Maluku: 1859–1860, *de Vriese & Teijsmann s.n.* (L). Nusa Tenggara Barat: Sumbawa, Sultanat Bima, Kologebirge, 8 Dec 1909, *Elbert 3668* (L). Nusa Tenggara Timur: Flores, Flores–Manggarai, 1 Nov 1979, *Schmutz 4262a* (L); Sumba, 29 Jul 1974, *Verheijen 4180* (L); West Timor, *Teysmann 7095* (L); Alor, Kgbola Peninsula, Adang–Jabandar–Alor ketjil, 1938, *Jaag 442* (L). Sumatra Barat: Mt. Sago, near Pajakumbuh, above Padang Mengatas, 8 Aug 1957, *Meijer 7196* (L). Sulawesi Tengah: Halfway Palu and Donggala, Lolu Pertamina, km 27, ca. 119˚ 45' E, 0˚ 45' S, 22 Apr 1979, *de Vogel 5016* (L). LAOS. Champasak: Khong, on Isl. and in Mekong R., 28 Apr 1998, *Maxwell 98–492* (L). Saravan: N of Saravan, 4 Aug 1928, *Poilane 15448* (P). MALAYSIA. Kedah: Langkawi, Pulau Chupah, 19 Nov 1941, *Corner SFN 37819* (L, SING). Penang: Nov 1937, *Henderson 257* (SING). MICRONESIA. Caroline Islands, Yap, Nov 1899–Jun 1900, *Volkens 445* (SING). MYANMAR. Bago (Pegu): 15 Aug 1892, *Kurz 3136* (K). Tanintharyi (Tenasserim): 1877, *Gallatly 982* (L). PAPUA NEW GUINEA. Central: W side of Waigani swamp, 8 Aug 1971, *Frodin 533* (L); Yule Isl., ca. 105 km NW of Port Moresby, 25 Sep 1980, *Salmang s.n.* (L). East Sepik: Angoram, Karawari R., 143˚ 35' E, 4˚ 40' S, 29 Jul 1967, *Millar & Dockrill NGF 35163* (K, L, SING). Morobe: Chivasing, 17 Dec 1959, *Henty NGF 11652* (K, L, SING). Western: Daru, Tanglide near Kunini, 143˚ 21' E, 9˚ 30' S, 9 May 1986, *Simaga 733* (L). SRI LANKA. Central: Kandy, along Mahaweli Ganga, Feb 1979, *Kostermans 27369* (L). North Central: Anuradhapura, Ritigala Strict Natural Reserve, 9 Aug 1973, *Jayasuriya 1312* (L). North Western: Kurunegala, 3 Jun 1973, *Kostermans 24939* (L). THAILAND. Chaiyaphum: Muang, Nafaii, Ban–Huagmarkdang, 15 Jan 1970, *Lekagul 64* (BKF). Chiang Mai: Chiengdao, Doi Chiengdao, 8 Apr 1940, *Garrett 1184* (A, L). Kanchanaburi: Huay Bankau, 90˚ 45' E, 14˚ 55' N, 10 Nov 1971, *van Beusekom et al. 3661* (BKF, L). Narathiwat: Waeng, Ban Bala, 7 Nov 2002, *Chantarasuwan 2002–0454* (BKF, THNHM). TIMOR ESTE. W of Díli, Tasitolu, 08˚ 33' 39" S 125˚ 30' 34" E, 26 Sep 2005, *Cowie 10650* (L). VIETNAM. Ninh Thuan: S of Phan rang, 11–14 Jun 1909, *d'Alleizette s.n.* (L). Quang Tri: 18 Mar 1917, *Poilane 13639* (L).

Note—We found this variety to be the most variable taxon in all morphological characters, e.g. (1) leaf size: smallest (*Schmutz SVD 4030*, Flores), 4.1–7.5 by 1.5–3 cm, largest (*Delavay s.n.*, Yunnan)13–21 by 5.6–9.5 cm; (2) Peduncle; sessile to up to 1 cm long in Shetty 1304 (India); (3) Diameter of receptacle; smallest (*Corner SFN 37819*, Lankawi) 0.4–0.5 cm diam., largest (*Wight KD 2635*, India) 1.1–1.2 cm diam.; and (4) Most receptacles are glabrous, but *Wiriadinata 2037* (Java) is pubescent.

27.2 ***Ficus virens*** Aiton var. ***dispersa*** Chantaras., var. nov.–TYPE: PAPUA NEW GUINEA. New Britain: West Nakanai, Rapuri village near Cape Hoskins, probably 5 Aug 1954, *A. Floyd NGF 6457* (holotype: L; isotypes: K, LAE)

Stipulae gemmas ovoideas terminales formantes, epidermis desquamarans. Flores masculi aut numerosi tum prope ostiolum pauci dispersi aut interdum pauci et tantum prope ostiolum.

Lamina ovate to lanceolate, base cuneate to round to subcordate; basal pair of veins up to 1/6–1/4(–1/3) the length of the lamina, sometimes branched; petiole 1–3(–5.5) cm long, epidermis persistent; stipules 0.3–0.9 cm long, glabrous or puberulous, forming an ovoid terminal bud, epidermis of bud scales flaking off. Figs axillary, just below the leaves, or on short spurs, solitary or in pairs; basal bracts 2–3 mm long, glabrous or minutely puberulous, apex usually lobed; receptacle 0.5–0.9 cm diam. when dry; ostiole 2–2.5 mm diam., upper ostiolar bracts glabrous. Staminate flowers abundant around the ostiole and a few dispersed or a few near the ostiole only; tepals usually connate. Figure 2-8.

Distribution and Habitat—This variety is distributed in Malaysia (Sabah), Indonesia (Borneo, Moluccas, Papua), Timor Este, Papua New Guinea, East Australia, Solomon Isl., New Caledonia, Vanuatu, and Micronesia; in rain forest, swamp forest, at low altitudes or up to 1,600 m in New Guinea.

Representative Specimens Examined—AUSTRALIA. Queensland: Atherton, State Forest Reserve, 145° 47' E, 17° 15' S, 16 Dec 1980, *Gray 1865* (K, L). INDONESIA. Kalimantan Timur: 117° 20' E, 0° 30' N, East Kutai Reserve, vicinity of Sengata and Mentoko R., 23 Feb 1979, *Leighton 527* (L). Maluku: Buru, NW Buru, Wae kosi, 3 Nov 1984, *Nooteboom 5081* (L). Papua: Mamberamo R., 1974, *Sauveur 3394* (L). MALAYSIA. Sabah: Dahad Datu, Ulu Sg. Segama, Orchid Plateau, 11 Jul 1970, *Cockburn SAN 70907* (L). MICRONESIA. Kusaie: Lela (Lele) Isl., Lela (Lele) Harbor, 19–21 Aug 1946, *Fosberg 26534* (L). Pohnpei (Ponape): Roi–pa, 29 Feb 1936, *Takamatsu 928* (K). Yap: Balabat, 17 May 1936, *Takamatsu 1880* (K). NEW CALEDONIA. Loyalty Isl.: Maré, Loy, 16 Jul 1951, Baumann–Bodenheim 14701, *14707* (L). South: Dumbea, Estuary of Dumbea R., 22 Apr 1956, *McKee 4466* (L). PAPUA NEW GUINEA. Bougainville: Buin, lower S slopes of lake Loloru crater, ca. 15 miles N of Buin, 30 Jul 1964, *Craven & Schodde 159* (L). Chimbu: E Highlands, 14 Aug 1957, *Robbins 653* (L). East Sepik: along Tiyangaram (Black R.), S of Ambunti, 21 Jun 1966, *Hoogland & Craven NGF 10326* (L). Morobe: near Piera, about 10 miles SE of Garaina, 19 Jan 1964, *Hartley TGH 12628* (L). SOLOMON ISLANDS. New Georgia: 29 Aug 1929, *Waterhouse 315* (K, L). Santa Isabel: Tiratona, 26 Nov 1932, *Brass 3224* (K, L). TIMOR ESTE. Dili: Nein Feto, 16 Jan 2004, *Paiva & Silveira T33* (L). VANUATU. Uri: Malekula, Selenamboro, 9 Nov 1992, *Curry 769* (L).

Note—Typical for this variety is the presence of a few staminate flowers dispersed througout the fig instead of only numerous staminate flowers around the ostiole. In this respect it resembles *F. prolixa*, but most characters are consistent with *F. virens*.

27.3 Ficus virens Aiton var. ***glabella*** (Blume) Corner, Gard. Bull. Singapore 17: 377. 1960.–*Ficus glabella* Blume, Bijdr.: 452. 1825; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 265, 286. 1867; King, Ann. Roy. Bot. Gard. (Culcutta) 1: 49, t. 60. 1887; in Hook.f., Fl. Brit. India 5: 511. 1888; Merr., Enum. Born.: 223. 1921; Ridl., Fl. Malay Penins. 3: 336. 1924; K. Heyne, Nutt. Pl. Ned.–Indië: 571. 1927; Gagnep. in Lecomte, Fl. Indo–Chine 5: 759. 1928; Burkill, Dict. Econ. Prod. Malay Penins.: 1009. 1935; Corner, Wayside Trees 1: 677. 1940; Blumea 6: 308. 1948.–*Urostigma glabellum* (Blume) Miq., Fl. Ind. Bat. 1, 2: 340. 1859; Fl. Ind. Bat., Suppl.: 437. 1961.—TYPE: INDONESIA. Java, Kiara beas, *Blume s.n.* (holotype: L; isotype: P).

Urostigma canaliculatum Miq., London J. Bot. 6: 579. 1847; Fl. Ind. Bat. 1, 2: 340. 1859.—TYPE: AUSTRALIA. Prince of Wales Island, *Hb. Hooker* (holotype: K; isotype: E).

Lamina mostly obovate or elliptic; base cuneate or subattenuate; basal lateral veins up to 1/6–1/4 the length of the lamina, unbranched; petiole 1.6–2.5 cm long, epidermis usually persistent; stipules 0.2–0.7 cm long, glabrous or puberulous, usually forming an ovoid terminal bud, epidermis of bud scales usually flaking off. Figs axillary, just below the leaves, or on 3–4 mm long spurs, solitary, in pairs, or up to 3 together on spurs; basal bracts 1.5–2 mm long, glabrous; receptacle 0.6–0.8 cm diam. when dry, glabrous or puberulous; ostiole (1–)2–3 mm diam., upper ostiolar bracts glabrous. Staminate flowers near the ostiole; tepals connate. Figure 2-5G.

Distribution and Habitat—This variety is distributed in Thailand, Vietnam, Malaysia, throughout Indonesia, Philippines, Timor Este, Papua New Guinea and Australia; in evergreen forest, deciduous forest, or secondary forest, at altitudes up to 800 m.

Representative Specimens Examined—INDONESIA. Jawa Tengah: Semarang, Karangasem, *Koorders 9266* (L); Pekalongan, *Koorders 22585* (L); Banjumas, *Koorders 9290* (L); Djapara, *Koorders 35708* (L); Tegal, *Koorders 9257* (L). Jawa Timur: Besoeki, *Koorders 38937* (L); Kediri, *Koorders 22785* (L); Madioen, *Koorders 38816* (L); Madura, *Koorders 21924* (L). Kalimantan Timur: Kutei, Susuk region, 2 Jul 1951, *Kostermans 5601* (L, SING). Maluku: Ambon, Waai, 31 Oct 1931, *Bank 600* (L); Morotai, Totodoku, 3 Jun 1949, *Kostermans 7870* (L, SING); Seram, 1859–1860, *Teijsmann s.n.* (L). Nusa Tenggara Timur: West Flores, S part of Mt. Ndeki, 14 Apr 1965, *Kostermans & Wirawan 250* (L); South Sumba, 12 Feb 1974, *Verheijen 3867* (L). Papua: near Jayapura, *Kostermans & Soegeng 831* (K, L); Jayawijaya, Angguruk area, 6 Jun 1975, *Sinke 63* (L). Sulawesi Selatan: S shore of Laka Matano, W of Soroako and Taipa, Pulau Lintu, 121° 15' E, 2° 29' S, 23 Jun 1979, *de Vogel 5942* (L). Sumatera Selatan: Bangka–Belitung, Sungai Liat, *Teysmann HB 6848* (L). MALAYSIA. Johore: Mawai, 13 May 1934, *Corner s.n.* (SING). Kedah: Rawei Isl., Aug 1911, *Ridley 15723* (SING). Perak, Larut, Sep

1883, *King 4884* (L). Sarawak: Kuching, Bau, Bau Rd. 19th mile, 26 Jun 1960, *Anderson 12734* (L). Trengganu: Dungun–Marang Rd. 37 ½ –38th miles, *Sinclair 39982* (L). PAPUA NEW GUINEA. Chimbu: E Highlands, near Wahgi R., S of Kundiawa, 14 Aug 1957, *Robbins 653* (L). Milne bay: Baniara, E of Nowata airstrip, 149˚ 44' E, 9˚ 59' S, 2 Jul 1969, *Kanis 1109* (L). Morobe: 19 Nov 1935, *Clemens 959* (L). PHILIPPINES. Abra: Banglas R., Gangal, Municipality of Sallapadan, 120˚ 49.6' E, 17˚ 28.0' N, 20 Nov 1996, *Fuentes PPI 38669* (K, L). Palawan: Mt. Pulgar, Apr 1911, *Elmer 13002* (K, L). Quezon: Tayabas, Jan 1884, *Vidal 909* (K). SINGAPORE. Tanglin post office, 22 Jun 1937, *Corner SFN 33565* (L). THAILAND. Nakhon Nayok: Muang, Khlong Sai, Khao Yai National Park, 101˚ 23' E, 14˚ 24.5' N, 19 Feb 1999, *Charienchai 742* (L). Phuket: Thalang, Khao Phra Tao Non–Hunting area, 98˚ 23' E, 8˚ 02' N, 21 Apr 2006, *Gardner ST 2606* (L). Songkhla: Rattapoom, Boripat Falls National Park, 2 Apr 1985, *Maxwell 85–364* (E, L). TIMOR ESTE. Ira Malaru: near Los Palos, 127˚ 04' 58" E, 08˚ 24' 00" S, 6 Oct 2005, *Cowie & Xavier 10841* (L). VIETNAM. Kontum: between Takha and Pakto, 13 Mar 1941, *Poilane 32314* (L).

***Note*—**Corner (1965) mentions that the Australian *Urostigma* canaliculatum Miq. is a synonym of *Ficus virens* Aiton var. *glabella*. However, so far no Australian specimens were found, thus we follow Corner with caution as the type specimen is not (re)found yet.

27.4 ***Ficus virens*** Aiton var. ***matthewii*** Chantaras., var. nov.—TYPE: INDIA. Tamil Nadu (Madras), Dist. Dindigul, Anna, Pachalur, below village, 1 Nov 1987, *K. M. Matthew RHT 50937* (holotype: L; isotypes: RHT, SHC).

Stipulae (albae) tomentosae gemmas ovoideas terminales et anguste ovoideas axillares formantes; receptaculum subglobosum vel subpyriforme (1.1–)1.2–1.5 cm diam. iin sicco pagina maculata rugosa in sicco.

Lamina usually broadest in the middle to below the middle; base cuneate to subattenuate to obtuse to (sub)cordate; basal lateral veins up to 1/6–1/4 the length of the lamina, sometimes branched; stipules 1.1–1.5 cm long, persistent at the shoot apex and forming a narrowly ovate terminal bud, (white) tomentose; usually forming an axillary bud. Figs axillary or below the leaves, solitary or in pairs; basal bracts 3–4 mm long, puberulous; receptacle (1.1–)1.2–1.5 cm diam. when dry, surface maculate and wrinkled when dry, glabrous, puberulous, or sometimes white tomentose; ostiole 3.5–4 mm diam., upper ostiolar bracts hairy. Staminate flowers near the ostiole; tepals connate. Figure 2-9.

***Distribution and Habitat*—**This variety is distributed in South India and Sri Lanka; in evergreen forest, at altitudes up to 1,300 m.

***Representative Specimens Examined*—**INDIA. Kerala: Kerala shoals, Devicolam–Periyar Rd., Cardamom hill, *Ridsdale 722* (L). Tamil Nadu (Madras): Dindigul, Pachalur, 1 Nov 1987, *Matthew RHT 50937* (L); Kodai kanal, Thadiankudisai–Adabur Rd., 4 Aug 1988, *Matthew RHT 53333* (L); Salem, Attur, Periakalrayans, Nagalur Forest, 10 Mar 1980, *Matthew RHT 26955* (L). SRI LANKA. North Central: Anuradhapura, Ritigala Strict Natural Reserve, 1 Oct 1972, *Jayasuriya 927* (L, K). Sabaragamuwa: Ratnapura, near Kalawana, 28 Jun 1972, *Hepper et al. 4532* (K).

***Note*—**This variety shows a distinctive larger receptacle, (1.1–)1.2–1.5 cm diam., than the other varieties.

Taxonomic treatment of *Ficus* sect. *Leucogyne*

Ficus L. subg. *Urostigma* (Gasp.) Miq. sect. *Leucogyne* Corner, Gard. Bull. Singapore 17: 371. 1960; C. C. Berg, Experientia 45: 605, 608. 1989.—TYPE: *Ficus rumphii* Blume

Growth intermittent. Leaves not articulate, with cystoliths at both sides of the lamina. Figs with (2)3 basal bracts; staminate flowers dispersed, usually pedicellate; pistille flowers with white ovaries.

Note*—Leucogyne*, containing two Indian species (*F. amplissima* and *F. rumphii*), was often placed in subsection *Urostigma* (e.g., Berg and Corner 2005). Berg (1989) already indicated the weak morphological difference between *Leucogyne* and *Urostigma*. However, molecular studies (Rønsted 2005, 2008) show that *F. rumphii* is embedded within section *Conosycea*. The two species differ from subsection *Urostigma* (see description), with which they mainly share the intermittent growth. They are pollinated by a special group of fig wasps, formerly the genus Maniella (see Wiebes 1979; Berg 1989), now called *Eupristina* subgenus *Parapristina* (Berg and Corner 2005: 603, *Leucogyne* erroneously called '*Leucosyce*'). Species of this group also pollinate some species in subsection *Conosycea*, another argument to place the species in this subsection, because subsection *Urostigma* is pollinated by figs from the genus *Platyscapa*. We refrain from placing the two species already in subsection *Conosycea*, because we first like to see *F. amplissima* sampled for phylogenetic analyses and a proper revision of *Conosycea*.

28. ***Ficus amplissima*** J. E. Sm. in Rees, Cycl. 14: n. 68. 1810, non Miq. 1867; Corner, Gard. Bull. Singapore 18: 84. 1961; 21: 11. 1965; K. M. Matthew, Fl. Tam. Carnatic 3: 1515. 1983.–*Tsjela* Rheede, Hort. Mal. 3: 85, t. 63. 1682, nom. inval.–*Ficus tsiela* Roxb, Hort. Bengal.: 66. 1826, nom. superfl.; Fl. Ind. 3: 549. 1832; King in Hook.f., Fl. Brit. India 5: 515. 1888.–*Ficus tsjela* Roxb. ex Buch. –Ham., Tr. Linn. Soc. 15: 149. 1826, nom. superfl.; King, Ann. Roy. Bot. Gard. (Culcutta) 1: t.74. 1887.–*Ficus indica* auct. non L.: L., Sp. Pl. 2: 1060. 1753; Vahl. Enum. Pl., ed. 2: 195. 1806; Willd., Sp. Pl., ed. 4, 4(2): 1146. 1806.—TYPE: Rheede (1682) t. 63, based on *Tsjela* Rheed.

Urostigma pseudobenjamineum Miq., London J. Bot. 6: 566. 1847.–*Ficus pseudobenjaminea* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867.—TYPE: INDIA. Luddaloor, *Wight s.n. in Herb. Rupel* (holotype: K).

Urostigma pseudotsiela Miq., London J. Bot. 6: 566. 1847.–*Ficus pseudotsiela* (Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: t. 74. 1887.—TYPE: *Wight. in Herb. Hook.* (holotype: K).

Tree up to 20 m tall. Branches drying grey–brown to brown, periderm flaking off or sometimes persistent. Leafy twigs 2.5–4 mm thick, glabrous, periderm flaking off. Leaves not articulate; lamina elliptic to ovate, 5.5–13.5(–17) by 3.2–7.5(–8.5) cm, coriaceous, apex acute to acuminate, the acumen blunt, base attenuate to cuneate to obtuse to rounded, both surfaces glabrous; lateral veins 8–10 pairs, the basal pair up to 1/4–1/2 the length of the lamina, sometimes branched, tertiary venation reticulate to partly parallel to the lateral veins; petiole 3.5–7 cm long, glabrous, epidermis persistent; stipules 1.3–1.5 cm long, glabrous or minutely puberulous, usually caducous, sometimes persistent at the shoot apex and forming a terminal bud. Figs axillary or just below the leaves, solitary or in pairs, sessile; basal bracts 3, 1–1.5 mm long, glabrous, persistent; receptacle obovate or subpyriform, 0.8–1 cm diam. when dry, glabrous, purple at maturity, apex flat; ostiole 1–1.5 mm diam., upper ostiolar bract glabrous; internal hairs absent. Staminate flowers dispersed, usually pedicellate; tepals 2–3, ovate or spathulate, free, red brown. Pistillate flowers sessile or pedicellate; tepals 2–3, ovate, free, red brown; ovary white.

***Distribution and Habitat*—**This species is distributed in South India and Sri Lanka; in evergreen forest, in rocky places, at altitudes up to 1,000 m.

***Representative Specimens Examined*—**INDIA. Andhra Pradesh: Kadapa (Cuddapah), Mar 1883, *Gamble 10942* (K); Feb 1883, *Gamble 10981* (K). Tamil Nadu (Madras): Kanchipuram, Chingleput, Jul 1885, *Gamble 16452* (K); Coimbatore, 18 Nov 1990, *Preyadarsaman 5* (L); Dharmapuri, Pennagaram, Hokainakkal, Cauvery banks, Veppalkovai pallam, 20 Dec 1978, *Matthew 20582* (K). SRI LANKA. Central: Matale, Sigiriya, 4 Nov 1949, *Worthington 4350* (K). Eastern: Kantalai, 9 May 1955, *Worthington 6737* (K). Sabaragamuwa: Ratnapura, near Turkama, between Nonagama and Ratnapura, 20 Jan 1968, *Wirawan 814* (K). Western: Negombo, Katunayake, 8 Sep 1962, Holmes & *Worthington 7639* (K).

***Note*—**Ramamoorthy and Gandhi (1976) described 4 basal bracts. We only found 3, however, bracts may be deeply lobed and erroneously appear to be an extra bract.

29.*Ficus rumphii* Blume, Bijdr. Fl. Ned. Ind. 9: 437. 1825; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867; King, Ann. Roy. Bot. Gard. (Calcutta) 1: 54, t. 67B. 1887; Gagnep. in Lecomte, Fl. Indo–Chine 5: 768. 1928; Corner, Wayside Trees 1: 687. 1940; Gard. Bull. Singapore 21: 11. 1965; C. C. Berg and Corner, Fl. Males. Ser. 1, 17 (2): 609. 2005.–*Urostigma rumphii* (Blume) Miq. in Zoll., Syst. Verz. 2: 90. 1854; Fl. Ind. Bat. 1, 2: 322. 1859.—TYPE: INDONESIA. Java, *Reinwardt 1121* (holotype: L; isotype: P).

[*Ficus populiformis* Schott ex Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867, nom. nud.]

Ficus religiosa L. var. ß "*Arbor conciliorum* etc." Lam., Encycl. 2, 2: 493. 1788. nom. illig.–*Ficus cordifolia* Roxb., Fl. Ind. (Carey ed.) 3: 548. 1832.–*Urostigma cordifolium* (Roxb.) Miq., London J. Bot. 6: 564. 1847.–*Ficus conciliorum* Oken, Allg. Naturgesch. 3: 1561. 1841, nom. superfl.—TYPE: based on Rumphius: *Arbor conciliorum* Rumph., Herb. Amboin. 3: t.91, 92. 1743.

Ficus damit Gagnep., Notul. Syst. (Paris) 4: 88. 1927; in Lecomte, Fl. Indo–Chine 5: 812, f. 93. 1928.—TYPE: VIETNAM. Quang–tri, Lao–bao, *Poilane 1337* (holotype: P).

Tree up to 20 m tall. Branches drying yellow–brown or brown. Leafy twigs 2–6 mm thick, glabrous or white puberulous, periderm flaking off. Leaves not articulate; lamina ovate (3–)4.5–17.6 by (2.8–)4–14.9 cm, (sub)coriaceous, apex acute, acuminate or cuspidate, the acumen sharp, base subcordate, subattenuate, broad cuneate or truncate, both surfaces glabrous; lateral veins 5–8 pairs, the basal pair up to 1/3–2/3 the length of the lamina, branched, below the major basal pair always a pair of smaller basal lateral veins, tertiary venation reticulate to subscalariform; petiole (1.8–)3.6–6.5(–9) cm long, glabrous or puberulous; stipules 1–3.8 cm long, glabrous, persistent at the shoot apex and forming a terminal bud or sometimes caducous. Figs axillary or below the leaves, solitary or in pairs, sessile; basal bracts (2 or) 3, 1–2 mm long, glabrous, persistent; receptacle subglobose or obovate, 1–1.5 cm diam., (usually) wrinkled when dry, glabrous, black at maturity, apex concave to flat to convex; ostiole 1.5–2.5 mm diam., the upper ostiolar bract glabrous; internal hairs absent. Staminate flowers dispersed, mostly pedicellate, usually with a bract at the base of the pedicel; tepals 2–3, ovate, oblong or spathulate, free, reddish brown or dark red. Pistillate flowers sessile or pedicellate; tepals 2–3(–4), ovate, oblong, or spahthulate, free, reddish brown to dark red; ovary white (or pale yellow). Figure 2-5C.

***Distribution and Habitat*—**This species is distributed in India, Nepal, Bhutan, Bangladesh, Myanmar, Thailand, Laos, Cambodia, Vietnam, and Indonesia (Java, Moluccas, Lesser Sunda Islands); in coastal and inland forest, often in rocky places (limestone), at altitudes up to 380 m.

***Representative Specimens Examined*—**BANGLADESH. Chittagong: 31 Dec 1850, *J.D. Hooker & T. Thomson 8046* (K). BHUTAN. Western: Samchi, 26° 54' N, 89° 06' E, 28 Feb 1982, *Grierson & Long 3284* (K). CAMBODIA.

Kampong Speu: 20 Jan 1928, *Poilane 14505* (K). Siem Reap: Puok, Borai forest, 17–20 km W from Siem Reap, 26 Mar 2001, *Huq & Phurin 10858* (L). Stung Treng: Thala Barevath, Preah Rum Kel, *Meng 155* (K, L). INDIA. Assam: Burnihat, Khasia hill, 4 Jun 1949, *Koelz 22871* (K, L). Jharkhand: Ranchi, 15 Nov 1915, *Haines 2504* (K). Tamil Nadu (Madras): Ganjam, 1889, *Gamble 21680* (K). South Andaman Islands: Shore Gaint hill, 6 Jan 1892, *King s.n.* (L). Uttarakhand: Mussoorie, Sainji to Kempti, 12 Jul 1944, *Stewart 21018* (K). INDONESIA. Java: Jakarta, *Reinwardt 1121* (L). Maluku: Ambon, Jul–Nov 1913, *Robinson 180* (L); Babar, Pulau Wetan, Herleh, 28 Nov 1956, *van Borssum Waalkes 3009* (L); Buru, Namlea, 5 Apr 1937, *Boschproefstation bb 22799* (L, SING); Obi, 30 Oct 1937, *Nodi 480* (L); Seram, Central Seram, Kecamatan Tehoru, Manusela National Park, 18 Feb 1985, *Kato et al. C–7604* (L). Nusa Tenggara Barat: Sumbawa, Sultanat Bima, 16 Dec 1909, *Elbert 3881* (L). Nusa Tenggara Timur: Sumba, 12 Jul 1974, *Verheijen 4224* (L); Alor, Kabola Peninsula, Adang–Sabandar–Alor ketjil, 4 May 1938, *Jaag 418* (L). LAOS. Champasak: Mehkong R., Khon Isl., Sompamit falls, 28 Apr 1998, *Maxwell 98–495* (L). MYANMAR. Kachin: Myitkyina, 16 Jan 1958, *McKee 6079* (K). Tanintharyi (Tenasserim): Tavoy, 12 miles from Paungdaw, ca. 98° 30’ E, 14° 00’ N, Paungdaw R. at the junction with the Banchaung R., 25 Aug 1961, *Keenan et al. 1203* (K).Yangon: Mingaladon, Dec 1937, *Dickason 6803* (L, SING). NEPAL. Eastern: Illam–Jog Mai–Ranga Pant, 8 Dec 1963, *Hara et al. 6300828* (K). THAILAND. Chiang Mai: Chiengdao, Doi Chiengdao, Ban Tham, 1 Mar 1958, *Bunchuai 756* (BKF). Chon Buri: Siracha, Si Chang Isl., at base of Kow Kwang and behind the shore, 13 Feb 1993, *Maxwell 93–143* (L). Kanchanaburi: Sangkhlaburi, Ban Sanehpawng, Lai Wo, Toong Yai Naresuan Wildlife Sanctuary, 17 Mar 1993, *Maxwell 93–272* (L). Prachuap Khiri Khan: Bangsaphan, 20 May 1890, *Keith 410* (SING). Sakon Nakhon: Phu Phan, 5 Dec 1962, *Suvarnakoses 2013* (BKF). Satun: Muang, Tarutao Isl., between Pante Malacca Bay and Ao Jahk, Tarutao National Park, 17 Apr 1987, *Maxwell 87–373* (BKF, L). VIETNAM. Ho Chi Minh (Saigon). Botanical Garden, 30 Jan 1919, *Chevalier 361*(K, L). Quang Tri: Lao Bao, 20 May 1921, *Poilane 1337* (P).

***Note*—**This species is often confused with *F. religiosa*, but differs in the acute, acuminate or cuspidate leaf apex, lateral veins 5–8 pairs, the basal pair up to 1/3–2/3 the length of the lamina, basal bracts of the fig 1–2 mm long (versus apex caudate, lateral veins 7–11 pairs, the basal pair up to (1/8–)1/7–1/5(–1/4) the length of the lamina, basal bracts 3–5 mm long in *F. religiosa*).

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Chapter 3

Leaf anatomy of *Ficus* subsection *Urostigma* (Moraceae)

Bhanumas Chantarasuwan, Pieter Baas, Bertie-Joan van Heuven, Claudia Baider and Peter C. van Welzen

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Abstract

Species of *Ficus* subsection *Urostigma* show much overlapping variation in vegetative morphology, which often precludes correct identification of the species. The aim of this study is to describe the leaf anatomical characters and their variation and to check their suitability for identification. Included were 41 samples belonging to 25 species of subsect. *Urostigma*, 4 samples belonging to 2 species of section *Leucogyne*, and one specimen of *Ficus glaberrima* subsp. *siamensis* of subsection *Conosycea*. Transverse sections of lamina, midrib, and petiole, and cuticular macerations were used. The observed anatomical characters are described per species. On the basis of a limited number of studied samples, the leaf anatomy shows little variation per species and each species has a unique combination of character states, which facilitates identification. *Ficus arnottiana* shows some leaf anatomical characters that are quite different from all other members of subsection *Urostigma*, such as a multiple epidermis and enlarged lithocysts on both sides of the leaf. Both characters are generally considered as typical for *Ficus* subsection *Conosycea*.

Additional keywords: cuticular sculpturing - indumentum - lithocysts - Section *Leucogyne* - stomata - Subsection *Conosycea* - vascular bundle patterns.

Introduction

Ficus L. subsection *Urostigma* C. C. Berg comprises 27 species, which occur in Africa, Madagascar, Asia, Australia, and the Pacific. Most species are deciduous and are found in semi-arid areas, some species grow in evergreen tropical forests or in swamp forests. The leaves are always spirally arranged, the lamina varies from broadest in the middle to broadest above the middle to broadest below the middle. The lamina is always symmetrical and varies from small (up to 10 cm long) to medium–sized (10–20 cm long), but those of *F. hookeriana* Corner can be up to 25 cm long. The lamina is subcoriaceous to coriaceous and mostly glabrous on both sides, though the young leaves of *F. cupulata* Haines are sometimes puberulous. The margin is always entire. The venation is basically pinnate and brochidodromous. The tertiary venation varies from clearly scalariform to reticulate and/or partly parallel to the secondary veins. The leaves are articulate in most species, therefore the lamina is often detached from the petiole in dry material; the African and Madagascan species are not articulate.

Renner (1907) was the first to study the leaf anatomy of 54 species of *Ficus* section *Urostigma*, which contained five species that are nowadays part of subsect. *Urostigma: F. saxophila*, *F. religiosa*, *F. tsjakela* , *F. virens* , and *F. salicifolia*. He showed the usefulness of anatomy for the classification of *Ficus*. Grambast (1954) also studied leaf anatomy, but he focused on stomatal characters. Sonibare et al. (2006) worked on the comparative leaf anatomy of 25 *Ficus* species from Nigeria, and agreed that foliar anatomical characters are significant and useful characters for the classification of *Ficus*. Berg & Corner (2005) reported on leaf anatomy of *Ficus* and suggested that the microscopic structures of the leaf help to distinguish subgenera, series, and even subseries, but for the species level more data are needed. However, Van Greuning et al. (1984) reported that anatomical characteristics of the leaves of Ficus are important for taxonomy even on the species level.

Corner (1959, 1981) used a mix of leaf anatomical and morphological characters in the classifications, e.g., the position of the lithocysts. Chew (1989) also combined leaf anatomy (e.g., lithocysts and hypodermis) with morphology to recognize subgenera, sections and series of *Ficus*. Berg & Corner (2005) and Berg et al. (2011) used epidermal characters next to lithocysts in their work.

Morphologically, many species of subsect. *Urostigma* are very variable, which makes it difficult to distinguish some species, such as *F. virens*. This species varies in the position of the figs, the shape of the lamina, the length of the petiole, and the formation of the terminal resting buds, whereby it overlaps in some characters with *F. geniculata* (Berg, 2007). *Ficus rumphii* and *F. amplissima*, previously placed in section *Leucogyne* by Corner (1959), were transferred to subsect. *Urostigma* by Berg & Corner (2005). Moreover, molecular phylogenetic research by Rønsted et al. (2005) showed that

F. rumphii is embedded in subsect. *Conosycea*. Thus, the systematic position of both species is still doubtful. To resolve these problems, extra morphological studies (Chantarasuwan et al., 2013) and leaf anatomy (this study) are applied to find more characters, while the phylogenetic distinctiveness of the species is analysed in molecular studies. Rønsted et al. (2005, 2008) already performed some phylogenetic analyses of DNA-sequences, but an extensive one of subsection *Urostigma* is in progress (Chantarasuwan et al., 2013).

Note: the authorities of all generic and lower level names can be found in the descriptive part.

Materials and methods

Material examined

Dry leaves from 41 samples belonging to 25 species of *Ficus* subsect. *Urostigma*, 4 samples belonging to 2 species of section *Leucogyne*, and 1 specimen of *Ficus glaberrima* subsp. *siamensis* of subsect. *Conosycea* were used for this study. They were mainly taken from herbarium specimens, though some were collected during field trips in Thailand. All specimens are stored in L (Leiden herbarium of Naturalis Biodiversity Center). When the species showed leaf morphological variation, at least two leaf samples per species were studied, whereby care was taken that they came from different collection areas. In case of some rare species or species without much morphological variation, a single sample was used. The specimens studied are mentioned in the anatomical description of each species.

Methods

Transverse and paradermal sections

Dry leaves were rehydrated by boiling in water until soft (leaves sink) and were then stored in 50% alcohol. Cross sections were made from three parts of each leaf: 1) the middle of the leaf including the midrib, 2) the margin where the leaf is broadest, and 3) three zones of the petiole, near the leaf blade, in the middle, and near the twig. Freehand paradermal sections were taken from each leaf surface. Half of the transverse sections and all paradermal sections were bleached in diluted household bleach (1:1) until the sections became transparent, after which they were rinsed 3–4 times with distilled water. All bleached sections were stained with safranin/haematoxylin for 15 seconds and rinsed with 50% alcohol for 2–3 seconds and then washed three times in distilled water. The stained and unstained sections were dehydrated in a series of increasing alcohol content (50%, 70%, 96%, and 99.5%), each step twice for 3 minutes. The dehydrated sections were soaked in Euparal essence for 2–3 minutes and then mounted in Euparal.

Cuticle macerations

Leaf samples (including midrib and margin) were placed in a mixture of 1:1

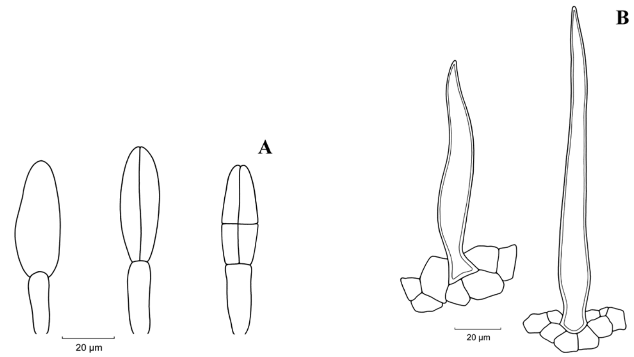

FIGURE 3-1. A. Glandular hairs with 1-, 2- or 4-celled heads, B. Simple hairs. Drawing: Esmée L. C. Winkel, 2013.

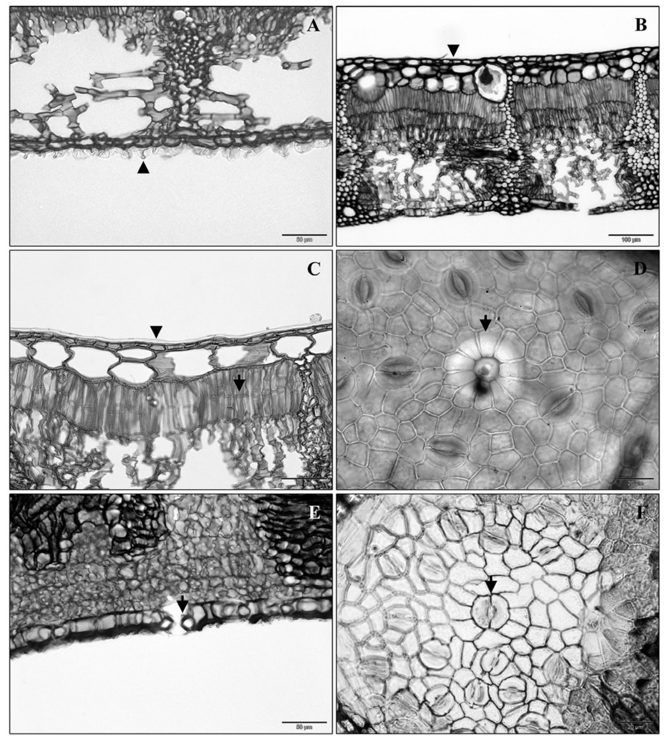

FIGURE 3-2. A. Cuticular ridges (arrowhead) (*F. hookeriana* from *Herb. Lugd. Bat.* [= L] *No 922312770*), B. Multiple epidermis (arrowhead) (*F. arnottiana* from *Haines 3546*), C. Multiple epidermis (arrowhead) and subdivided palisade cells (arrow) (*F. hookeriana* from *Herb. Lugd. Bat.* [= L] *No 922312770*), D. Radiating epidermal cells in surface-view (arrow) (*F. concinna* from *B. Chantarasuwan 071010-1*), E. Inner stomata ledge (arrow) (*F. densifolia* from *C. Baider CB 2421*), F. Giant stomata (arrow) (*F. middletonii* from *D. J. Middleton, S. Suddee, S. J. Davies & C. Hemrat 1178*). All photographs by B. Chantarasuwan.

of glacial acetic acid (96%) and hydrogen peroxide (30%) at 60° C overnight. The next day the maceration mix was rinsed with distilled water and the air in the leaves was removed by using an exsiccator. The macerated leaf material was carefully removed from the cuticle with a fine brush. The cleaned cuticle was stained with 5% Sudan IV in 70% alcohol at 30–40° C for 2–3 hours. Stained cuticles were rinsed with alcohol 70% for a few minutes and then rinsed with distilled water three times. The cleaned cuticles were placed in a 1:1 mixture of glycerin (87%) and distilled water after which they were mounted in glycerin gelatin preheated to 40° C.

Results

Survey of leaf anatomical characters

The following twelve leaf anatomical features/character syndromes were analysed for their systematic and diagnostic significance (Table 3-1).

Indumentum—Glandular hairs can be found on the young parts and they are often caducous in the adult leaves. In subg. *Urostigma* these hairs are elongate, cylindrical with 1- or 2-celled heads, or ellipsoid with 4-celled heads (Berg & Corner, 2005) (Fig. 3-1A). Simple hairs are mostly single-celled and have a pointed tip (Fig. 3-1B); they are common on the petiole of some species, but also on the lamina of *F. ingens* and *F. middletonii*. Most species of subsect. *Urostigma* are generally glabrous on the adult leaves. Some species, such as *F. concinna*, *F. prolixa*, and *F. salicifolia* show simple hairs on the petiole and glandular hairs with 1- or 2-celled heads on the lamina. *Ficus alongensis* only has simple hairs on the petiole. Some species, such as *F. chiangraiensis*, *F. cordata*, and *F. religiosa* have only glandular hairs on the lamina. *Ficus ingens* and *F. saxophila* are glabrous or have simple unicellular hairs on the petiole.

Cuticle—The cuticle is usually smooth or striate abaxially in some species, thin above the lamina and thicker over the leaf margin, midrib and petiole. Some species (*F. hookeriana* and *F. orthoneura*) show a strongly sculptured abaxial cuticle. The cuticular ridges then create an impression of papillae in transverse sections (Fig. 3-2A).

Epidermal cells—The epidermis of *Ficus* differs conspicuously between species, and is, therefore, of taxonomic as well as phylogenetic importance (Van Greuning et al., 1984). The epidermis is mostly single-layered and generally thicker at the adaxial side of the leaf, although it may have proliferated to form a multiple epidermis in several *Ficus* species (Rudall, 1992), of which three species occur in subsect. *Urostigma: F. arnottiana*, *F. hookeriana*, and *F. orthoneura*. However, there are two forms of multiple epidermis: 1) The outer and inner epidermal cells are similar in shape and only gradually increase in size from the periphery to the deeper layers (in *F. arnottiana*) (Fig. 3-2B), or 2); or the cells in

the second layer are much larger than in the outer layer and both layers resemble an epidermis with a separate hypodermis (*F. hookeriana* and *F. orthoneura*) (Fig. 3-2C).

In surface view the bases of the lithocysts (enlarged epidermal cells with a cystolith, see below) are surrounded by radiating epidermal cells, presenting a rosette-like appearance in surface-view. In subgen. *Urostigma* there are usually 5–8 pericentral cells (Berg & Corner, 2005), but this can vary to up to 16 cells (Fig. 3-2D). The anticlinal walls of unspecialized epidermal cell are straight. In transverse section epidermal cells are commonly horizontally elongate but can also be square or vertically elongate (upright).

Mesophyll—Most species in *Ficus* subsect. *Urostigma* have a dorsiventral mesophyll with predominantly one or two layers of adaxial palisade cells and a big layer with spongy cells, or there may be a compact mesophyll consisting of multiple layers which gradually change from top (palisade) to bottom (more spongy). Some species have more or less isobilateral mesophyll with palisade cells on both the adaxial and abaxial side, but abaxially the cells are much shorter than the adaxial palisade cells. In the palisade of *F. hookeriana* and *F. orthoneura* some long palisade cells are subdivided. (Fig. 3-2C).

The stomatal complex—The stomata of *Ficus* subsect. *Urostigma* are only present on the abaxial surface and are anomocytic to actinocytic. In many species the stomatal cells are level with the epidermis but in some species they are slightly sunken; in *F. saxophila* the stomata are commonly level with the epidermis, but some are slightly raised. Grambast (1954) reported that the stomata of *F. salicifolia* and *F. verruculosa* are level with the epidermis, but they look slightly sunken, because the outer epidermal walls are domed unlike those of the subsidiary or neighbouring cells. The guard cells always have outer cuticular ledges, but in some species inner ledges are present too, e.g., *F. densifolia* and *F. religiosa* (Fig. 3-2E). "Giant stomata or hydathode stomata" (sensu Van Cotthem, 1971), much larger than the normal stomata (Fig. 3-2F), occur over the veins or are mixed with normal stomata in some species, such as *F. middletonii*, *F. religiosa*, and *F. virens*.

Crystals—Two types of crystals are common in the leaves of the Moraceae: prismatic crystals, which occur in bundle sheath cells, and druse crystals that are located in the mesophyll and bundle sheaths (according to Wu & Kuo–Huang, 1997). *Ficus* subsect. *Urostigma* shows both types of crystals. Druse crystals (Fig. 3-3A) are commonly present in the palisade and spongy mesophyll, but also occur in the phloem parenchyma of midrib and petiole. Some species show druses in the epidermis above the midrib or petiole. Prismatic crystals (Fig. 3-3B) are mainly found in the bundle sheaths above and below the veins, but in some species all around the veins. Prismatic crystals also occur in the parenchyma cells of midrib and petiole and then they are usually more abundant near the sclerenchyma caps. Where prismatic crystals occur in cells directly adjoining sclerenchyma, the cell walls of the crystalliferous cells are often unilaterally thickened and lignified, resulting in so-called cristarque cells (Baas, 1972; Van Welzen & Baas, 1984) Many species form a peripheral sclerenchyma ring in the petiole and then the prismatic crystals occur in the parenchyma outside the ring, usually in cristarque cells. Prismatic crystals rarely occur in the phloem parenchyma of midrib and petiole.

Lithocysts—In subg. *Urostigma*, the lithocysts are generally cells with a short spike (cystolith base) in the interior, resembling an abortive hair (Berg & Corner, 2005). There are two forms of lithocysts within subsect. *Urostigma*: 1) The "enlarged lithocysts" consist of large cells, which are deeply intruding into the palisade or spongy mesophyll and which are surrounded by radiating epidermal cells in surface-view (Fig. 3-3C). They mostly appear on the abaxial side of the lamina, except in *F. arnottiana*, which shows abundant enlarged lithocysts adaxially and very few abaxially (Fig. 3-3D). 2) The other type are smaller lithocysts in ordinary adaxial epidermal cells of normal size, but they are not always consistently present in all species. (Fig. 3-3E).

Silicified cells—Most leaf anatomical studies ignore the presence or absence of individual or groups of silicified cells (i.e., wholly or partly impregnated with amorphous silica that produces a glass-like appearance of the cells), but Baas et al. (1982) have shown that this type of silification can be highly diagnostic at the genus level in Olacaceae. We therefore also explored their potential systematic significance in *Ficus* subsection *Urostigma*. The silicified cells may occur in the epidermis (Fig. 3-3F) and mesophyll (Fig. 3-4A). Some guard cells of *F. prasinicarpa* and *F. pseudoconcinna* also become silicified (Fig. 3-4B). There is a great variation in the conspicuousness and abundance of silicified cell groups, and one has to look for them very carefully.

Petiole and midrib vascularization—The vascular system of the petiole consists of a cylinder of separate or partially merged vascular bundles. Central pith vascular collateral bundles or phloem strands are present or absent. One type of vascular system in the midrib consists of opposed adaxial and abaxial arcs (Fig. 3-4C). Sometimes the arc consists of separate bundles (Fig. 3-4D), which can be partially merged or become a more or less closed ring of vascular tissue (Fig. 3-4E) and contain or do not contain central vascular bundles or phloem strands (Fig. 3-4D). There are intermediates between these different character states in some species.

Veins and bundle sheaths—The characters of veins and bundle sheaths were already considered of diagnostic value by Solereder (1908). Within *Ficus* subsect. *Urostigma*, the bundle sheaths of the primary and secondary veins show two forms. 1) Vertically transcurrent (Fig. 3-4F), then the bundle sheaths are not only around the veins but they also extend upwards and downwards to both epidermal layers. 2) Circular (Fig. 3-5A), with the sclerenchymatous bundle sheaths present around the veins, but not extending to the abaxial epidermis, although the parenchymatous bundle sheath may extend to the adaxial epidermis. The tertiary veins of all

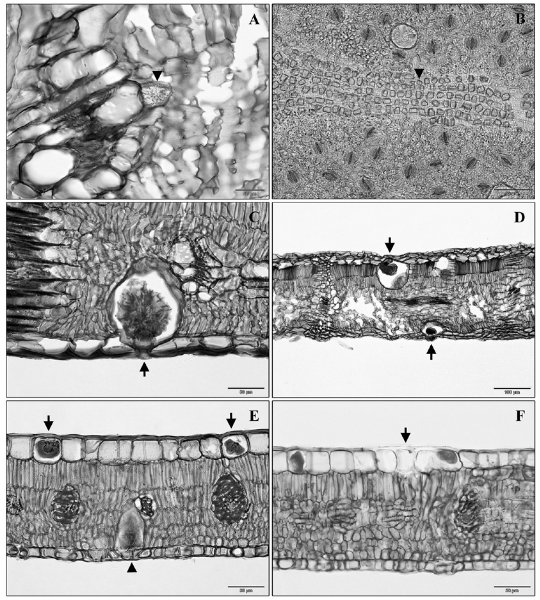

FIGURE 3-3. A. Druse crystal (arrowhead) (*F. salisifolia* from *O. Beccari 39*), B. Prismatic crystals (arrowhead) (*F. concinna* from *B. Chantarasuwan 071010-1*), C. Enlarged lithocysts (arrow) (*F. salisifolia* from *O. Beccari 39*), D. Enlarged lithocysts adaxially and abaxially (arrow) (*F. arnottiana* from *Haines 3546*). E. Smaller lithocysts in ordinary adaxial epidermal cells (arrow) and enlarged litho-cysts (arrowhead) (*F. religiosa* from *B. Chantarasuwan 150910-2*), F. Silicified cells in the epidermis (arrow) (*F. religiosa* from *B. Chantarasuwan 150910-2*). All photographs by B. Chantarasuwan.

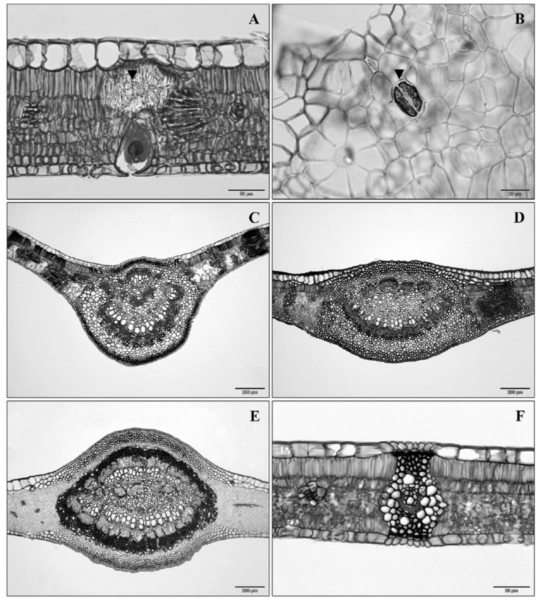

FIGURE 3-4. A. Silicified cells in mesophyll (arrowhead) (*F. religiosa* from *B. Chantarasuwan 150910-2*), B. Guard cells silicified (arrowhead) (*F. prassinicarpa* from *A. J. G. H. Kostermans 1593*), C. Midrib vascularization with opposed adaxial and abaxial arcs with central vascular bundles (or phloem strands) (*F. caulocarpa* from *B. Chantarasuwan 071010-2*), D. Adaxial arcs consist of separate bundles (*F. densifolia* from *C. Baider CB 2421*), E. Partially merged bundles or more or less closed ring of vascular tissue (*F. religiosa* from *B. Chantarasuwan 150910-2*), F. Vertically transcurrent of veins and bundle sheath (*F. superba* from *P. J. A. Kessler 714*). All photographs by B. Chantarasuwan.

species have circular bundle sheaths (usually parenchymatous only) and are embedded in the mesophyll.

Sclerenchyma fibres and sclerified ground tissue—Sclerenchyma layers are commonly associated with the vascular tissue of *Ficus* subsect. *Urostigma*. Fibre caps or sheaths mainly occur associated with peripheral phloem tissue in petiole and midrib, although they also form part of the bundle sheaths in some species. Sclerified ground tissue (initially parenchyma or collenchyma) can also be found close to the epidermis, where it usually forms adaxial and abaxial plates in the midrib (Fig. 3-5B) or a subepidermal ring in the petiole (Fig. 3-5C). Sclerenchyma also occurs in the leaf margin of many species (Fig. 3-5D).

Laticifers—Laticifers are present in all species of subsect. *Urostigma*, and they occur mainly in the vicinity of the vascular tissue, in the mesophyll and between epidermal cells and mesophyll layers. The laticifers are typical for the entire family, and thus not useful for species recognition.

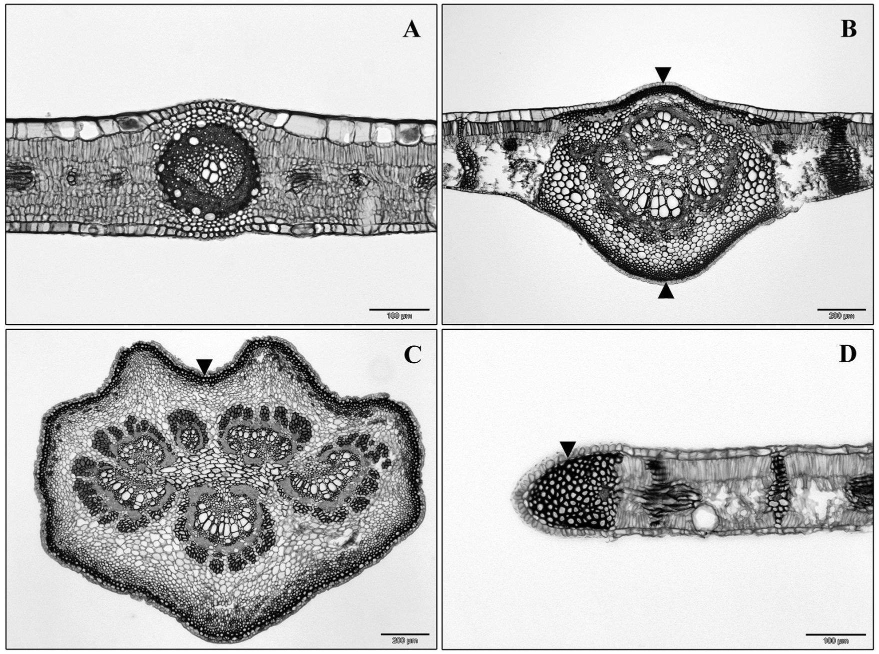

FIGURE 3-5. A. Circular bundle of veins and bundle sheath (*F. religiosa* from *B. Chantarasuwan 150910-2*), B. Adaxial and abaxial sclerified ground tissue subepidermal in midrib (arrowhead) (*F. geniculata* from *B. Chantarasuwan 220910-1*). C. Sclerified ground tissue in the petiole (arrowhead) (*F. virens* from *B. Gray 1994*). D. Marginal sclerenchyma(arrowhead) (*F. caulocarpa* from *Garcia, Fuentes, Romero PPI 18502*). All photographs by B. Chantarasuwan.

TENTATIVE KEY TO SPECIES OF *FICUS* SECT. *LEUCOGYNE*, SUBSECT. *UROSTIGMA*, AND SUBSECT. *CONOSYCEA* (*FICUS GLABERRIMA* SUBSP. *SIAMENSIS*) BASED ON LEAF ANATOMY

1. Epidermis multi-layered (2–3 layers) … … … … … … … … … … … … … … … 2
1. Epidermis single-layered … … … … … … … … … … … … … … … … … … … 7
2. Enlarged lithocysts mainly adaxially or on both sides … … … … … … … … 3
2. Enlarged lithocysts only abaxially … … … … … … … … … … … … … … … … 6
3. Simple hairs absent on petiole … … … … … … … … … … … … … … … … … 4
3. Simple hairs present on petiole … … … … … … … … … … … … … *F. rumphii*
4. Internal cuticular ledges of stomata present … … … … … … … … … … … … 5
4. Internal cuticular ledges of stomata absent … … … … … … … … *F. arnottiana*
5. Palisade 1-layered, subepidermal sclerification above midrib absent … … … … … … … … … … … … … … … … … … *F. glaberrima* subsp. *siamensis*
5. Palisade 2-layered, subepidermal layer above midrib sclerified … *F. amplissima*
6. Marginal sclerenchyma strands absent, peripheral ground tissue in petiole not sclerified … … … … … … … … … … … … … … … … … … … *F. hookeriana*
6. Marginal sclerenchyma strands present, peripheral ground tissue in petiole sclerified … *F. orthoneura*
7. Cuticular ridges absent … 8
7. Cuticular ridges present abaxially… … … … … … … … … … … … … *F. tsjakela*
8. Midrib vascularisation consisting of two opposing vascular arcs to a closed ring, pith bundles in petiole present … … … … … … … … … … … … … … 9
8. Midrib vascularisation composed of a cylinder of separate bundles, pith bundles in petiole absent … … … … … … … … … … … … … … *F. alongensis*
9. Bundle sheaths of veins circular or only transcurrent to the adaxial epidermis … 10
9. Bundle sheaths of veins vertically transcurrent … … … … … … … … … … 13
10. Subepidermal ground tissue in midrib and petiole sclerified … … … … … 11
10. Subepidermal ground tissue in midrib and petiole not sclerified … *F. saxophila*
11. Marginal sclerenchyma strands absent, stomata slightly sunken … … … 12
11. Marginal sclerenchyma strands present, stomata level with epidermis … *F. religiosa*
12. Internal cuticular ledges of stomata absent … … … … … … … … … *F. cordata*
12. Internal cuticular ledges of stomata present … … … … … … … … *F. tsjakela*
13. Peripheral ground tissue in petiole sclerified … … … … … … … … … … 14
13. Peripheral ground tissue in petiole not sclerified … … … … … … … … … 23
14. Palisade 1-layered … 15
14. Palisade 2–5-layered … 18
15. Simple hairs present on petiole … … … … … … … … … … … … … … … 16
15. Simple hairs absent … 17
16. Glandular hairs present on petiole and lamina, radiating epidermal cells around lithocysts 8–16 … … … … … … … … … … … … … … … … *F. prolixa*
16. Glandular hairs absent, radiating epidermal cells around lithocysts 5–8 … … … … … … … … … … … … … … … … … … *F. subpisocarpa* subsp. *pubipoda*

17. Silicified cells present … … … …. … *F. prasinicarpa* and *F. pseudoconcinna*
17. Silicified cells absent … … … … … … … … … … … … … … … … … .. *F. superba*
18. Silicified cells absent … . 19
18. Silicified cells present … … … … … … … … … … … … … … … … … … … . 20
19. Simple hairs absent … … … … … … … … … … … … … … … … … *F. geniculata*
19. Simple hairs present on both petiole and midrib … … … … *F. middletonii*
20. Giant stomata present … 21
20. Giant stomata absent … … … … … … … … … … … … … … … .. *F. caulocarpa*
21. Lithocysts resembling ordinary epidermis cells absent … … … … … … 22
21. Lithocysts resembling ordinary epidermis cells present … … … … … … …
… … … … … … … … … … … … … … … … … … … .. *F. ingens* and *F. virens*
22. Simple hairs absent … … … … … … … … … … … … … … … *F. chiangraiensis*
22. Simple hairs present on the petiole … … … … … … … … … … . *F. concinna*
23. Marginal sclerenchyma strands present … … … … … … … … … … … … . 24
23. Marginal sclerenchyma strands absent … … … … … … … … … … … … .. 26
24. Radiating epidermal cells around lithocysts 5–8, glandular hairs present
… 25
24. Radiating epidermal cells around lithocysts 8–12, glandular hairs absent
… *F. henneana*
25. Stomata level with epidermis, lithocysts resembling ordinary epidermis cells present … ... *F. densifolia*
25. Stomata slightly sunken, lithocysts resembling ordinary epidermis cells absent … ... *F. salicifolia*
26. Silicified cells absent, stomata with inner cuticular ledges … … ... *F. lecardii*
26. Silicified cells present, stomata without inner cuticular ledges
… . ... … … *F. verruculosa*

Leaf anatomy of *Ficus* subsect. *Urostigma*

In surface view: Indumentum absent to present, simple, elongate, single-celled or glandular with 1- or 2- or even 4-celled heads. Cuticle smooth adaxially and mostly also abaxially, sometimes striate or strongly ridged abaxially. Anticlinal walls straight. Epidermal cells 5–16 in a radiating pattern around lithocyst bases in abaxial epidermis (seldom also adaxially so). Stomata restricted to the abaxial surface, anomocytic to actinocytic, generally in level with epidermis, guard cells of moderate size (15–38 µm); giant stomata present in some species.

In transverse section: Epidermis single-layered or multiple (2–3)-layered, in the latter all cells of more or less the same size or gradually increasing in size inwardly or second layer hypodermis-like with much enlarged cells, outer epidermal cells square to horizontally or vertically elongated. Stomata in level with epidermis or slightly sunken, guard cells with conspicuous outer and sometimes also inner cuticular ledges. Enlarged lithocysts mainly abaxially or on both sides, lithocysts in ordinary, unenlarged cells present or absent in adaxial epidermis. Silicified cells in epidermis or mesophyll present or absent. Mesophyll dorsiventral (to seldom isobilateral). Adaxial palisade of one, two,

or multiple (up to 5) layers thick that gradually change to a compact spongy tissue. Midrib vascularization consisting of two opposing arcs or separate to partially merged bundles or a closed ring of vascular tissue. Petiole with separate to partially merged bundles, each with a cap of fibres. Pith bundles or phloem strands mostly present in petiole and midrib (but absent in midrib of three species). Veins vertically transcurrent or embedded and circular; minor veins embedded in mesophyll. Marginal sclerenchyma strands present or absent. Crystals abundant as druses and/or prismatic ones. Cristarque cells present or absent. Laticifers present.

Leaf anatomical descriptions of species of *Ficus* subsect. *Urostigma*

Prominent leaf anatomical features of 25 species of *Ficus* subsect. *Urostigma* are described below in a standard format.

1. *Ficus alongensis* Gagnep.

Material studied: CHINA. Guangdong, *T. M. Tsui 524*.

In surface view: Indumentum absent on lamina, but unicellular simple hairs abundant on petiole. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 28–32 µm long and 18–28 µm wide.

In transverse section: Cuticle 1–3 µm thick above the lamina, the abaxial cuticle slightly thicker than the adaxial one, above midrib and margin 3–5 µm thick. Epidermis single-layered on both sides, adaxial cells larger than abaxial ones, cells mostly horizontally elongated, but small above the main veins. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts present abaxially. Mesophyll dorsiventral. Palisade 1(–2)-layered. Midrib composed of a cylinder of separate bundles surrounded by fibre caps; subepidermal layers on both sides sclerified. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; subepidermally sclerified and crystalliferous cell layers apparent around petiole. Pith bundles absent in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of the midrib; prismatic crystals present, partly in cristarque cells, or in the periphery of the bundle sheaths above and below the veins, in the parenchyma of midrib and petiole, few in the phloem parenchyma of midrib and petiole.

2. *Ficus arnottiana* (Miq.) Miq. (Figs. 3-2B, 3-3D)

Material studied: SRI LANKA. Anuradhapura, *A. H. M. Jayasuriya 1293*. INDIA; Courtallum, *Haines 3546*.

In surface view: Indumentum of glandular hairs with 1- or 2-celled heads present on abaxial and adaxial surface. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8(–9), mainly confined to adaxial surface. Stomata 19–28 µm long and 14–19 µm wide; giant stomata 28–33 µm long and 19–24 µm wide.

In transverse section: Cuticle less than 1 µm thick on adaxial lamina, above midrib and margin 2–3 µm thick. Epidermis multi-layered at both sides. Stomata level with epidermis, only outer stomatal ledges present. Enlarged lithocysts present on both sides, but very infrequent and smaller abaxially than adaxially. Mesophyll isobilateral. Palisade 2-layered adaxially, 1-layered abaxially. Midrib with two opposing vascular arcs surrounded or not by fibre caps. Petiole with a cylinder of separate to partially merged bundles, each with or without a fibre cap; phloem strands present in pith of midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands very weakly developed. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of the petiole, few in the bundle sheaths around the veins; prismatic crystals extremely rare or absent in the parenchyma of midrib and petiole.

Note: The two specimens studied differ rather strongly in the amount of sclerification and fibre tissue associated with the vascular bundles.

3. *Ficus caulocarpa* (Miq.) Miq. (Figs. 3-4C, 3-5D)

Material studied: THAILAND. Nakhon Si Thammarat, *B. Chantarasuwan 071010–2*. PHILIPPINES, Luzon, Cagayan, *Garcia*, *Fuentes*, *Romero PPI 18502*.

In surface view: Indumentum present, simple hairs on petiole and glandular hairs with 1- or 2-celled heads on the lamina abaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 23–28 µm long and 19–26 µm wide.

In transverse section: Cuticle 1–2 µm thick above lamina, above midrib and margin 4–5 µm thick. Epidermis single-layered. Stomata level with epidermis, only outer stomatal ledges present. Enlarged lithocysts present abaxially, sometimes cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral; some silicified cells present, especially near the abaxial epidermis. Palisade 2-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; subepidermal ground tissue of petiole sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of the midrib; prismatic crystals present (partly in cristarque cells) in the periphery of the bundle sheaths above and below the veins, the parenchyma of midrib and petiole, abundant in the cell layer between epidermis and peripheral sclerified ground tissue.

4. *Ficus chiangraiensis* Chantaras.

Material studied: THAILAND. Chiang Rai, *J. F. Maxwell 06–517*.

In surface view: Indumentum present abaxially, glandular hairs with 1- or 2-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 23–28 µm long and 19–24 µm wide; giant stomata 28–38 µm long and 19–28 µm wide.

In transverse section: Cuticle 1–2 µm thick above the lamina, above midrib and margin 5–7 µm thick. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts present abaxially. Mesophyll dorsiventral; some silicified cells present, especially near the abaxial epidermis. Palisade 2-layered. Midrib with two opposing arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; subepidermal ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of the midrib; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths above and below the veins, the parenchyma of midrib and petiole, abundant in the cell layer between the epidermis and sclerified peripheral ground tissue.

5. *Ficus concinna* (Miq.) Miq. (Fig. 3-2D, 3-3B)

Material studied: THAILAND. Nakhon Si Thammarat, *B. Chantarasuwan 071010–1*.

In surface view: Indumentum present, simple hairs on petiole and glandular hairs with 1- or 2-celled heads on the lamina abaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 19–24 µm long and 16–21 µm wide; giant stomata 21–31 µm long and 19–21 µm wide.

In transverse section: Cuticle ca. 1 µm thick above the lamina, above midrib and margin 2–3 µm thick. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts present abaxially. Mesophyll dorsiventral; groups of silicified cells present, usually near the abaxial epidermis. Palisade 3–5-layered, gradually changing to compact spongy tissue. Midrib composed of two opposing arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, absent in the epidermis; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths above and below the veins, the parenchyma of midrib and petiole, abundant in cell layer between the epidermis and the peripheral sclerified ground tissue.

6. *Ficus cordata* Thunb.

Material studied: BOTSWANA. Northern district, *P. A. Smith 3462*. Without locality, *Dinter 275*. SOUTH AFRICA. Okongawa, *R. Seydel 3186*.

In surface view: Indumentum present abaxially, glandular hairs with 1- or 2-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–16 abaxially. Stomata 23–28 µm long and 19–24 µm wide; giant stomata 30–33 µm long and 29–26 µm wide.

In transverse section: Cuticle less than 1 µm thick above the lamina, above midrib and margin 4–7 µm thick. Epidermis single-layered on both sides. Stomata slightly sunken, only outer cuticular ledges present. Enlarged lithocysts sometimes present abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral; silicified cell groups present, especially near the stomata of the abaxial epidermis or sometimes absent. Palisade multi-layered, gradually changing to compact chlorenchyma tissue. Midrib with two opposing arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins circular, embedded in the mesophyll or only transcurrent to adaxial epidermis. Marginal sclerenchyma strands absent. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, also in the epidermis above the lamina and midrib; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths around the veins, the parenchyma of midrib and petiole, few in the phloem parenchyma of midrib and petiole, abundant in the cell layer between epidermis and peripheral sclerified tissue.

7. *Ficus densifolia* Miq. (Figs. 3-2E, 3-4D)

Material studied: MAURITIUS. *C. Baider CB 2421*.

In surface view: Indumentum present abaxially, glandular hairs with 1- or 2-celled heads. Cuticle smooth adaxially, striated abaxially. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 28–33 µm long and 23–33 µm wide.

In transverse section: Cuticle 1–3 µm thick above the lamina and midrib, 3–4 µm thick above margin. Epidermis single-layered on both sides. Stomata level with epidermis, inner and outer cuticular ledges present. Enlarged lithocysts abaxially. Mesophyll dorsiventral. Palisade 2–5-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue not sclerified. Pith bundles absent in midrib and present in the base of the petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, also in the epidermis of the petiole; prismatic crystals present in the periphery of the bundle sheaths above and below the veins and the parenchyma of midrib and petiole.

8. *Ficus geniculata* Kurz (Fig. 3-5B)

Material studied: THAILAND. Phitsanulok, *B. Chantarasuwan 220910–1*.

In surface view: Indumentum present abaxially, glandular hairs with 1- or 2-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 23–28 µm long and 16–19 µm wide; giant stomata 28–31 µm long and 16–21 µm wide.

In transverse section: Cuticle 1–3 µm thick above lamina, above midrib and margin 5–7 µm thick. Epidermis single-layered on both sides, adaxially thicker than abaxially, cells mostly horizontally elongated, small above the main veins. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral. Palisade 2-layered. Midrib with two opposing arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of midrib and petiole; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths above and below the veins, the parenchyma of midrib and petiole, abundant in the cell layer between the epidermis and peripheral sclerified tissue.

9. *Ficus henneana* (Miq.) Corner

Material studied: AUSTRALIA. Queensland, *B. Hyland 8086*. New South Wales, *R. Coveny 9750*.

In surface view: Indumentum absent. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 23–28 µm long and 19–24 µm wide; giant stomata 28–33 µm long and 28–31 µm wide.

In transverse section: Cuticle less than 1 µm thick above lamina, above midrib and margin 4–5 µm thick. Epidermis single-layered on both sides, cells square to vertically elongated, rarely horizontally elongated adaxially but more commonly so abaxially, small above the main veins. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral (to partly isobilateral). Palisade 2-layered, sometimes a discontinuous palisade layer also abaxially. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue not sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in the phloem parenchyma of midrib and petiole, few in the parenchyma cells near the epidermis of the petiole; prismatic crystals present in the periphery of the bundle sheaths above and below the veins, the parenchyma of midrib and petiole, and abundant in the parenchyma cells near the epidermis of the petiole.

10. *Ficus hookeriana* Corner (Figs. 3-2A, C)

Material studied: FRANCE. Cultivated in Cap d'Antibes, *Herb. Lugd. Bat.* [= L] *No 922312770.*

In surface view: Indumentum abaxially of glandular hairs with 1- or 2-celled heads. Cuticle smooth adaxially, strongly ridged abaxially. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 23–28 µm long and 16–19 µm wide; giant stomata 28–33 µm long and 23–26 µm wide.

In transverse section: Cuticle 4–5 µm thick above lamina, above midrib and margin 7–9 µm thick. Epidermis multi-layered adaxially with the outer cells much smaller than the inner cells; abaxially outer periclinal epidermal wall and cuticle strongly ridged, creating the impression of papillae in transverse section. Stomata level with epidermis, only outer cuticular ledges

present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral. Palisade 1- to partly 2-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue not sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma absent. Druses present in mesophyll, phloem parenchyma of midrib and petiole, few in the epidermis of the petiole; prismatic crystals present in the periphery of the bundle sheaths around the veins, the parenchyma of midrib and petiole, also mixed with druses in the phloem parenchyma of midrib and petiole.

11. *Ficus ingens* (Miq.) Miq.

Material studied: ZAMBIA. Lusaka, *C. C. Berg & M. G. Bingham 1368*, *C. C. Berg & M. G. Bingham 1395.*

In surface view: Indumentum: simple hairs absent or on petiole and/or on both sides of midrib; glandular hairs with 1-celled heads present abaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–16 abaxially. Stomata 16–24 µm long and 14–17 µm wide; giant stomata 26–33 µm long and 21–28 µm wide.

In transverse section: Cuticle less than 1 µm thick above lamina, above midrib and margin 3–5 µm thick. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral; some silicified cells present, especially near the abaxial epidermis. Palisade 2–5-layered, gradually changing to a compact chlorenchyma tissue. Midrib with two opposing arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of the petiole; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths above and below the veins, the parenchyma and phloem parenchyma of midrib and petiole, abundant in the cell layer between epidermis and peripheral sclerified tissue.

12. *Ficus lecardii* Warb.

Material studied: IVORY COAST. *A. J. M. Leeuwenberg 1960.*

In surface view: Indumentum absent. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 6–9 abaxially. Stomata

30–38 µm long and 28–36 µm wide; stomata above veins slightly smaller than stomata above lamina, 28–33 µm long and 23–31 µm wide.

In transverse section: Cuticle less than 1 µm thick above lamina, above midrib and margin 4–5 µm thick. Epidermis single-layered on both sides. Stomata slightly sunken, outer and inner cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral. Palisade 1-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; peripheral ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue not sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands absent. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, also in the epidermis of the petiole; prismatic crystals present in the periphery of the bundle sheaths above and below the veins, and the parenchyma of midrib and petiole.

13. *Ficus middletonii* Chantaras. (Fig. 3-2F)

Material studied: THAILAND. Prachuap Khiri Khan, *D. J. Middleton, S. Suddee, S. J. Davies & C. Hemrat 1178*.

In surface view: Indumentum present, simple hairs on petiole and midrib, and/or glandular hairs with 1–4-celled heads on both surfaces. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 14–19 µm long and 9–17 µm wide; giant stomata above veins, 21–24 µm long and 19–21 µm wide.

In transverse section: Cuticle less than 1 µm thick above lamina, above midrib and margin 2–6 µm. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially. Mesophyll dorsiventral. Palisade 4–5-layered, gradually changing to compact spongy tissue. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of midrib and petiole; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths above and below the veins, the parenchyma and phloem parenchyma of midrib and petiole, abundant in the cell layer between the epidermis and the peripheral sclerified ground tissue.

14. *Ficus orthoneura* H. Lév. & Vaniot

Material studied: VIETNAM. Nihn Binh, N. M. Cuong, *D. T. Kien and M. V. Sinh 765*. THAILAND. Phatum Thani (Cultivated), *B. Chantarasuwan s.n.*

In surface view: Indumentum abaxially of glandular hairs with 1-celled heads. Cuticle smooth adaxially, strongly ridged abaxially. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 21–26 µm long and 14–21 µm wide; giant stomata present above veins, 26–28 µm long and 19–24 µm wide, some cuticular ridges obscuring the stomata.

In transverse section: Cuticle 4–5 µm thick above lamina, above midrib and margin 4–10 µm thick. Epidermis multi-layered adaxially, cells in outer layer smaller than in the inner layer; abaxially outer periclinal epidermal wall and cuticle strongly ridged resulting in seemingly papillate appearance in sectional view. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially. Mesophyll dorsiventral. Palisade 1- to partly 2-layered, the inner layer consisting of short cells. Midrib composed of a cylinder of separate to partially merged bundles to two opposing arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands weakly developed. Druses present in mesophyll, phloem parenchyma of midrib and petiole, few in the epidermis of the petiole; prismatic crystals present in the periphery of the bundle sheaths around the veins, the parenchyma of midrib and petiole, or mixed with druses in the phloem parenchyma of midrib and petiole, also abundant in the peripheral tissue of the petiole.

15. *Ficus prassinicarpa* Elmer ex C. C. Berg (Fig. 3-4B)

Material studied: PAPUA NEW GUINEA. Central district, *J. Wiakabu et al. LAE 70408*. INDONESIA. Moluccas, Morotai, *A. J. G. H. Kostermans 1593*.

In surface view: Indumentum present abaxially, glandular hairs with 1-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–9 abaxially. Stomata 23–28 µm long and 19–24 µm wide; giant stomata above veins, 26–31 µm long and 19–26 µm wide. Silicified adaxial epidermal or guard cells present.

In transverse section: Cuticle less than 1 µm thick above the lamina, above midrib and margin 3–5 µm thick. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral. Palisade 1-layered. Some silicified cells present, especially near the abaxial epidermis. Midrib with two opposing vascular arcs, the vascular bundles in the upper arc separate or partially merged, fibre caps present; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll and epidermis, the phloem parenchyma of midrib and petiole; prismatic crystals present in the periphery of the bundle sheaths above and below the veins, the parenchyma and phloem parenchyma of midrib and petiole, abundant in the subepidermal cell layer.

16. *Ficus prolixa* G. Forst.

Material studied: MARQUESAS. Nukuhiva, *B. H. Gagne 1281*. MARIANAS. Saipan, *F. R. Fosberg 31278*.

In surface view: Indumentum present on petiole and lamina, simple hairs on petiole, glandular hairs with 1- or 2-celled heads common on lamina and few with 2- or 4-celled heads on petiole. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–16 abaxially. Stomata 26–33 μm long and 19–24 μm wide.

In transverse section: Cuticle less than 1 μm thick above the lamina, above midrib and margin 2–4 μm thick. Epidermis single-layered on both sides, some epidermal cells silicified. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral. Palisade 1-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of midrib and petiole; prismatic crystals with very few of them in poorly differentiated cristarque cells present in the periphery of the bundle sheaths above and below the veins, the ground tissue parenchyma and phloem parenchyma of midrib and petiole, and abundant in the cell layer between the peripheral sclerenchyma and epidermis.

17. *Ficus pseudoconcinna* Chantaras.

Material studied: INDONESIA. Northern Sulawesi, *T. C. Whitmore & K. Sidiyasa TCW 3429*.

In surface view: Indumentum abaxially of glandular hairs with 1- or 2-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 23–28 μm long and 14–19 μm wide; giant stomata above veins or mixed with normal stomata in the lamina, 33–36 μm long and 26–28 μm wide. Silicified adaxial epidermal or guard cells present.

In transverse section: Cuticle 1–2 μm thick above the lamina, above midrib and margin 4–5 μm thick. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral, some silicified cells present, especially near the abaxial epidermis. Palisade 1-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll and phloem parenchyma of midrib and petiole, absent in epidermis; prismatic crystals present in the periphery of the bundle sheaths above and below the veins, few in the phloem parenchyma of midrib, parenchyma and phloem parenchyma of the petiole, abundant in the cell layer between epidermis and peripheral sclerified tissue.

18. *Ficus religiosa* L. (Figs. 3-3E, F, 3-4A, E, 3-5A)

Material studied: THAILAND. Kanchanaburi, *B. Chantarasuwan 150910–2*. VIETNAM. Hanoi, *C. d'Alleizette s.n.*

In surface view: Indumentum present abaxially, glandular hairs with 1-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 28–33 μm long and 23–28 μm wide; giant stomata above veins, 33–36 μm long and 28–33 μm wide.

In transverse section: Cuticle less than 1 μm thick above the lamina, above midrib and margin 4–9 μm thick. Epidermis single-layered on both sides. Stomata level with epidermis, outer and inner cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral. Palisade multi-layered, gradually changing to a compact chlorenchyma tissue; some cell groups silicified especially near the abaxial epidermis. Midrib with a closed ring of vascular tissue sheathed by fibres; subepidermal ground tissue weakly sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins circular, not transcurrent, xylem and phloem sheathed by fibres; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, the phloem parenchyma of midrib and petiole, also in the epidermis of the midrib; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths around the veins, the phloem parenchyma and parenchyma of midrib and petiole, also in the cell layer between the epidermis and the peripheral sclerified tissue.

19. *Ficus salicifolia* Vahl (Figs. 3-3A, C)

Material studied: ETHIOPIA. Abita, *O. Beccari 39*. SAUDI ARABIA. *J. Bornmüller 646*.

In surface view: Indumentum of simple hairs on the petiole, glandular hairs with 1- or 2-celled heads abaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 33–42 μm long and 28–33(–38) μm wide, giant stomata above veins or mixed with normal stomata in the lamina, 47–52 μm long and 33–38(–43) μm wide.

In transverse section: Cuticle less than 1 μm thick above the lamina, above midrib and margin 2–3 μm thick. Epidermis single-layered on both sides. Stomata slightly sunken, outer and inner cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral. Palisade 2-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue not sclerified. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap in the distal part of the petiole, peripheral ground tissue not sclerified. Pith bundles present in petiole and present or absent from midrib. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, the phloem parenchyma of the midrib, and the phloem parenchyma and parenchyma of the petiole, few in the bundle sheaths around the veins; prismatic crystals present in the parenchyma of midrib and petiole.

Note: Both samples differed somewhat, the stomata in the Arabian sample (Bornmüller 646) are bigger in size than in the Ethiopian specimen and the midrib showed a pith bundle. In all other characters the specimens were similar.

20. *Ficus saxophila* Blume

Material studied: THAILAND. Saraburi, *B. Chantarasuwan 180910–1*. INDONESIA. Timor, *C. d'Alleizette s.n.*

In surface view: Indumentum present, simple hairs absent or present on petiole, glandular hairs with 1- or 2-celled heads abaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 8–12 abaxially. Stomata 23–28 μm long and 19–24 μm wide; giant stomata above veins or mixed with normal stomata in the lamina, 35–43 μm long and 33–38 μm wide.

In transverse section: Cuticle less than 1 μm thick above the lamina, above midrib and margin 4–6 μm thick. Epidermis single-layered on both sides. Stomata level with epidermis, and sometimes slightly raised or slightly sunken, outer and inner cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral. Palisade 1- or 2-layered. Midrib with a more or less closed vascular ring, intergrading with two opposing arcs, sheathed by fibres; subepidermal tissue not sclerified. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue not sclerified. Pith bundles present in midrib and petiole. Veins circular, not transcurrent, xylem and phloem sheathed by fibres; minor veins embedded in mesophyll. Marginal sclerenchyma strands absent. Druses present in mesophyll, the phloem parenchyma of midrib and petiole, also in the epidermis of the midrib and petiole; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths around the veins, the phloem parenchyma and the parenchyma of midrib and petiole.

21. *Ficus subpisocarpa* Gagnep. subsp. *pubipoda* C. C. Berg

Material studied: THAILAND. Rayong, *B. Chantarasuwan 120910–6*.

In surface view: Indumentum present at base of petiole, composed of simple hairs. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 23–28 μm long and 19–24 μm wide, giant stomata above veins, 28–33 μm long and 21–24 μm wide.

In transverse section: Cuticle less than 1 μm thick above the lamina, above midrib and margin 2–3 μm thick. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral. Palisade 1-layered. Midrib with two opposing vascular arcs surrounded by fibre caps; subepidermal tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and the phloem parenchyma of midrib and petiole, few in the epidermis of the midrib; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths above and below the veins, the parenchyma of midrib and petiole, and abundant in the cell layer between the epidermis and peripheral sclerified tissue.

22. *Ficus superba* (Miq.) Miq. (Fig. 3-4F)

Material studied: THAILAND. Rayong, *B. Chantarasuwan 120910–1*. INDONESIA. East Java, *P. J. A. Kessler 714*.

In surface view: Indumentum abaxially of glandular hairs with 1-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 6–9 abaxially. Stomata 28–33 µm long and 23–28 µm wide; giant stomata above veins, 33–38 µm long and 23–28 µm wide.

In transverse section: Cuticle less than 1 µm thick above the lamina, above midrib and margin 4–6 µm thick. Epidermis single-layered on both sides. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially. Mesophyll dorsiventral, some silicified cells present, especially near the abaxial epidermis. Palisade 1-layered. Midrib with two opposing vascular arcs intergrading with a ring of vascular bundles sheathed by fibres; subepidermal ground tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, parenchyma and phloem parenchyma of midrib and petiole, few in the epidermis of midrib and petiole; prismatic crystals present in the periphery of the bundle sheaths above and below the veins, the parenchyma of midrib and petiole, and abundant in the cells between the epidermis and the peripheral sclerified tissue.

23. *Ficus tsjakela* Burm.f.

Material studied: SRI LANKA. Paradeniya, *A. J. G. H. Kostermans 27682*. INDIA. Nedunkayany, *D. R. Priyadarsanan 4*.

In surface view: Indumentum abaxially of glandular hairs with 1-celled heads. Cuticle smooth adaxially, slightly ridged abaxially. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 28–38µm long and 23–28 µm wide; giant stomata above veins, 37–43 µm long and 33–38 µm wide.

In transverse section: Cuticle 2–5 µm thick above the lamina, above midrib and margin 6–10 µm thick. Epidermis single-layered on both sides; sometimes outer periclinal abaxial epidermal wall and cuticle slightly ridged, producing a papillae-like appearance. Stomata slightly sunken, outer and inner cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral. Palisade multi-layered, gradually changing to a compact chlorenchyma tissue; some groups of palisade cells silicified. Midrib with partially merged bundles forming two opposing arcs surrounded by fibre caps; subepidermal tissue sclerified on both sides. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap, peripheral tissue not sclerified. Pith bundles present in midrib and petiole. Veins circular, not transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands absent. Druses present in mesophyll, phloem parenchyma and parenchyma of midrib and petiole, few in the epidermis of lamina; prismatic crystals (partly in weakly differentiated cristarque cells) present in the periphery of the bundle sheaths around the veins, few in the parenchyma of midrib and petiole.

Note: Both samples differ somewhat, abaxial epidermal wall and cuticle ridged, producing papillae-like appearance present in the sample (*Kostermans 27682*) from Sri Lanka, but very weak (or absent) in the Indian sample (*Priyadasanan 4*).

24. *Ficus verruculosa* Warb.

Material studied: ZAMBIA. Southern Province, *C. C. Berg & M. G. Bingham 1374*. Lusaka, *M. G. Bingham 2124*.

In surface view: Indumentum present abaxially of glandular hairs with 1-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 6–9 abaxially. Stomata 37–43 µm long and 28–33 µm wide; giant stomata 37–47 µm long and 33–38 µm wide.

In transverse section: Cuticle less than 1 µm thick above the lamina, above midrib and margin 3–5 µm thick. Epidermis single-layered on both sides. Stomata level with epidermis or slightly sunken, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells occasionally present adaxially. Mesophyll dorsiventral, some silicified cells present, especially near the abaxial epidermis. Palisade 1(–2)-layered. Midrib with two opposing vascular arcs of partially merged bundles sheathed by fibres; subepidermal tissue not sclerified. Petiole with a cylinder of separate to partially merged bundles, without fibre caps, peripheral tissue not sclerified. Pith bundles present in the petiole, absent or present in the midrib. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands absent. Druses present in mesophyll, phloem parenchyma and parenchyma of midrib and petiole, few in the epidermis of midrib and petiole; prismatic crystals present in the periphery of the bundle sheaths above and below the veins, abundant in the parenchyma of midrib and petiole, few in the phloem parenchyma of midrib and petiole.

25. *Ficus virens* Aiton (Fig. 3-5C)

Material studied: THAILAND. Kanchanaburi, *J.F. Maxwell 93–1186*. AUSTRALIA. Queensland, *B. Gray 1994.*

In surface view: Indumentum abaxially of glandular hairs with 1-celled heads. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 7–12 abaxially. Stomata 15–21 μm long and 12–19 μm wide, giant stomata 21–28 μm long and 18–26 μm wide.

In transverse section: Cuticle less than 1 μm thick above the lamina, above midrib and margin 3–5 μm thick. Epidermis single-layered on both sides; some epidermal cells silicified. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially, cystoliths in ordinary epidermal cells adaxially. Mesophyll dorsiventral. Palisade multiple layered, gradually changing to a compact spongy tissue. Midrib of two opposing vascular arcs surrounded by fibre caps; subepidermal ground tissue sclerified. Petiole with a cylinder of separate to partially merged bundles, each with a fibre cap; peripheral ground tissue sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, phloem parenchyma of midrib and petiole; prismatic crystals (partly in cristarque cells) present in the periphery of the bundle sheaths above and below the veins, the parenchyma and phloem parenchyma of midrib and petiole, and abundant in cell layer between the peripheral sclerified tissue and epidermis.

Leaf anatomical descriptions of species of *Ficus* section *Leucogyne*

26. *Ficus amplissima* J. E. Sm.

Material studied: SRI LANKA. North-Western Province, Puttalan district *L. H. Cramer 4670*. INDIA. Coimbatore, *D. R. Priyadarsanan 5.*

In surface view: Indumentum of glandular hairs with 1- or 2-celled heads abaxially and adaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8, mainly confined to adaxial surface. Stomata 32–43 μm long and 23–28 μm wide; giant stomata 47–52 μm long and 32–38 μm wide

In transverse section: Cuticle 2–3 μm thick adaxially, above midrib and margin 5–8 μm thick. Epidermis 2–3-layered on both sides. Stomata slightly sunken, outer and inner cutucular ledges present. Enlarged lithocysts present both adaxially and abaxially. Mesophyll dorsiventral, silicified cell groups present or absent. Palisade 2-layered. Midrib with two opposing vascular arcs surrounded by fibre caps, subepidermal ground tissue sclerified. Petiole with a cylinder of separate to partially merged bundles, each with or without a fibre cap; phloem strands present in pith of midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, ground tissue parenchyma and phloem parenchyma of midrib and petiole, few in the bundle sheaths around the veins; prismatic crystals extremely rare or absent in the parenchyma of midrib and petiole.

Note: The two specimens studied differ rather strongly in silicified cell groups, which are absent in sample from Sri Lanka (*Cramer 4670*).

27. *Ficus rumphii* Blume

Material studied: THAILAND. Ratchaburi, *B. Chantarasuwan 140910–1*. CAMBODIA. Stoeung Treng, *M. Meng 155*.

In surface view: Indumentum of simple hairs on the petiole, glandular hairs with 1- or 2-celled heads present adaxially and abaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8, mainly confined to adaxial surface. Stomata 23–38 μm long and 18–26 μm wide; giant stomata 42–47 μm long and 32–38 μm wide

In transverse section: Cuticle 1–2 μm thick adaxially, above midrib and margin 7–10 μm thick. Epidermis 2(–3)-layered at both sides, cells in outer layer smaller than in the inner layer(s). Stomata level with epidermis, outer and inner cuticular ledges present. Enlarged lithocysts present both adaxially and abaxially. Mesophyll dorsiventral, silicified cell groups absent. Palisade 1–2-layered. Midrib with two opposing vascular arcs surrounded by fibre caps, subepidermal ground tissue not sclerified. Petiole with a cylinder of separate to partially merged bundles, each with or without a fibre cap; phloem strands present in pith of midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, ground tissue parenchyma and phloem parenchyma of midrib and petiole, few in the bundle sheaths around the veins; prismatic crystals extremely rare or absent in the parenchyma of midrib and petiole.

Leaf anatomical descriptions of species of *Ficus* subsection *Conosycea*

28. *Ficus glaberrima* Blume subsp. *siamensis* (Corner) C. C. Berg

Material studied: THAILAND. Sa Kaeo, *B. Chantarasuwan 110910–3*.

In surface view: Indumentum of glandular hairs with 1- or 2-celled heads present abaxially and adaxially. Cuticle smooth. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8, mainly confined to adaxial surface. Stomata 18–24 μm long and 16–19 μm wide; giant stomata 32–38 μm long and 28–33 μm wide.

In transverse section: Cuticle less than 2 μm thick adaxially, above midrib and margin 3–6 μm thick. Epidermis 2(–3)-layered on both sides, cells in outer layer smaller than in the inner layer. Stomata level with epidermis, outer and inner cuticular ledges present. Enlarged lithocysts present adaxially and abaxially. Mesophyll dorsiventral, silicified cell groups absent. Palisade

1-layered. Midrib with two opposing vascular arcs surrounded by fibre caps, subepidermal ground tissue not sclerified. Petiole with separate to partially merged bundles, each with fibre caps; phloem strands present in pith of midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Marginal sclerenchyma strands present. Druses present in mesophyll, ground tissue parenchyma and phloem parenchyma of midrib and petiole, few in the bundle sheaths around the veins; prismatic crystals extremely rare or absent in the parenchyma of midrib and petiole.

Discussion

Does leaf anatomy enable species recognition?

Many species of subsect. *Urostigma* show such a high amount of morphological variation (Chantarasuwan et al., 2013), that identification may be troublesome. The results of our present study show, that in case of multiple samples per species, the leaf anatomical variation is fairly low, but not significant. This suggests that leaf anatomical characters may facilitate an accurate identification of species, especially when used together with morphological characters. However, not all anatomical characters are useful, which we will discuss per character:

1) ***Indumentum***. Sonibare et al. (2005) consider the type of indumentum to be of little diagnostic value. However, in the present subsection hair types are typical for several species, e.g., 1- or 2-celled capitate glandular hairs are typical for many species of subsect. *Urostigma*, also sect. *Leucogyne* and subsect. *Conosycea*, a view consistent with Berg & Corner (2005). Simple hairs on the petiole are characteristic for some species such as *F. caulocarpa*, *F. concinna* and *F. middletonii*.

2) ***Epidermis.*** Van Greuning et al. (1984) indicated that the multiple epidermis is typical for several species. Indeed, the multiple epidermis types (see results) are typical for sect. *Leucogyne*, subsect. *Conosycea*, and three species of subsect. *Urostigma: Ficus arnottiana* with a "normal" multiple epidermis, and *F. hookeriana* and *F. orthoneura* with enlarged, hypodermis-like cells in the "subepidermal" layer. In the latter a new developmental study would be needed to determine whether the "subepidermal" layer is derived from the ground meristem or from the protoderm to know for sure whether these species have a true hypodermis or a multiple epidermis.

3) ***Stomatal size.*** Wilkinson (1979) reviewed the literature on stomatal size variation. She mentioned that stomatal size may vary according to environmental conditions and that the diagnostic value of stomatal size needs to be tested in each case. In the same lamina differences may also exist, caused by the time of development, as the earliest stomata along the veins are larger than those in the areolae (Berg & Corner, 2005). Most authors agree that stomatal size is usually sufficiently stable to be used as a diagnostic character, but some authors consider that stomatal size is too variable to be of diagnostic value, and the term 'small' is generally applied to stomata with guard cell of less than c. 15 µm long, and 'large' to stomata with guard cells of more than c. 38 µm long (Wilkinson, 1979). In *Ficus* subsect. *Urostigma* stomata usually are of intermediate size (e.g., *F. salicifolia* shows the full range, from medium to large), but in view of the limited number of specimens studied we refrain from using the size of stomata for species recognition. The occurrence of giant stomata seems suitable for species recognition, however, more samples are required, especially of rare species, to really appreciate this character.

4) ***Radiating epidermal cells.*** The radiating epidermal cells around the base of lithochysts generally occur in the lower leaf surface, but are found on both sides in Sect. *Leucogyne*, *F. glaberrima* subsp. *siamensis* (subsect. *Conosycea*) and *F. arnottiana*. There are usually 5–8 radiating cells in subsect. *Urostigma* (Berg & Corner, 2005), but we also found many species with 8–12 cells, and some species even with 8–16 cells, which increases the range for subsect. *Urostigma* to 5–16 cells The number of radiating cells is rather constant per species.

5) ***Lithocysts.*** Most lithocysts are inflated and mostly present in the lower part of the mesophyll. However, they form a part of the abaxial epidermis but the cells have intruded into the spongy tissue or abaxial palisade layer (if present). The only exception in subsection *Urostigma* is *F. arnottiana*, where they occur on both sides, a character shared with subsect. *Conosycea* (Berg & Corner, 2005) and sect. *Leucogyne*. The unenlarged lithocysts in ordinary epidermal cells, occur generally adaxially and are found in many species of subsect. *Urostigma*. They were already reported for *F. religiosa* (Solereder, 1899; Sajwan et al., 1977) and *F. salicifolia* (Renner, 1910), we also found them in *F. cordata*, *F. prolixa*, *F. saxophila* and *F. tsjakela*. Moreover, we found that the lithocysts in ordinary epidermal cells are absent in sect. *Leucogyne*, *F. glaberrima* subsp. *siamensis* (subsect. *Conosycea*), *F. arnottiana*, and *F. orthoneura*, which all have a multiple epidermis; *F. hookeriana* is the only species with an adaxial multiple epidermis with the cystoliths in ordinary epidermal cells.

6) ***Crystals and Silicified cells.*** Prismatic crystals are mainly found in the bundle sheaths of the veins, but they also occur in the parenchyma cells of midrib and petiole and they are usually more abundant near the sclerenchyma caps where they often occur in the cristarque cells. Many species form a peripheral sclerenchyma ring in the petiole and then the prismatic crystals occur in the parenchyma outside the ring, usually in cristarque cells. They rarely occur in the phloem parenchyma of midrib and petiole. We found few prismatic crystals in the leaves of sect. *Leucogyne* and *F. glaberrima* subsp. *siamensis* (subsect. *Conosycea*). They are more abundant in the leaves of subsect. *Urostigma*, though *F. arnottiana* is the only exception with absent or rare prismatic

crystals, in which it resembles the two other groups. The crystals may provide good characters for section recognition. The diagnostic value of the presence or absence of silicified cell groups in *Ficus* appears to be fairly limited. In the eight species of *Urostigma*, in which they occur and of which more than one specimen was studied they appeared to vary in no less than four species (see table 3-1). Absence of silicified cell groups appeared to be "constant" in five species. More samples are obviously needed to further test this character, that appeared so diagnostic in the Olacaceae (Baas et al., 1982).

7) ***Bundle sheath extensions.*** We agree with Van Greuning et al. (1984) that the two forms of the bundle sheath, circular or transcurrent, are useful in the identification of species, although the difference is not a totally absolute one: also the tertiary bundles with circular fibre sheaths may have very minor parenchyma bundle sheath extensions to the upper (and more rarely also lower) epidermis.

8) ***Sclerenchyma.*** Several types of sclerenchyma (strands in the leaf margins, sclerified peripheral ground tissue in petiole and midrib) occur in subsect. *Urostigma*. The presence or absence of subepidermal sclerified layers in midrib and petiole, as well as marginal sclerenchyma strands seems diagnostic (Table 3-1), although in some species (*F. arnottiana*) they are very poorly developed.

With the available data, admittedly based on a very limited number of samples per species, it was quite easy to produce an identification key to most individual species, with often two individual leaf anatomical characters available in the final leads separating two look-alike species. The African species *F. ingens* and the Asian *F. virens* could not be separated by leaf anatomical characters. However, in this case the widely different geographic distribution easily resolves any identification problem.

The diagnostic value of many leaf anatomical characters raises the question of their value in phylogeny reconstruction. This question will be addressed in our ongoing study on the phylogeny of subsection Urostigma, in which we will optimize leaf anatomical character states on the most robust phylogeny of this subsection and its sister clades.

The position of *Ficus amplissima* and *Ficus rumphii*

Berg & Corner (2005) placed *F. amplissima* and *F. rumphii* (sect. *Leucogyne* of Corner, 1959) in subsect. *Urostigma*, based on the presence of intermittent growth (long internodes alternating with short internodes, apparent by the grouped leaves) and the difference in colour between the older branches from the former season and the current growth branches. However, the flowers of both species differ strongly from most species in subsect. *Urostigma*, therefore, Chantarasuwan et al. (2013) placed both species in sect. *Leucogyne*. The leaf

anatomical characters of *F. amplissima* show similarity with *F. arnottiana* of subsect. *Urostigma* whereas *F. rumphii* show similarity with *F. glaberrima* subsp. *siamensis* (subsect. *Conosycea*). Moreover, the molecular phylogeny of Rønsted et al. (2005) shows that *F. rumphii* is embedded within subsect. *Conosycea*, which makes the leaf anatomy congruent with Rønsted's work. Thus *F. rumphii* can be a member of subsect. *Conosycea*. while *F. amplissima* should be in the same clade with *F. arnottiana*. Further phylogenetic research has to substantiate this.

The position of *Ficus arnottiana*

Morphologically, *F. arnottiana* is typically a member of subsect. *Urostigma*, though the distribution of the staminate flowers (abundant around the ostiole and a few dispersed or if few staminate flowers are present then only near the ostiole; Chantarasuwan et al., 2013) is intermediate between subsect. *Conosycea* (staminate flowers dispersed) and subsect. *Urostigma* (staminate flowers mostly around the ostiole). Leaf anatomically, *F. arnottiana* also shows similarities with subsect. *Conosycea* and sect. *Leucogyne* (though the latter may be a part of subsect. *Conosycea*, see former paragraph), like the enlarged lithocysts present on both sides (not only abaxially) and the presence of a multiple epidermis (Berg & Corner, 2005). Current molecular studies on subsect. *Urostigma* and all species of sect. *Leucogyne* are still unfinished, but preliminary results show that most samples of *F. arnottiana* are placed unambiguously in subsect. *Urostigma* (Chantarasuwan et al., in prep.).

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Table 3-1. Leaf anatomical features of *Ficus* subsection *Urostigma* (Gasp.) C.C.Berg

Species	Epidermis	No. of radiating epidermal cells around lithocysts	Cuticular ridges	Occurrence of enlarged lithocysts	Cristarque cells	Epidermal lithocysts	No. of Palisade layers	Marginal sclerenchyma	Vascular bundle in midrib	Pith bundle		Bundle sheaths	Silicified cells		Simple hair		Glandular hairs		Giant stomata	Inner stomata ledge	Stomatal level	Subepidermal sclerified layer	
										Midrib	Petiole		Mesophyll	Epidermis	Petiole	lamina	Petiole	Lamina				petiole	midrib
subsect. *Urostigma* *F. alongensis*	S	8–12	–	Ab	+	–	1	+	Sep	–	–	V	–	–	+	–	–	–	–	–	L	+	+
F. arnottiana	M (2-3)	5–8	–	Ad, Ab	–	–	(1–) 2	±	N	+	+	V	–	–	–	–	–	+	+	–	L	–	–
F. caulocarpa	S	8–12	–	Ab	+, –	–	2	+	N	+	+	V	+	–	+	–	–	+	–	–	L	+	+
F. chiangraiensis	S	5–8	–	Ab	+	–	2	+	N	+	+	V	+	–	–	–	–	+	+	–	L	+	+
F. concinna	S	8–12	–	Ab	+	–	3-5	+	N	+	+	V	+	–	+	–	–	+	+	–	L	+	+
F. cordata	S	8–16	–	Ab	+	+,–	2–5	–	N	+	+	C	+,–	–	–	–	–	+	+	–	Sun	+	+
F. densifolia	S	5–8	–	Ab	–	–	2–5	+	N	–	+	V	–	–	–	–	–	+	–	+	L	–	+
F. geniculata	S	8–12	–	Ab	+	+	2	+	N	+	+	V	–	–	–	–	–	+	+	–	L	+	+
F. henneana	S	8–12	–	Ab	–	+	2	+	N	+	+	V	–	–	–	–	–	–	+	–	L	–	+
F. hookeriana	M (2)	5–8	+	Ab	+,–	+	1–2	–	N	+	+	V	–	–	–	–	–	+	+	–	L	–	+
F. ingens	S	8–16	–	Ab	+	+	2–5	+	N	+	+	V	+,–	–	+,–	+,–	–	+	+	–	L	+	+
F. lecardii	S	6–9	–	Ab	+,–	+	1	–	N	+	+	V	–	–	–	–	–	–	–	+	Sun	–	+
F. middletonii	S	8–12	–	Ab	+	–	4–5	+	N	+	+	V	–	–	+	+	–	+	+	–	L	+	+
F. orthoneura	M (2)	5–8	+	Ab	–	–	1–2	+	Sep	+	+	V	–	–	–	–	–	+	+	–	L	+	+
F. prasinicarpa	S	5–9	–	Ab	+,–	+,–	1	+	N	+	+	V	+	+	–	–	–	+	+	–	L	+	+
F. prolixa	S	8–16	–	Ab	+,–	+,–	1	+	N	+	+	V	+	+,–	+	–	+	+	–	–	L	+	+

Table 3-1. Continued

Species	Epidermis	No. of radiating epidermal cells around lithocysts	Cuticular ridges	Occurrence of enlarged lithocysts	Cristarque cells	Epidermal lithocysts	No. of Palisade layers	Marginal sclerenchyma	Vascular bundle in midrib	Pith bundle		Bundle sheaths	Silicified cells		Simple hair		Glandular hairs		Giant stomata	Inner stomata ledge	Stomatal level	Subepidermal sclerified layer	
										Midrib	Petiole		Mesophyll	Epidermis	Petiole	lamina	Petiole	Lamina				petiole	midrib
F. pseudoconcinna	S	5–8	–	Ab	+	+,–	1	+	N	+	+	V	+	+	–	–	–	+	+	–	L	+	+
F. religiosa	S	8–12	–	Ab	+	+,–	2–5	+	N, CR	+	+	C	+	+	–	–	–	+	+	+	L	+	+
F. salicifolia	S	5–8	–	Ab	–	+	2	+	N	+,–	+	V	–	–	+	–	–	+	+	+	Sun	–	–
F. saxophila	S	8–12	–	Ab	+	+,–	1–2	–	N, CR	+	+	C	–	–	+,–	–	–	+	+	+	L, R, Sun	–	–
F. subpisocarpa subsp. *pubipoda*	S	5–8	–	Ab	+	+	1	+	N	+	+	V	–	–	+	–	–	–	+	–	L	+	+
F. superba	S	6–9	–	Ab	+	–	1	+	N	+	+	V	–	–	–	–	–	+	+	–	L	+	+
F. tsjakela	S	5–8	+,–	Ab	+,–	+,–	2–5	–	N	+	+	C	+,–	–	–	–	–	+	+	+	Sun	+	+
F. verruculosa	S	6–9	–	Ab	+,–	+,–	1(–2)	–	N	+,–	+	V	+	+	–	–	–	+	+	–	L, Sun	–	–
F. virens	S	7–12	–	Ab	+	+	4–5	+	N	+	+	V	+	+	–	–	–	+	+	–	L	+	+
sect. Leucogyne *F. amplissima*	M (2-3)	5-8	–	Ad	–	–	2	+	N	+	+	V	+,–	+,–	–	–	–	+	+	+	Sun	–	+, ±
F. rumphii	M (2-3)	5-8	–	Ad	–	–	2	+	N	+	+	V	–	–	+	–	–	+	+	+	L	–	–
subsect. Conosycea *F. glaberrima* subsp. *siamensis*	M (2-3)	5-8 (-9)	–	Ad, Ab	–	–	1	+	N	+	+	V	–	–	–	–	–	+	+	+	L	–	–

** Ab = abaxial, Ad = adaxial, C = circular, CR = closed vascular, E = epidermis, L = level to epidermis, M(n) = multiple with number of layers, N = normal vascularization with cylinder 2 opposing arcs, R = raised, S = simple, Sep = separate bundles, Sun = slightly sunken,V = vertically transcurrent, + = present, – = absent, ± = character weakly developed.

Chapter 4

Pollen morphology of *Ficus* subsection *Urostigma* (Moraceae)

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Abstract

The pollen morphology of *Ficus* subsection *Urostigma* has been studied using light microscopy and scanning electron microscopy. It conforms to the description of *Ficus* pollen in the literature except for the observed rare occurrence of 4-porate pollen, which was unknown so far in the genus. Due to minor variability it was not possible to distinguish any pollen types. No significant pollen morphological differences were found between species with active pollination and species with passive pollination.

Key words: *Ficus*, Moraceae, pollen, pollination.

Introduction

Ficus L. subsect. *Urostigma* (Gasp.) Berg and *F.* subsect. *Conosycea* (Miq.) Berg form section *Urostigma* (Gasp.) Endl. of *F.* subgenus *Urostigma* (Gasp.) Miq. *Ficus* subsect. *Urostigma* comprises 28 species, which are distributed from West Africa and Madagascar through the Asian mainland to Japan and through southern Malesia to Australia and the Pacific (Berg & Wiebes, 1992; Berg & Corner, 2005; Chantarasuwan et al., 2013). All species are trees, many are hemi-epiphytic, some are terrestrial. The syconiums (figs) are usually borne below the leaves, sometimes on the older branches. Staminate flowers occur mostly near the ostiole of the syconium or are regularly dispersed among the pistillate flowers; in some species (e.g., *F. arnottiana* (Miq.) Miq. and *F. virens* Aiton var. *dispersa* Chantaras.) they occur both around the ostiole (abundant) and dispersed (scarce). *Ficus* subsect. *Conosycea* comprises 66 species (Berg & Corner, 2005), their figs are mostly sessile and the staminate flowers are dispersed, as in some of the species of subsect. *Urostigma* (see above).

Literature on the pollen morphology of *Ficus* is scarce (Langeveld & van der Ham, 2005). Recent studies include those by Khan et al. (2001) and Tzeng et al. (2009). The latter provided detailed descriptions and scanning electron micrographs of 28 *Ficus* taxa occurring in Taiwan, three of which belong to subsect. *Urostigma*. According to the available studies, pollen grains of *Ficus* are very small to small monads (largest = equatorial diameter 6–22 μm), 2- or sometimes 3-porate, and quite uniform. The shape of 2-porate grains is ellipsoid, often slightly asymmetrical, one side being more convex than the other (Fig. 4-1G; 4-2E, M; 4-3 E,K). The orientation of the polar axis in 2-porate grains is hard or impossible to determine. The shape of 3-porate grains is triangular in polar view and oblate in equatorial view. Nearly all species have 2-porate pollen, many species (c. 50% according to the literature studied) have minor percentages of 3-porate pollen as well. *Ficus palmata* Forssk. (= *F. pseudosycomorus* Decne.) is reported to have exclusively 3-porate pollen (Horowitz & Baum, 1967). The pores are circular and vary in size from 0.7–2.5 μm. The exine is thin, flexible, up to 1 μm thick and tectate. Mostly, the nexine and sexine are equally thick; sometimes the nexine is slightly thicker. The infratectum is granular with indistinct columellae. The ornamentation is psilate or slightly scabrate.

The relationship between *Ficus* and its pollinators is a classical story (Ramirez, 1969; Wiebes, 1979). All species are pollinated by fig wasps (Agaonidae). Two pollination types have been distinguished: 1. Active pollination, in which pollen is deliberately collected by the wasps and stored in their pollen pockets, and 2. Passive pollination, in which the wasps receive the pollen from the flowers, scattered over their body. Both passive and active pollination are found in section *Urostigma* (Kjellberg et al., 2001).

The aims of the present study is to describe the pollen of *Ficus* subsect. *Urostigma*, trying to find pollen morphological markers supporting the taxonomy (Chantarasuwan et al., 2013) and phylogeny (Chantarasuwan et al., in prep.) of this group, and to assess if there is any difference between the pollen of species with the passive pollination type and species with the active type.

Materials and methods

All material studied belongs to *Ficus* section *Urostigma*. Pollen of 12 out of the 28 species of subsect. *Urostigma* and two species of subsect. *Conosycea* (*F. altissima* Blume and *F. amplissima* J.E.Sm.) was examined (Table 1). The latter two species were included for comparison, because the species of subsect. *Conosycea* share some morphological characters with subsect. *Urostigma* (e.g., deciduousness, staminate flowers dispersed, and the colour of the ovaries partly red). The classification used is according to Chantarasuwan et al. (2013). Among the species studied, *F. prolixa* G.Forst. and *F. virens* var. *dispersa* could have passive pollination, while the other species (including *F. virens* Aiton var. *matthewii* Chantaras.) probably have active pollination (Kjellberg et al., 2001; Kjellberg personal communication, 2012). The pollen samples were taken from collections preserved in the herbaria of the Naturalis Biodiversity Center at Leiden (L) and the Muséum National d'Histoire Naturelle in Paris (P).

All samples were prepared for light microscopy (LM) and scanning electron microscopy (SEM), following the techniques described by Van der Ham (1990). Ten pollen grains per sample were measured. The terminology used follows Punt et al. (2007). The shape of asymmetrical 2-porate pollen grains is described as 'gibbous' in the present study. Although the orientation of the polar axis in 2-porate grains is hard or impossible to determine, the smallest diameter of the grains is still given here as P.

Results

Ficus subsection *Urostigma*

The pollen grains are very small to small, 2– or sometimes 3–porate, rarely 4–porate monads; P x E = 7.7–13.6 x 11.4–19.7 µm. The shape 2–porate grains is ellipsoid or gibbous, while that of 3–porate grains is triangular in polar view and oblate in equatorial view; 4–porate grains are quadrangular in polar view; P/E = 0.56–0.81. The pores are circular and 1.2–4.7 µm diam. The exine is less than 1 µm thick, and the ornamentation is nearly always scabrate (elements < 1 µm: finely punctate, microrugulate or microverrucate).

Table 4-1 Pollen characters of *Ficus* subsect. *Urostigma* and *Conosycea*

Taxa	Distribution	P x E (µm)	P/E	Shape	Aperture system	Pore (µm)	Ornamentation	Figures
Subsect. *Urostigma*								
F. arnottiana	India, Sri Lanka, Nepal	9.8 x 16.4	0.60	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3	microverrucate	4-1 A–C
F. cordata	Africa	11.8 x 16.4	0.72	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3–3.9	microverrucate	4-1 D–F
F. densifolia	India, Sri Lanka	11.5 x 15.5	0.73	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3	microrugulate	4-1 G–I
F. geniculata var. geniculata	SE Asia	9.7 x 15.4	0.62	ellipsoid, gibbous	2-porate	1.6	indistinctly punctate	4-1 J–L
F. ingens	Africa	11.6 x 16.2	0.71	ellipsoid, gibbous	2-porate	2.3–3.1	indistinctly punctate	4-1 M–O
F. orthoneura	SE Asia	11.5 x 14.1	0.81	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	1.6	microrugulate	4-2 A–C
F. prolixa	W Pacific	7.7 x 11.4	0.67	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	1.2	indistinctly microverrucate	4-2 D–F
F. pseudoconcinna	Sulawesi	9.3 x 14.0	0.66	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.0	indistinctly microverrucate	4-2 G–I
F. religiosa	India to SE Asia	13.6 x 18.9	0.72	ellipsoid, gibbous	2-porate	1.6–2.3	indistinctly microverrucate	4-2 J–L
F. salicifolia	Africa	12.9 x 19.7	0.65	ellipsoid, gibbous, triangular, quadrangular	2-, 3- and 4-porate (50 : 20 : 1)	3.9–4.7	microverrucate	4-2 M–O
F. superba	SE Asia, W Malesia	8.3 x 13.0	0.63	ellipsoid, gibbous	2-porate	1.6	indistinctly microverrucate	4-3 A–C
F. virens var. dispersa	Malesia, W Pacific	10.8 x 16.5	0.65	ellipsoid, gibbous	2-porate	2.3	indistinctly microverrucate	4-3 D–F
F. virens var. matthewii	India, Sri Lanka	11.9 x 17.0	0.70	ellipsoid, gibbous, triangular	2- and 3-porate (50 : 1)	2.3–3.9	microverrucate	4-3 G–I
Subsect. *Conosycea*								
F. altissima	SE Asia, Malesia	10.7 x 14.8	0.72	ellipsoid, gibbous	2-porate	2.3	microverrucate	4-3 J–L
F. amplissima	India, Sri Lanka	9.2 x 16.4	0.56	ellipsoid, gibbous	2-porate	2.3	psilate	4-3 M–O

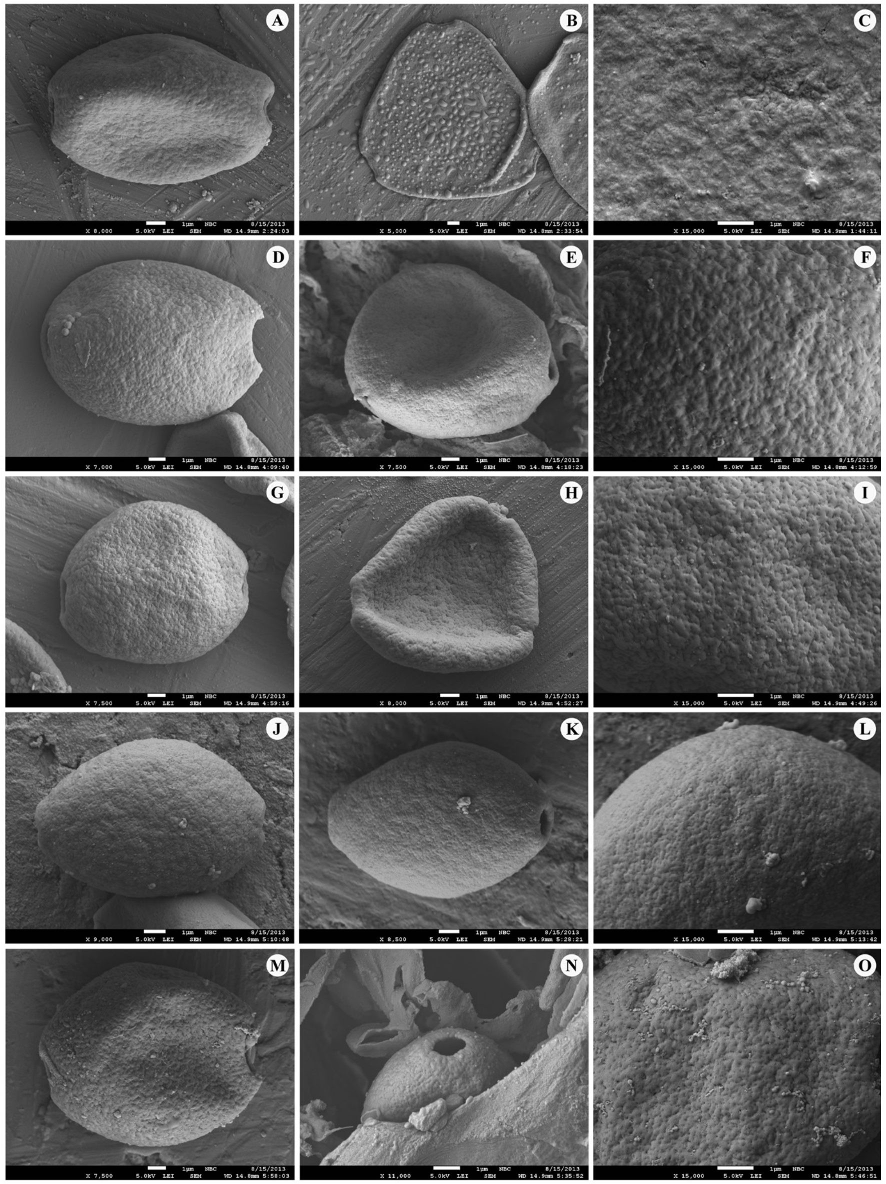

FIGURE 4-1. A-C. Pollen of *F. arnottiana* (from *Kurz s.n.*): A. ellipsoid grain, B. triangular grain in polar view, C. indistinctly microverrucate surface; D-F. Pollen of *F. cordata* (from *Robert J. Rodin 2969*): D. ellipsoid grain, E. triangular grain in surface view, *F.* indistinctly microverrucate surface; G-I. Pollen of *F. densifolia* (from *Etienne 5156*): G. gibbous grain, H. triangular grain in polar view, I. microrugulate surface; J-L. Pollen of *F. geniculata* var. *geniculata* (from *Chantarasuwan 220910-1*): J. gibbous grain, K. grain with circular pore, L. indistinctly punctate surface. M-O. Pollen of *Ficus ingens* (from *Lotsy & Goddijn 379*): M. ellipsoid grain, N. circular pore, O. indistinctly punctate surface. All photographs by B. Chantarasuwan.

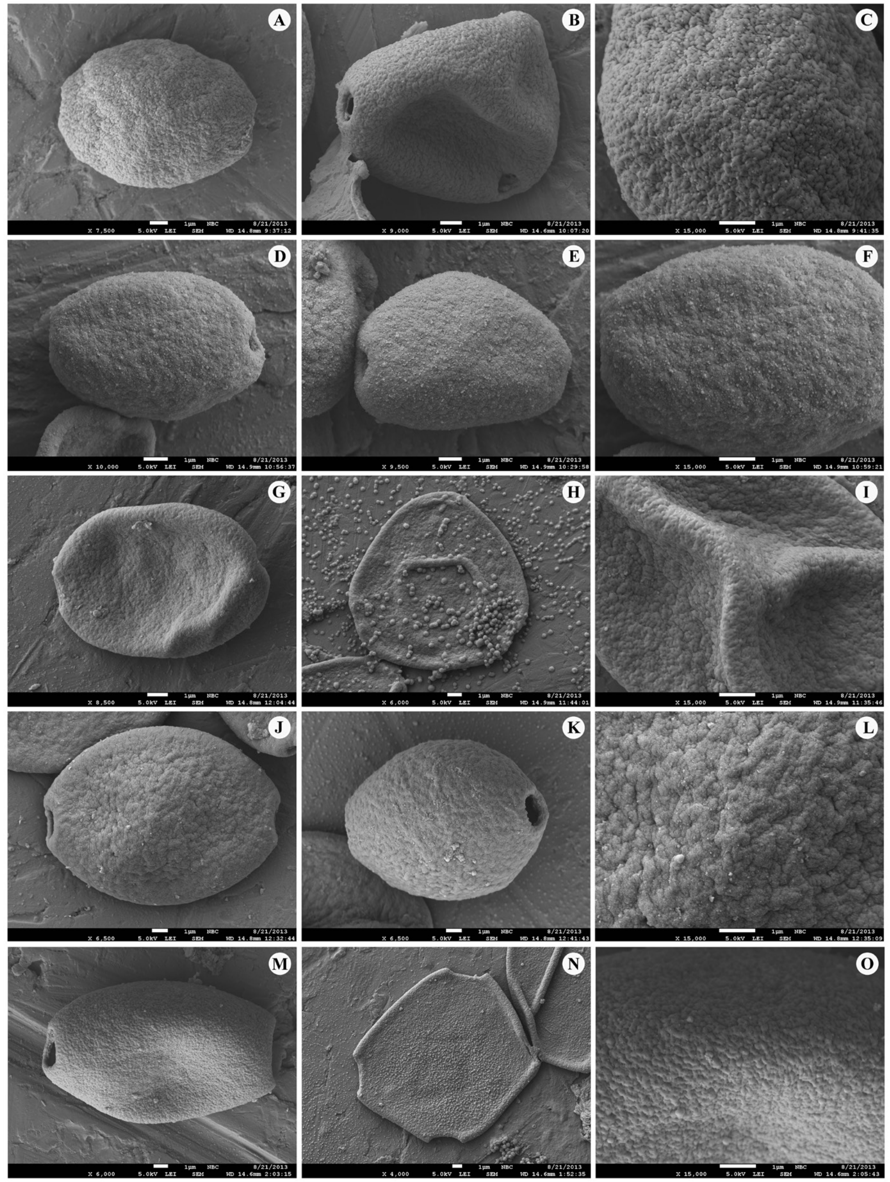

FIGURE 4-2. A-C. Pollen of *F. orthoneura* (from *M.M. Cavalerie & Fortunat 2050*): A. ellipsoid grain, B. triangular grain in polar view, C. microrugulate surface; D-F. Pollen of *F. prolixa* (from *Florence 10308*): D. ellipsoid grain, E. gibbous grain, F. indistinctly microverrucate surface; G-I. Pollen of *F. pseudoconcinna* (from *T.C. Whitmore & K. Sidiyasa TCW3429*): G. ellipsoid grain, H. triangular grain in polar view, I. indistinctly microverrucate surface; J-L. Pollen of *F. religiosa* (from *W. Koelz 4030*): J. ellipsoid grain, K. grain with circular pore, L. indistinctly microverrucate surface; M-O. Pollen of *Ficus salicifolia* (from *J. Léonard 4959*): M. ellipsoid grain, N. quadrangular grain in polar view, O. microverrucate surface. All photographs by B. Chantarasuwan.

Ficus arnottiana **(Miq.) Miq. (Fig. 4-1A–C)**
Material: Sri Lanka. Maison, 1864, *Kurz s.n.* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 9.8 x 16.4 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.60. Proportion of 2– and 3–porate grains about 50/1. Pores circular, about 2.3 µm diam. Exine thin (<1 µm), microverrucate.

Ficus cordata **Thunb. (Fig. 4-1D–F)**
Material: South–West Africa. Namib desert, 17 Dec 1947, *Robert J. Rodin 2969* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.8 x 16.4µm. Shape of 2–porate grains ellipsoid or gibbous, of 3– porate grains triangular in polar view and oblate in equatorial view; P/E = 0.72. Proportion of 2– and 3–porate grains about 50/1. Pores circular, 2.3–3.9 µm diam. Exine thin (< 1 µm), microverrucate.

Ficus densifolia **Miq. (Fig. 4-1G–I)**
Material: Réunion. 7 Apr 1975, *Etienne 5156* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.5 x 15.5 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.73. Proportion of 2– and 3–porate grains about 50/1. Pores circular, about 2.3 µm diam. Exine thin (<1 µm), microrugulate.

Ficus geniculata **Kurz. var.** ***geniculata*** **(Fig. 4-1J–L)**
Material: Thailand. Phitsanulok, 22 Sept 2010, *Chantarasuwan 220910-1*(L).

Pollen grains small, 2–porate; P x E = 9.7 x 15.4 µm. Shape ellipsoid or gibbous; P/E = 0.62. Pores circular, about 1.6 µm diam. Exine thin (<1 µm), indistinctly punctate.

Ficus ingens **(Miq.) Miq. (Fig. 4-1M–O)**
Material: South Africa. Magaliesberge, Aug 1925, *Lotsy & Goddijn 379* (L)

Pollen grains small, 2–porate; P x E = 11.6 x 16.2 µm. Shape ellipsoid or gibbous; P/E = 0.71. Pores circular, 2.3–3.1 µm diam. Exine thin (<1 µm), indistinctly punctate.

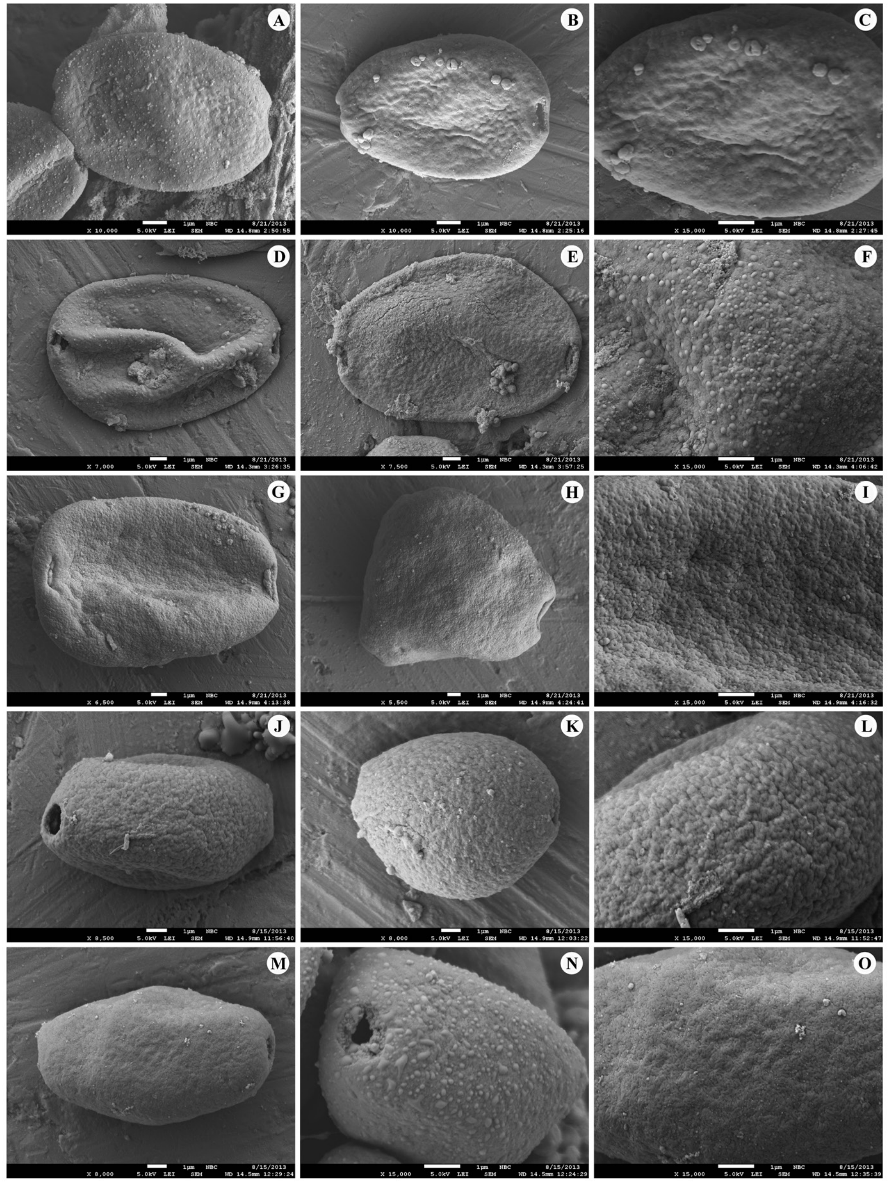

FIGURE 4-3. A-C. Pollen of *F. superba* (from *F.S.P. Ng FRI 5047*): A. ellipsoid grain, B. a grain show circular pore, C. indistinctly microverrucate surface; D-F. Pollen of *F. virens* var. *dispersa* (from *Floyd NGF 6457*): D. a grain show 2–porate, E. gibbous grain, F. indistinctly microverrucate surface; G-I. Pollen of *F. virens* var. *matthewii* (from *Ridsdale 722*): G. ellipsoid grain, H. triangular grain in polar view, I. microverrucate surface; J-L. Pollen of *F. altissima* (from *Chantarasuwan 281111-2*): J. ellipsoid grain with circular pore, K. gibbous grain, L. microverrucate surface; M-O. Pollen of *Ficus amplissima* (from *Wirawan et al. 1133*): M. ellipsoid grain, N. circular pore, O. psilate surface. All photographs by B. Chantarasuwan.

Ficus orthoneura **H.Lév. & Vaniot (Fig. 4-2A–C)**
Material: China. Kouy–Tchéou, 6 Jun 1904, *M.M. Cavalerie & Fortunat 2050* (P).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.5 x 14.1 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.81. Proportion of 2– and 3–porate grains about 50/1. Pore circular, about 1.6 µm diam. Exine thin (<1 µm), microrugulate.

Ficus prolixa **G. Forst. (Fig. 4-2D–F)**
Material: Tahiti. Mont Hiurai, 10 May 1990, *Florence 10308* (L).

Pollen grains very small, 2– or 3–porate; P x E = 7.7 x 11.4 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.67. Proportion of 2–porate and 3–porate grains about 50/1. Pore circular, about 1.2 µm diam. Exine thin (<1 µm), indistinctly microverrucate.

Ficus pseudoconcinna **Chantaras. (Fig. 4-2G–I)**
Material: Indonesia. Sulawesi, 17 Sep 1984, *T.C. Whitmore & K. Sidiyasa TCW3429* (L).

Pollen grains small, 2– or sometimes 3–porate; P x E = 9.3 x 14.0 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.66. Proportion of 2– and 3–porate grains about 50/1. Pores circular, about 2.0 µm diam. Exine thin (<1 µm), indistinctly microverrucate.

Ficus religiosa **L. (Fig. 4-2J–L)**
Material: India. Punjab, 23 Jan 1933, *W. Koelz 4030* (L).

Pollen grains small, 2–porate; P x E = 13.6 x 18.9 µm. Shape ellipsoid or gibbous; P/E = 0.72. Pores circular, about 1.6–2.3µm diam. Exine thin (<1 µm), indistinctly microverrucate.

Ficus salicifolia **Vahl (Fig. 4-2M–O)**
Material: Libye. Djebel Uweinat, 12 Dec 1968, *J. Léonard 4959* (P).

Pollen grains small, 2– or sometimes 3–porate, rarely 4–porate; P x E = 12.9 x 19.7 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view, of 4–porate grains quadrangular in polar view; P/E = 0.65. Proportion of 2– , 3– and 4–porate grains about 50/20/1. Pore circular, 3– 4.7 µm diam. Exine thin (<1 µm), microverrucate.

Ficus superba **(Miq.) Miq. (Fig. 4-3A–C)**
Material: Malaysia. Johore, 16 Apr 1967, *F.S.P. Ng FRI 5047* (L).

Pollen grains very small, 2–porate; P x E = 8.3 x 13.0 µm. Shape ellipsoid or gibbous; P/E = 0.63. Pores circular, about 1.6 µm diam. Exine thin (< 1 µm), indistinctly microverrucate.

Ficus virens Aiton var. dispersa **Chantaras. (Fig. 4-3D–F)**
Material: Papua New Guinea. New Britain, West Nakanai, *Floyd NGF 6457* (L).

Pollen grains small, 2–porate; P x E = 10.8 x 16.5 µm. Shape ellipsoid or gibbous; P/E = 0.65. Pores circular, about 2.3 µm diam. Exine thin (< 1 µm), indistinctly microverrucate.

Ficus virens Aiton var. matthewii **Chantaras. (Fig. 4-3G–I)**
Material: India. South India, Cardamom Hills, *Ridsdale 722* (L).

Pollen grains small, 2– or sometimes 3–porate; P x E = 11.9 x 17.0 µm. Shape of 2–porate grains ellipsoid or gibbous, of 3–porate grains triangular in polar view and oblate in equatorial view; P/E = 0.70. Proportion of 2– and 3–porate grains about 50/1. Pore circular, 2.3–3.9 µm diam. Exine thin (< 1 µm), microverrucate.

Ficus subsect. Conosycea
The pollen grains are very small to small, 2–porate; P x E = 9.2–10.7 x 14.8–16.4 µm. The shape 2–porate grains is ellipsoid or gibbous; P/E = 0.56–0.72. The pores are circular and about 2.3 µm diam. The exine is less than 1 µm thick, and the ornamentation is nearly always scabrate (elements < 1 µm: finely punctate, microverrucate), or sometimes psilate.

Ficus altissima **Blume (Fig. 4-3J–L)**
Material: Thailand. Chiang Rai, Doi Po, 28 Nov 2011, *Chantarasuwan 281111-2* (L).

Pollen grains small, 2–porate; P x E = 10.7 x 14.8 µm. Shape ellipsoid or gibbous; P/E = 0.72. Pores circular, about 2.3 µm diam. Exine thin (< 1 µm), microverrucate.

Ficus amplissima **J.E. Sm. (Fig. 4-3M–O)**
Material: Sri Lanka. Wilpattu National Park, 13 Jul 1969, *Wirawan et al. 1133* (P).

Pollen grains small, 2–porate; P x E = 9.2 x 16.4 µm. Shape ellipsoid or gibbous; P/E = 0.56. Pores circular, about 2.3 µm diam. Exine thin (< 1 µm), psilate.

Discussion

The pollen morphology of the species of *Ficus* subsect. *Conosycea* and *F.* subsect. *Urostigma* described in the present study conforms to the general description of *Ficus* pollen in the literature (see Introduction), though, as far as known, 4-porate pollen grains (observed in *F. salicifolia*) were unknown in the genus. Subsect. *Urostigma* shows very little pollen diversity, which is the general picture in the genus *Ficus* (Langeveld & van der Ham, 2005). Minor variation occurs in all characters, but this does not seem to be useful in distinguishing pollen types, subdividing subsection *Urostigma* or supporting clades as found by Chantarasuwan et al. (in prep.).

Neither is much difference observed between subsect. *Urostigma* and the two species of subsect. *Conosycea*. In our study, subsect. *Conosycea* showed only 2-porate pollen, but only two species were included in the observation and five out of the 12 species of subsect. *Urostigma* also have exclusively 2-porate pollen.

The pollen of the two species, which could have passive pollination (*F. prolixa* and *F. virens* var. *dispersa*), cannot be distinguished from the other species, which show active pollination. This supports the results found earlier in larger sets of species (Khan et al. 2001; Kjellberg, 2001; personal communication F. Kjellberg, 2012; Rønsted et al., 2005, 2008; Tzeng et al., 2009; Cruaud et al., 2012). Our conclusion is that pollen morphology is not useful in distinguishing taxonomic groups, clades, or groups of species with either the active or passive pollination mode.

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Chapter 5

A new classification of *Ficus* subsection *Urostigma* (Moraceae) based on four nuclear DNA markers (ITS, ETS, G3pdh, and ncpGS), morphology and leaf anatomy

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Abstract

Ficus subsection *Urostigma* as currently circumscribed contains 27 species, distributed in Africa, Asia, Australia and the Pacific and is of key importance to understanding the origin and evolution of *Ficus* and the fig-wasp mutualism. The species of subsect. *Urostigma* are very variable in morphological characters and exhibit a wide range of often partly overlapping distributions, which makes identification often difficult. The systematic classification within and between this subsect. and others is problematic, e.g., it is still unclear where to classify *F. amplissima* and *F. rumphii*. To clarify the circumscription of subsection *Urostigma*, we present a phylogenetic reconstruction based on four nuclear DNA markers (ITS, ETS, G3pdh, and ncpGS) combined with morphology and leaf anatomy. The combined phylogenetic tree shows that *F. madagascariensis*, a Madagascan species, is sister to the remainder of subsect. *Urostigma*. *Ficus amplissima* and *F. rumphii*, formerly constituting sect. *Leucogyne*, appears to be imbedded in subsect. *Conosycea*. The result of the phylogenetic analysis necessitates nomenclatural adjustments. A new classification of *Ficus* subsect. *Urostigma* is presented along with morphological and leaf anatomical characters to recognise it. Two new species are described, one in subsect. *Urostigma*, the other in *Conosycea*. One variety is raised to species level.

Keywords classification; *Ficus* subsection *Urostigma; Ficus* subsection *Conosycea;* morphology; leaf anatomy.

Introduction

Despite substantial effort, the origin and evolution of *Ficus* L. and the fig-wasp mutualism remain unclear due to lack of resolution of the backbone of the phylogeny of *Ficus* (Cruaud et al., 2012; Rønsted et al., 2005; 2008). One of the key clades of uncertain placement is *Ficus* subsection *Urostigma* (Berg 2004; Chantarasuwan et al, 2013). *Ficus* subg. *Urostigma* sect. *Urostigma* subsect. *Urostigma* (Gasp.) C.C. Berg includes 27 species as currenly circumscribed with *Ficus religiosa* L. as the type. The distribution of the subsection ranges from West Africa and Madagascar via the Asian mainland to Japan and through (southern) Malesia to Australia and the Pacific. Typical characters of subsect. *Urostigma* are: Trees, many of which are hemi-epiphytic and some terrestrial, aerial roots not abundant, usually intermittent growth, leaves often deciduous, spirally arranged, and articulate or subarticulate (some African-Madagascan species lack the articulation), inflorescences often borne below the leaves and in some species they are borne on the spurs of the older branches, the colour of the syconium can change from whitish to pinkish, then to purplish, and finally blackish, although the final stage may never develop (Berg & Wiebes, 1992; Berg & Corner, 2005). *Urostigma*, was first described in 1844 when Gasparrini (1844) broke up the genus *Ficus* into several genera. Later Miquel (1867) abandoned this idea and reunited *Ficus*, but divided the genus into six subgenera. Subgen. *Urostigma* was further divided by him into series based on distribution, six series for species in Asia and Australia, three series for African species, and five series for species in America. The species presently included in subsect. *Urostigma* were mainly placed in series *Infectoriae* Miq. and *Religiosae* Miq. of Asia and Australia. The African representatives of the subsection were classified in series *Grandiores* Miq., *Oblongifoliae* Miq., and *Ellipticifoliae* Miq. Later, morphological characters were used to classify the genus, e.g. King (1887) divided *Ficus* into seven sections based on leaf morphology. Corner (1960) used the colour of the ovary and the position of the lythocists for his classification, an idea shared by Berg (2004). However, the concept of the sections varied between Corner's (1960) and Berg's (2004) classifications. Berg (2004) expanded Corner's section *Urostigma* by including former sections *Conosycea* and *Leucogyne* (Corner, 1959) and Corner's concept of section *Urostigma* was consequently reduced to the status of subsection. The relationship of the two species (*F. amplissima* J.E.Sm. and *F. rumphii* Blume) of former sect. *Leucogyne* was questioned when Rønsted et al. (2005) published a molecular phylogenetic hypothesis, which showed that *F. rumphii* belongs to subsect. *Conosycea* (Miq.) C.C.Berg (*F. amplissima* was not included in their study).

At present, molecular phylogenetic analyses have become the major basis for improving classifications. In an early molecular study of *Ficus* by Weiblen (2000) using the ITS marker together with morphological data, only three species of *Ficus* subsect. *Urostigma* (*F. prasinicarpa* Elmer ex C.C.Berg, *F. superba* (Miq.) Miq. and *F. virens* Aiton) were included. This study was the first to suggest that the monoecious subgenus *Urostigma* (Gasp.) Miq. is not monophyletic, because section *Urostigma* (Gasp.) Endl. appeared to be the sister clade of a functionally dioecious clade, but support for this relationship was weak. Jousselin et al. (2003) combined ITS and ETS markers to construct the phylogenetic relationships of 41 species of *Ficus*, including three other species of subsection *Urostigma* (*F. prolixa* G. Forst., *F. religiosa* L., and *F. salicifolia* Vahl). Their results again suggested that subsection *Urostigma* forms a separate group from the remainder of subgenus *Urostigma*. Rønsted et al. (2005) also combined ITS and ETS in their work, which included nine species of subsect. *Urostigma* and *F. rumphii* of sect. *Leucogyne*. Their results indicated that *Ficus* subsect. *Urostigma* is monophyletic to the exclusion of *F. rumphii*, but subsect. *Urostigma* has to be excluded from the rest of subgenus *Urostigma*, and *F. rumphii* is embedded in sect. *Conosycea*. Addition of other nuclear markers and more species to the global analysis of *Ficus* have subsequently confirmed a narrow concept of subsection *Urostigma* excluding *F. rumphii* (Rønsted et al, 2008; Xu et al., 2011; Cruaud et al, 2013). However, more than half of the species of subsect. *Urostigma* and *F. amplissima* of (former) sect. *Leucogyne* are not included in any phylogenetic analysis yet, thus the monophyly and circumscription of the group is still far from clear.

To solve the problem of the classification of *Ficus* subsect. *Urostigma* and closely related subsections, we began a revision of *Ficus* subsect. *Urostigma* (Chantarasuwan et al., 2013) in its traditional classification, congruent with that of Berg (2004). However, we realised that morphology alone did not provide typical characters or a typical combination of characters to solve the classification problem. Leaf anatomy (Chantarasuwan et al., 2014) appeared to show more consistent characters and less variation within species than the morphological characters previously studied and, especially when combined with morphology, leaf anatomical characters provided a highly accurate tool for species recognition, enabling recognition of some of the morphologically highly variable species (e.g., *F. virens*). However, leaf anatomical evidence suggested that *F. amplissima* more closely resembles *F. arnottiana* (Miq.) Miq. (subsection *Urostigma*) than *F. rumphii* (former sect. *Leucogyne*). A result that upsets the present classification (Chantarasuwan et al, 2013).

Therefore, the main aim of this study is (1) to create a comprehensive and well supported phylogenetic hypothesis of subsection *Urostigma* by analysing several molecular markers (ITS, ETS, G3pdh, and ncpGS) for almost all known species of subsect. *Urostigma* and related groups and (2) to propose a new new classification of subsection *Urostigma* based on the resulting phylogenetic hypothesis.

Materials and methods

Taxon sampling

In total, 76 taxa were represented corresponding to thirty–six species out of c. 280 spp. of *Ficus* subgen. *Urostigma*, including 24 out of 27 species of subsect. *Urostigma*, and five (out of 60) species representating *Urostigma* subsect.

Conosycea (*F. cf. rumphii*, *F. altissima* Blume, *F. benjamina* L., *F. glaberrima* Blume subsp. *siamensis* (Corner) C.C. Berg and *F. menabeensis* H. Perrier), as well as two species from each of sect. *Americana* (*F. americana* Aubl., *F. aurea* Nutt.; c. 100 species), sect. *Stilpnophyllum* subsect. *Malvanthera* (*F. pleurocarpa* F. Muell., *F. blachypoda* (Miq.) Miq.; c. 20 species), one species of sect. *Leucogyne* (*F. rumphii*), and one species of sect. *Galoghycia* (*F. bubu* Warb.; c. 72 species). Two species of subgenus *Pharmacosycea* (*F. maxima* Mill. and *F. tonduzii* Standl.) were included as outgroup representing the first diverging lineage of *Ficus* as currently understood (Cruaud et al, 2013).

Thirty–seven dried leaf samples from herbarium collections and 26 leaf samples dried on silica gel (collected in the field) were used for DNA extraction (for voucher information see Appendix 1). DNA sequence data were sampled for four nuclear DNA markers (ITS, ETS, G3pdh, ncpGS). In total, 233 sequences were used in the analysis, including 198 new sequences and 35 sequences downloaded from GenBank. All new sequences are available from GenBank (Appendix 1).

DNA extraction, amplification, and sequencing

About 20–50 mg of dried leaf tissue from each sample was used for extraction using the Qiagen DNeasy Plant Kit and following the manufacturers protocol. The ITS region was amplified using the primers 17SE_its and 26SE_its and ITS_5_F, ITS_4_R (Sun et al., 1994; Rønsted et al., 2008). The ETS region was amplified using primers ETS_Hel1_F, 18S_ETS_R and ETS_FIG1_F, 18S_ETS_R (Rønsted et al., 2008). The G3pdh gene was amplified using the primers GPDX7_F and GPDX9_R (Strand et al., 1997). The ncpGS region was amplified with the primers ncpGS_3_F and ncpGS_4_R (Rønsted et al., 2008). The primer sequences for all markers are shown in Table 5-1. The Polymerase chain reactions (PCR) were performed with 1µl of DNA product, 10 µl of Red-Sigma buffer (Qiagen Inc.), 2µl of each 10 µM primers (foreward and reverse), 0.4 µl of BSA (Promega, Madison, Wisconsin, USA) and 6.6 µl of H2O, in a total volume of 20 µl. The PCR programmes followed are summarised in Table 5-2. PCR fragments were checked for length and yield

Table 5-1. Sequences of primers used in this study.

Regions	Primer sequences
ITS	ITS_5F : 5´ - GGA AGT AAA AGT CGT AAC AAG G - 3´ ITS_4R : 5´ - TCC TCC GCT TAT TGA TAT GC - 3´ ITS_17SE : 5´ - ACG AAT TCA TGG TCC GGT GAA GTG TTC G - 3´ ITS_26SE : 5´ - TAG AAT TCC CCG GTT CGC TCG CCG TTA C - 3´
ETS	ETS_Hel1 : 5´ - GCT CTT TGC TTG CGC AAC AAC T - 3´ 18S_ETS : 5´ - GCA GGA TCA ACC AGG TAG CA- 3´
G3pdh	GPDX7F : 5´ - GAT AGA TTT GGA ATT GTT GAG G - 3´ GPDX9R : 5´ - AAG CAA TTC CAG CCT TGG - 3´
ncpGS	GS_3F : 5´ - GTT GTG ATT WAC CAT GCT - 3´ GS_4R : 5´ - AGA TTC AAA ATC GCC TTC - 3´

by gel electrophoresis on 2% agarose gels and cleaned using the Qiagen PCR clean-up kit before sequencing on an ABI 377 Genetic Analyzer according to the manufacturer's protocols (Applied Biosystems). Both strands were sequenced for each region for the majority of taxa.

DNA sequence alignments

Sequences were initially edited and improved by eye using CodonCode Aligner (CodonCode Corporation, Dedhem, USA) and MacClade 4.08 OSX (Maddison & Maddison, 2011), and forward and reverse sequences were assembled. All assembled sequences were blasted against the GenBank database to check for possible contamination with non-*Ficus* DNA. The alignment of whole sequences was done online with Phylogeny.fr (2008) and SeaView 3.2 (Galtier et al., 1996). Gaps were treated as missing data and indels were excluded from the alignments. Missing markers were also coded as missing data.

Morphological and leaf anatomical data

The morphological data matrix was constructed using the most recent taxonomic revision of *Ficus* subsection *Urostigma* (Chantarasuwan et al., 2013). The same specimens used in the revision were also the primary source for compiling the data matrix. In addition, specimens, stored in L, representing the species from other infrageneric taxa were also used to score data. In total, 43 qualitative morphological characters were coded for analysis (see Appendix 2 for characters, and Appendix 3 for the data matrix). The leaf anatomical data are based on recent work by Chantarasuwan et al. (2014), to which the character states of non-subsect. *Urostigma* species were added, either studied (*F. cf. rumphii*) or extracted from Berg and Corner (2005). In total 23 qualitative characters were coded for analysis (see Appendix 2 for characters,and Appendix 3 for the data matrix). All characters were treated as unordered and of equal weight, missing data were coded as unknown.

Table 5-2. PCR programs used for each molecular marker.

Regions	PCR program
ITS	2 min. at 94˚C followed by 35 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (63˚C), and 1 min. extension (72˚C) and 10 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (60˚C), and 1 min. extension (72˚C). After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.
ETS	2 min. at 94˚C followed by 45 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (60˚C), and 1 min. extension (72˚C). After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.
G3pdh	2 min. at 94˚C followed by 40 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (62˚C), and 1 min. extension (72˚C) and 10 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (56˚C), and 1 min. extension (72˚C). After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.
ncpGS	2 min. at 94˚C followed by 45 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (57˚C), and 1 min. extension (72˚C) After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.

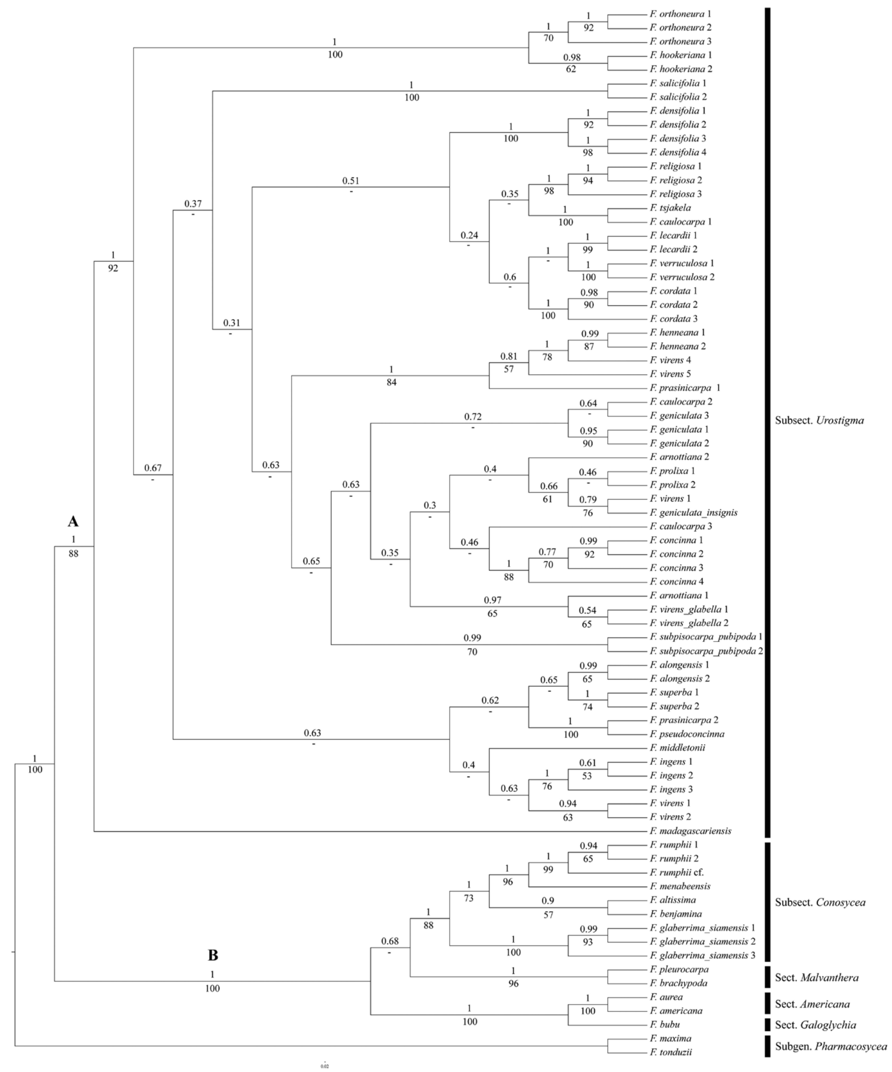

FIGURE 5-1: Majority rule consensus tree from Bayesian analysis of four combined DNA markers (ITS, ETS, G3pdh, and ncpGS) with posterior probabilities (PP) above and bootstrap supports (BS) below the branches.

Phylogenetic analysis

The analyses of the four combined molecular DNA markers were conducted under Maximum Parsimony (MP) and Bayesian Inference (BI). The morphology and leaf anatomy dataset was analysed under Maximum Parsimony (MP). Both datasets were subsequently combined and analysed under MP and BI.

The MP analyses were run using PAUP* v4.0b10 (Swofford, 2003) and heuristic searches with 3000 replicates, ten random taxon additions, tree-bisection-reconnection branch swapping (TBR), MulTrees option active, and no more than 10 trees saved per replicate. Branch support was performed in PAUP with bootstrap analyses (Felsenstein, 1995) with 1000 replicates and similar settings. Bootstrap percentages (BS) are defined as high (85–100%), moderate (75–84%), low (50–74%) or no support (<50%). Model selection for the Bayesian analysis was conducted using the model selection tool available through the online HIV sequence database site (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). The chosen model was HKY+G for ITS, GTR+G for ETS, HrN+G for G3pdh, and HKY+G for ncpGS. The datasets were analysed online using MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003) with 100,000,000 generations via the Cipres science gateway (http://www.phylo.org). Bayesian inference produces posterior probabilities that are relatively higher than the corresponding bootstrap frequencies (Erixon et al., 2003), thus we only used posterior probabilities (PP) above 0.9 as (high) support. A 10% burn-in was executed, after Tracer 1.6 (Rambaut et al., 2013) was used for each tree file to check whether or not the effective sampling sizes (ESS) of all parameters exceeded 200, indicating that they are a good representation of the posterior distributions. TreeAnnotator v.1.8.0 (part of BEAST v.1.8.0 package, Drummond & Rambaut, 2007, Drummond et al., 2012) was used to create a Maximum Clade Credibility (MCC) tree.

Mesquite v.2.7.5 (Maddison & Maddison, 2011) was used to map the morphological and anatomical characters on the MCC tree from the Bayesian analysis of the combined datasets.

Results

Analysis of four combined DNA markers

Seventy six taxa were included in the combined dataset, of which 74 taxa had ITS data, 68 taxa had ETS sequences, 53 taxa with G3pdh sequences, and 38 with ncpGS sequences. The combined aligned data matrix was 2674 bp long with 472 potentially informative characters. The MP analysis resulted in 1300 most parsimious trees (MPTs) with a length = 1636, consistency index (CI) = 0.68, and retention index (RI) = 0.78.

The strict consensus tree of 1300 most parsimonious trees (MPTs) (Fig. 5-1) splits into two clades. Clade A comprises all members of subsect. *Urostigma*

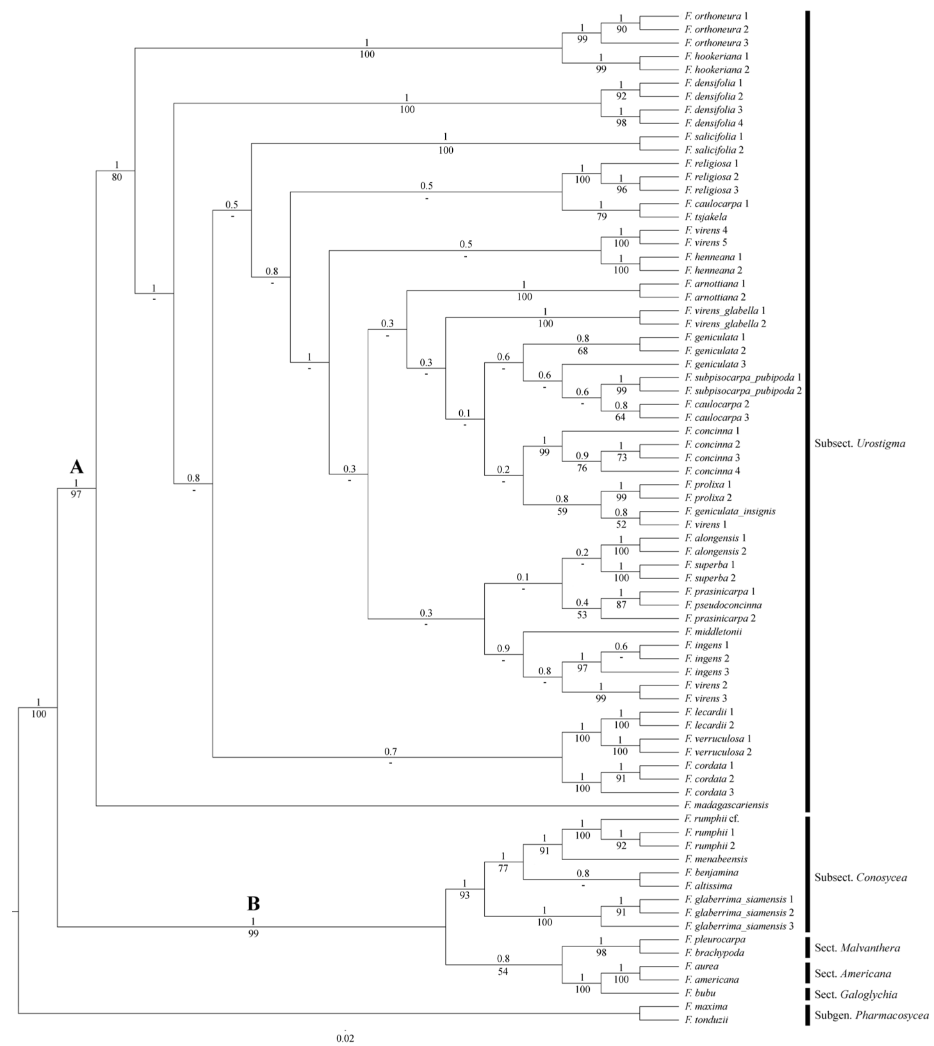

FIGURE 5-2. Total evidence majority rule consensus tree from Bayesian analysis of four DNA markers, morphology and leaf anatomy. Posterior probabilities (PP) above and bootstrap supports (BS) below the branches.

with a support of BS=88 and PP=1. *Ficus madagascariensis* is sister to the rest of this clade (high support, BS=92 and PP=1), but within clade A most internal nodes show low support, while the support for most nodes that unite the various specimens of a species is usually high. Clade B contains the members of sect. *Americana*, sect. *Galoghycia*, sect. *Malvanthera*, subsect. *Conosycea*, and *F. rumphii* of sect. *Leucogyne* with BS=100 and PP=1.

Analysis of morphological and leaf anatomical data

A total of 43 morphological and 23 leaf anatomical characters were used. The MP analysis resulted in 1368 most parsimonious trees with a length = 280, CI = 0.25, and RI = 0.77. The strict consensus tree is one large polytomy of all taxa (not shown here).

Analysis of DNA markers combined with morphology and leaf anatomy

A total of 2740 characters, 2674 DNA (ITS, ETS, G3pdh, and ncpGS) and 66 qualitative morphological and leaf anatomical characters were used; 538 characters were parsimony informative. The MP analysis resulted in 81 most parsimonious trees with a tree length = 1964, CI = 0.60, and RI = 0.76 (strict consensus not shown). Tracer(Rambaut et al., 2013) showed that all variables in the results of the BI analysis had an effective sampling size far above 200 (326–1851). The MCC tree, made of the cladograms in set 1 with TreeAnnotator, is shown in Fig. 5-2.

The cladogram (Fig. 5-2) shows the same two distinctive subclades as found in the analysis of the four combined DNA markers (Fig. 5-1). Clade A is composed of all species of subsect. *Urostigma* and it has high support, BS=97 and PP=1. *Ficus madagascariensis* is sister to the remainder of subsection *Urostigma* s.s. and the remaining clade is well supported, BS=80, and PP=1. Relationships within the remainder of clade A are not well supported in the combined analysis as was also the case in the 4-gene analysis alone (Fig. 5-1). The species that are represented by several samples usually form clades with high Bootstrap and Bayesian support except for *F. caulocarpa*, *F. geniculata*, *F. prasinicarpa* and *F. virens*. *Ficus prasinicarpa* is paraphyletic because of the inclusion of *F. pseudoconcinna*. The clade itself has low support (BS = 53, PP=0.4), but *F. prasinicarpa 2* and *F. pseudoconcinna* have high support (BS high= 87, PP high = 1). *Ficus geniculata 3* groups with *F. caulocarpa 2* and *3* and *F. subpisocarpa* Gagnep. subsp. *pubipoda*, but with very low support (BS<50, PP=0.6).

Two species, represented by several samples, appear to be polyphyletic, *F. caulocarpa* (Miq.) Miq. and *F. virens*. Of the three samples of *F. caulocarpa*, *F. caulocarpa 1* forms a clade with *F. tsjakela* Burm.f. (BS moderate =79, PP high = 1), while *F. caulocarpa 2* and *3* form a clade together as described above. Accessions of *F. virens* appears in four places; variety virens appears

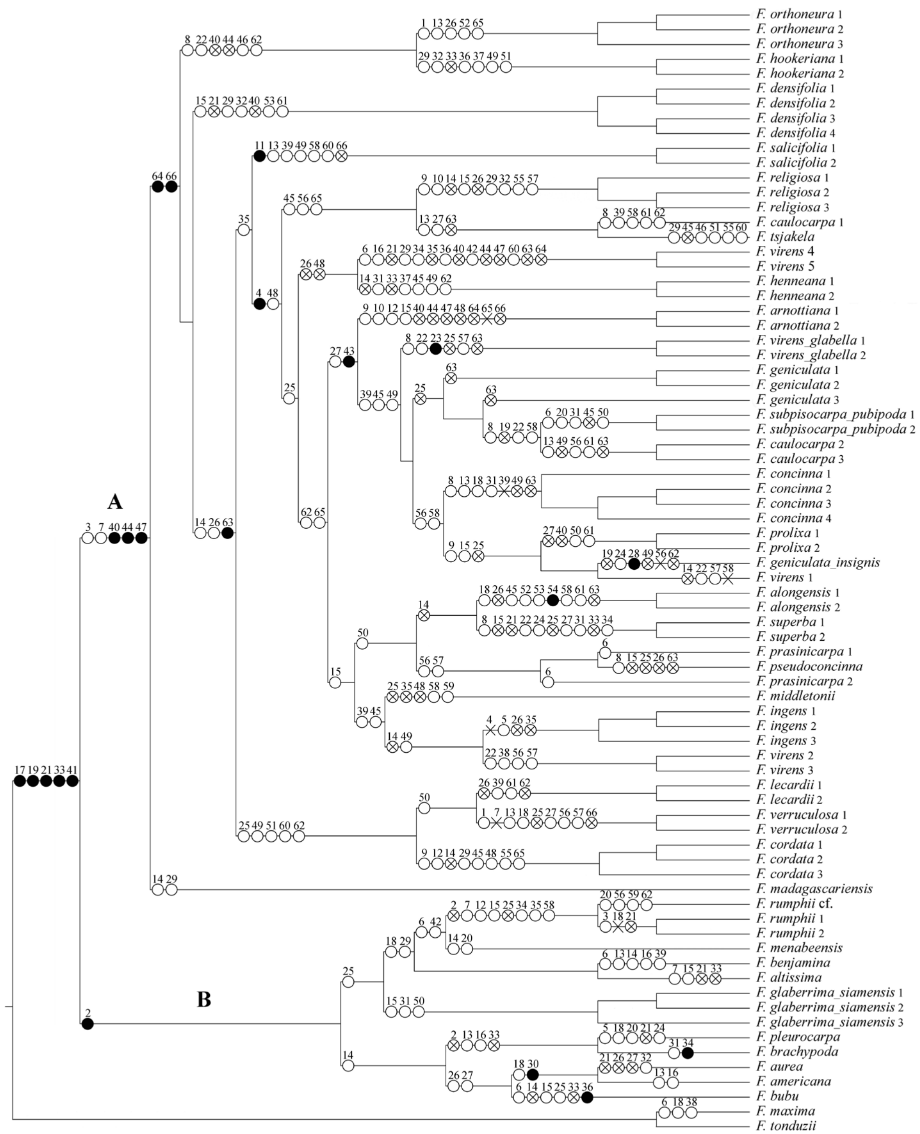

FIGURE 5-3. Character state changes of the morphological characters traced on the majority rule consensus Bayesian tree of the total evidence matrix (Fig. 5-2). ● = unique apomorphy; ○ = parallelism; ✕ = reversal; ⊗ = parallel reversal.

in three clades, *F. virens 1* groups with *F. geniculata_insignis* (low support, BS=52, PP=0.8), *F. virens 2* and *3* group together (strong support, BS=99 and PP = 1) and are further linked to the three specimens of *F. ingens* (Miq.) Miq., and *F. virens 4* and *5* group together (strong support, BS=100 and PP=1) and further group with two specimens of *F. henneana* Miq. The two specimens of *F. virens* var. *glabella* (*F. virens_glabella 1* and *F. virens_glabella 2*) also form a separate clade with high support (BS = 100 and PP = 1).

Clade B is composed of members of sect. *Americana*, sect. *Galoghycia*, subsect. *Malvanthera*, subsect. *Conosycea*, and *F. rumphii* of sect. *Leucogyne* and is well supported in this analysis. (BS=99, PP=1). Within this clade, subsect. *Conosycea* is well suppported (BS=93 and PP=1) and includes three accessions of *F. rumphii* (BS=100 and PP = 1).

Character mapping

The morphological and leaf anatomical character state changes are summarised in Fig. 5-3. Subsect. *Urostigma* (clade A in Fig. 5-3) is supported by the following apomorphies: intermittent growth (character 3, state 2; shared in parallel with *F. rumphii* of subsect. *Conosycea*, clade B), deciduous leaves (char. 7, state 1; reversal in *F. verruculosa*, parallel with some species of subsect. *Conosycea*: *F. altissima*, *F. rumphii* and *F. cf. rumphii*), staminate flowers near ostiole (char. 40, state 1; parallel reversals in *F. arnottiana*, *F. densifolia*, *F. hookeriana F. orthoneura*, *F. prolixa*, and *F. virens 4* and *5*), single-layered epidermis (char. 44, state 1; parallel reversals in *F. arnottiana*, *F. virens 4* and *5*, *F. orthoneura*, and *F. hookeriana*), abaxial enlarged lithocysts (char. 47, state 1; parallel reversals in *F. arnottiana* and *F. virens 4* and *5*).

Discussion

Phylogenetic circumscription of of *Ficus* subsect. *Urostigma*

Our results based on comprehensive sampling of subsection *Urostigma* are consistent with recent previous studies at the genus level supporting a narrow concept of subsection *Urostigma* s.s. excluding former section *Leucogyne* (Rønsted et al. 2005, 2008, Xu et al., 2011; Cruaud et al., 2012). Unfortunately the extraction of DNA from *Ficus amplissima*, the other species of sect. *Leucogyne*, was unsuccessful in our study, but a partial ITS sequence of *F. amplissima* (Rønsted unpublished; specimen Matthew 20582 (K)) forms a clade together with *F. rumphii* embedded in the *Conosycea* clade. This is supported by evidence from the pollinators, because *F. amplissima* (Wiebes, 1992) and *F. rumphii* (Berg and Corner, 2009) are pollinated by a wasp genus that is only known to be associated with subsect. *Conosycea*. Based on these two independent pieces of evidence we support the placement of *F. amplissima* in subsection *Conosycea*, which means that the complete sect. *Leucosyce* should now be synonymised with subsect. *Conosycea*. *Ficus madagascariensis* is the sister to all other members of subsect. *Urostigma*, which may imply that the origin of this subsection could be in Madagascar. Corner (1958) considered *F. prolixa*, a Polynesian species, to group with sect. *Americana*, because the

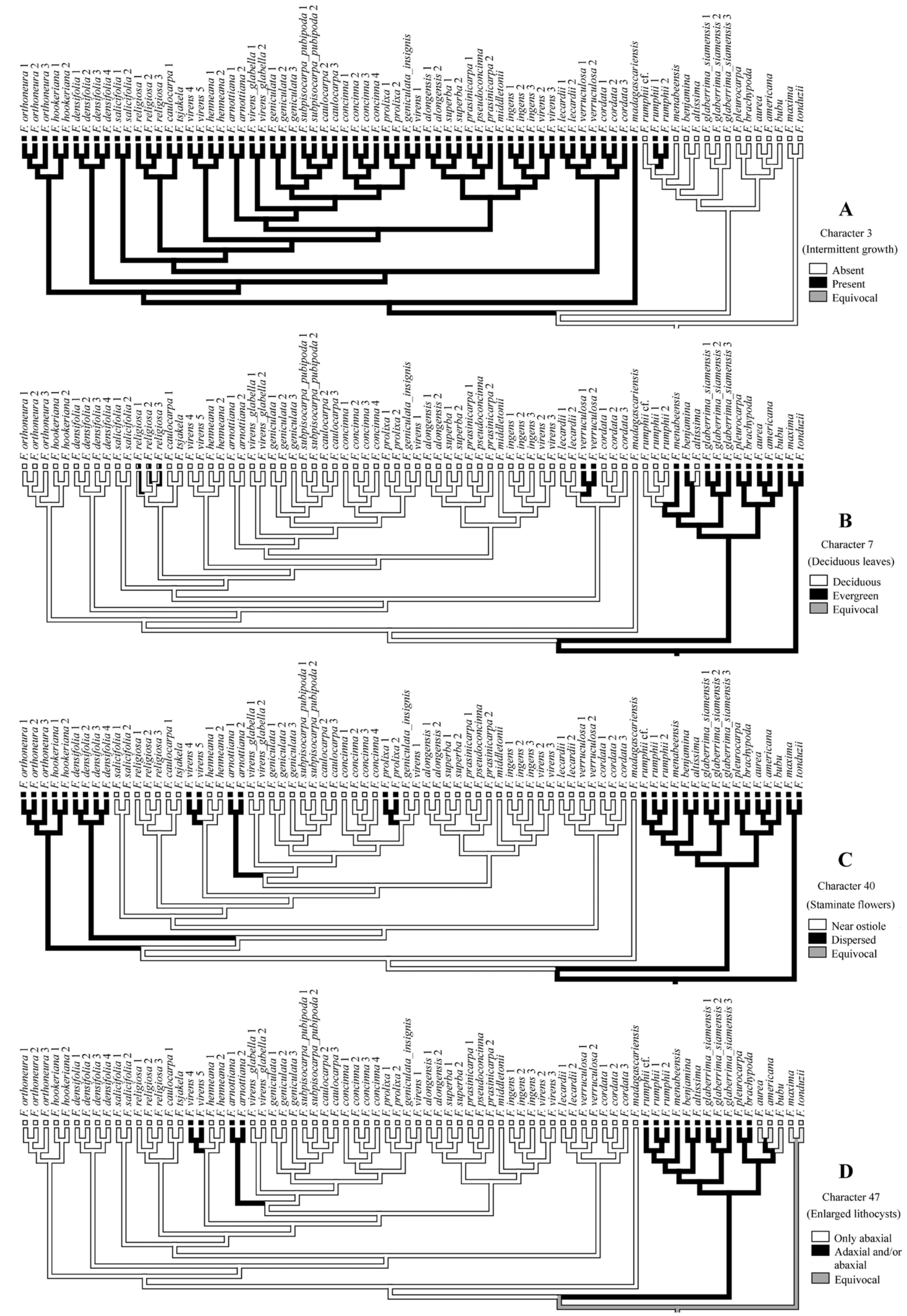

FIGURE 5-4. Evolution of some selected morphological and leaf anatomical characters optimized onto the phylogeny tree (Fig. 2) using Mesquite v.2.7.5. A: Intermittent growth (character 3), B: Deciduous leaves (character 7), C: Staminate flowers (character 40), and D: Enlarged lithocysts (character 47).

staminate flowers are scattered in the fig, which is similar to a large group of American hemi-epiphytic figs (over 100 species; section *Americana*). However, *F. prolixa* has three basal bracts and not two as in sect. *Americana*. Our phylogenetic results clearly show that there is no close relation between *F. prolixa* (clade A) and sect. *Americana* (clade B).

Relationships within subsection *Urostigma* s.s. are still not well supported based on four nuclear genes, morphology and leaf anatomy, and further work possibly using massive parallel sequencing is needed before subdivision of the subsection, and additional biogeographical analysis can meaningfully be conducted enabling our understanding of the evolution of this widespread group of *Ficus*. For example, *F. ingens*, an African species morphologically (Corner, 1958) and leaf anatomically close to *F. virens* (Chantarasuwan et al., 2014), forms a clade (Fig. 5-2) together with *F. virens 2* and *3* and *F. middletonii* from Asia constituting a biogeographical puzzle.

Molecular versus Total Evidence

The combination of all DNA and morphological data (total evidence analysis) resulted in a phylogenetic tree (Fig. 5-2) supporting the same major clades A and B and the position of *F. madagascariensis*, *F. orthoneura*, and *F. hookeriana* However, the tree (Fig. 5-2) resulting from analysis including morphological data differs in details from the tree solely based on molecular data (Fig. 5-1). Interestingly the total evidence tree groups within a clade all the Asian species presenting an leaf articulated on the petiole, supporting the idea of Wiens (2004) that morphology and leaf anatomy add valuable data to the phylogeny reconstruction when combined with molecular data. However, the support for relationships among species is low in both analyses precluding an infrageneric classification.

Comparing the phylogeny with traditional classifications

To some degree, our phylogenetic results support Miquel's classification (1867), with the taxa arranged per continent, e.g., a group of African species separate from Asian species, but with a few exceptions. In our results (Fig. 5-1) one African species, *F. ingens*, is placed among Asian species, and Sino-Himalayan *F. hookeriana* and *F. orthoneura* are among African species. Thus, a purely continental classification is not attainable. Corner (1959, 1965) divided section *Urostigma* (similar to subsection *Urostigma* here) of Asia and Australia into four series, *Religiosae* Miq., *Superbae* Corner, *Caulobotryae* (Miq.) Corner, and *Orthoneurae* Corner. However, species in the various series of Corner do not form monophyletic groups, but are mixed in our phylogenetic tree and the relationships among clades are not well supported. Moreover, Corner never included the African species, precluding direct comparison with his subdivision. Berg (2004) re-classified section *Urostigma* and included African species and recognized two subsections, *Urostigma* and *Conosycea*. He did not further subdivide subsect. *Urostigma* as Corner (1959, 1965) did. Berg's classification compares very well with ours and previous works (Rønsted et al, 2005, 2008, Xu et al, 2011; Cruaud et al, 2012) showing

two clades, which cannot easily be subdivided into recognisable subgroups (low support for most branches and no distinct character combinations in Fig. 5-3). *Ficus amplissima* and *F. rumphii* (formerly in *Leucosyce*) were united in subsect. *Urostigma* by Berg, which is now shown to be incorrect as they should instead by included in subsect. *Conosycea*.

Suitable characters for recognising subsection *Urostigma*

The character mapping showed three unique apomorphies for the subsect. *Urostigma* clade (Fig. 5-3), one morphological character (40.1: staminate flowers near ostiole), and two leaf anatomical characters (44.1: epidermis simple; 47.1: enlarged lythocysts only abaxially), of which especially the enlarged lythocysts are typical. Two morphological characters (3.1: intermittent growth present; 7.1: leaves deciduous) show parallel apomorphies in *Conosycea*, though the combination is unique. All characters were previously used for the recognition of subsection *Urostigma* by Berg (2004), Berg & Corner (2005), and Chantarasuwan et al. (2013). These results imply that morphology alone is not sufficient when trying to separate both subsections, whereas the combination with leaf anatomy allows a distinct subsectional recognition.

Intermittent growth (char. 3, Fig. 5-4A) was always the main character used to recognise subsection *Urostigma*, but also occurs in parallel in *F. amplissima* and *F. rumphii* (subsect. *Conosycea*). Thus this character has to be treated carefully and should be used in combination with others.

Deciduousness (char. 7, Fig. 5-4B) should also be used in combination with other characters, because subsection *Urostigma* has exceptions, *F. verruculosa* is evergreen and *F. religiosa* becomes evegreen when growing in wet areas. Moreover, many species of subsect. *Conosycea* are also deciduous. Thus, this is not a decisive character to be used for taxonomic recognition.

The character staminate flowers around the ostiole (char. 40, Fig. 5-4C) is the only typical morphological character, but also this character shows parallel reversals in *F. arnottiana*, *F. hookeriana*, *F. orthonera*, *F. prolixa*, and *F. virens 4* and *5*. The character was used to recognise the subsection by Berg (2004), Berg & Corner (2005), and Chantarasuwan et al. (2013).

Of the leaf anatomical characters, Corner (1959) and Berg & Corner (2005) used the enlarged lythocysts on only the abaxial surface (chr. 47, Fig. 5-4D) as typical for subsect. *Urostigma*. However, the leaf anatomical work of Chantarasuwan et al. (2014) revealed that *F. arnottiana* and *F. virens 4* and *5* show enlarged lithocysts on both the adaxial and abaxial sides, which is similar to subsect. *Conosycea*. Thus, this character also is not unique for subsection *Urostigma*.

The articulation of the leaf (char. 4) only occurs in Asian and Australian species, for which it is a unique apomorphy within the *Urostigma* clade, but again there are reversals to absence in *F. hookeriana* and *F. orthoneura* (probably related to their non-deciduousness).

Circumscription of subsect. *Urostigma* and subsect. *Conosycea*

Ficus amplissima and *F. rumphii*, together constituting former section *Leucogyne*, were united because of the lythocysts at both sides of the leaf blade, staminate flowers dispersed, and whitish ovaries, while typical for subsect. *Urostigma* were the lythocysts at the abaxial side only, staminate flowers generally around the ostiole and red(-brown) ovaries. Both groups are pollinated by different fig wasps, *Eupristina* in section *Leucogyne* and *Platyscapa* in subsection *Urostigma* (Berg & Wiebes, 1992; Berg & Corner, 2005; Cruaud et al., 2009). However, section *Leucogyne* is not supported by phylogenetic evidence and both species have to be included in subsect. *Conosycea*. Section *Leucogyne* will then become a synonym of subsect. *Conosycea*.

Because of the reclassification of the species of former section *Leucogyne* the recognition of the subsection *Urostigma* and the subsection *Conosycea* changes compared to Berg (2004) Berg and Corner (2005).

Typical for subsect. *Urostigma* are: plants deciduous, intermittent growth present, leaf articulation present or not, petioles relatively long, enlarged lithocysts generally only abaxially to present at both sides, epidermis a single to multiple layers, staminate flowers near the ostiole or dispersed.

Typical for subsect. *Conosycea* are: plants evergreen or deciduous, without clear indication of intermittent growth, leaves without articulation, petioles relatively thick and short, enlarged lithocysts present at both sides, figs more frequently sessile than pedunculate, staminate flowers dispersed.

Paraphyletic species within subsect. *Urostigma*

The sampled specimens of two species show these to be paraphyletic:

Ficus geniculata var. *geniculata*

The two samples of *F. geniculata* var. *geniculata* (*1 & 2*) form a clade but with low support, while the other one (*F. geniculata 3*) forms a clade with *F. caulocarpa* and *F. subpisocarpa* subsp. *pubipoda*, also with low support. Consequently, *F. geniculata* is paraphyletic. However, the support at the internal nodes of the clades are low, therefore we refrain from changing the species concepts until more molecular information becomes available.

Ficus prasinicarpa

The sample *F. prasinicarpa 1* forms a clade with *F. pseudoconcinna* with high support. The two together are sister to *F. prasinicarpa 2*, but with low support.

Morphologically, the two specimens of *F. prasinicarpa* show a few differences, but because of the low support for the clade we do not make any decision about possible cryptic species.

Polyphyletic species within subsect. *Urostigma*

Besides the two paraphyletic species, three out of the 24 species included in our study appear to be polyphyletic:

Ficus caulocarpa

Three specimens of *F. caulocarpa* var. *caulocarpa* were included in this study. *F. caulocarpa 1* was separated from *F. caulocarpa 2* and *F. caulocarpa 3* and forms a clade with *F. tsjakela* with high PP support, while *F. caulocarpa 2* and *F. caulocarpa 3* form a separate clade. The three specimens share many morphological characters, but *F. caulocarpa 1* deviates in a few characters from *F. caulocarpa 2* and *F. caulocarpa 3* such as the stipule forming an ovoid terminal bud, the figs only on short spurs on the branches, and the figs solitary or in pairs. Based on these differences *F. caulocarpa 1* is described here as a separate species, *F. pseudocaulocarpa* (see below). However, in our phylogenetic analysis, the full genetic variation within *F. caulocarpa* is still not covered, because only samples with a narrow leaf form could be included.

Ficus geniculata

Four specimens of *F. geniculata* were analysed, three belong to *F. geniculata* var. *geniculata* and one to *F. geniculata* var. *insignis*. The three samples of var. *geniculata* show paraphyly, but the var. *insignis* specimen groups separately with *F. virens 1*, but with low support. Both varieties can be recognised at the species level, but because the support for the clades was low we refrain to make this decision until more molecular information becomes available.

Ficus virens

Chantarasuwan et al. (2013) recognised four varieties within the *F. virens* complex, var. *virens*, var. *glabella*, var. *matthewii*, and var. *dispersa*. Unfortunately, we only succeeded to amplify DNA sequences from two varieties (var. *virens* and var. *glabella*). Both varieties are separated in the resulting cladogram (Fig. 5-2), and the five samples of var. *virens* even proved to be polyphyletic. The clade of *F. virens* var. *glabella* is strongly supported, its morphology is clear, thus we will reinstate the species level for this taxon. We will maintain *F. virens* with three varieties, var. *virens*, var. *dispersa*, and var. *matthewii*. *F. virens* var. *virens* was represented by five samples in our analyses, which became divided into three groups (Figs. 5-1, 5-2), see above. *Ficus virens 1* shows some morphological differences with *F. virens 2–5*, but the support is low, thus we will not change the status of *F. virens 1*. The morphology and leaf anatomy of the united and highly supported *F. virens 4* and *F. virens 5* are distinctive rom *F. virens 1–3*. Both samples coincide with the previous name *F. wightiana* (Wall. ex Miq.) Benth., which King (1887) treated as *F. infectoria* Roxb. var. *wightiana* (Wall. ex Miq.) King, and which Corner (1965) accepted as synonym of *F. virens*. Therefore, we will reinstate *F. wightiana*.

Taxonomic Treatment

In this part we will officially make the necessary changes in taxonomy on the basis of our phylogeny. Much of the nomenclature and descriptions can be found in Chantarasuwan et al. (2013) and these will not be repeated here.

***Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. subsect. *Urostigma* (Gasp.) C.C. Berg**

For nomenclature and the subsection description, see Chantarasuwan et al. (2013)

The following species can be recognized in subsection *Urostigma*:
***Ficus virens* Aiton**, Hort. Kew. 3: 451. 1789 — TYPE: Introduced to Kew about 1762 by James Gordon (holotype: BM). For more nomenclature and description see Chantarasuwan et al. (2013: 679). Only three varieties will be recognised:
***Ficus virens* Aiton var. *virens* Corner** (Chantarasuwan et al., 2013: 679).
***Ficus virens* Aiton var. *dispersa* Chantaras.** (Chantarasuwan et al., 2013: 681).
***Ficus virens* Aiton var. *matthewii* Chantaras.** (Chantarasuwan et al., 2013: 683).

***Ficus glabella* Blume**, Bijdr.: 452. 1825 ≡ *Urostigma glabellum* (Blume) Miq., Fl. Ind. Bat. 1, 2: 340. 1859 ≡ *Ficus virens* Aiton var. *glabella* (Blume) Corner, Gard. Bull. Singapore 17: 377. 1960 — TYPE: INDONESIA. Java, Kiara beas, *Blume s.n.* (holotype: L; isotype: P).

= *Urostigma canaliculatum* Miq., London J. Bot. 6: 579. 1847 — TYPE: AUSTRALIA. Prince of Wales Island, *Hb. Hooker* (holotype: K; isotype: E).

The former variety is here reinstated as species again. For more nomenclature and description see Chantarasuwan et al. (2013: 681, under *F. virens* var. *glabella*).

Ficus wightiana (Wall. ex Miq.) Benth., Fl. Hongk.: 327. 1861 ≡ *Urostigma wightianum* Wall. ex Miq., London J. Bot. 6: 566. 1847 ≡ *Ficus infectoria* Roxb. var. *wightiana* (Wall. ex Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: 60, 63, t 75-77. 1887 — TYPE: INDIA. Bangaloor, *Wallich 4540* (Herb. Wight.) (holotype: K; isotype: E).

Tree. Branches drying brown or grey-brown. Leafy twigs 3–3.5 mm thick, glabrous. Leaves with (sub)articulation; lamina elliptic, 3.8–11.0 by 2.5–5.2 cm, (sub)coriaceous, apex acuminate, the acumen sharp, base attenuate, both

FIGURE 5-5. *Ficus pseudocaulocarpa* Chantaras. A: Twig with leaves and figs. B: Fig. C: Fig in longitudinal section. D: Staminate flower. E and F: Pistillate flowers.-Drawing: Pajaree Inthachup, 2014.

surfaces glabrous; lateral veins 6–10 pairs, the basal pair up to 1/5–1/3 the length of the lamina, unbranched, tertiary venation reticulate, partly parallel to lateral veins; petiole 2.0–6.5 cm long, glabrous, epidermis persistent; stipules 0.4–1.7 cm long, glabrous, persistent at the shoot apex, forming a terminal bud. Figs axillary or below the leaves, solitary or in pairs, sessile, basal bracts 1.5–3 mm long, glabrous, persistent; receptacle subglobose, 0.9–1.1 cm diam. when dry, glabrous, apex convex; ostiole 1–1.5 mm diam., the upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers dispersed, mostely petiolate; tepals 2 – 3, reddish brown; stamen one. Pistillate flowers sessile or pedicellate; tepals 2–3, lanceolate or ovate, free or connate, reddish brown; ovary white to pale brown.

Note: Some samples of this species are very similar to *F. amplissima*. Distinctive are the elliptic leaves with an attenuate base and acuminate apex with sharp acumen. The samples *Gamble 16452* (K), *Preyadarsaman 5*(L), and *Worthington 4350*(K) were misidentified as *F. amplissima* by Chantarasuwan et al. (2013).

Ficus pseudocaulocarpa Chantaras., sp. nov. — TYPE : PHILIPPINES, Palawan, Tatay municipality, Lake Manguao(Danao), 5 April 1984, *C.E. Ridsdale SMHI 323* (holotype : L)

Resembling *Ficus caulocarpa* (Miq.) Miq. Lamina elliptic-ovate to oblong, 3.8–11.8 by 1.8–5.2 cm, subcoriaceous; stipules 0.7–1.1 cm long, puberulous, persistent at the shoot apex, forming an ovoid terminal bud. Figs on short spurs on the older wood, solitary or in pairs.

Tree. Branches drying brown or grey-brown. Leafy twigs 3–6 mm thick, puberulous. Leaves with articulation; lamina elliptic-ovate to oblong, 3.8–11.8 by 1.8–5.2 cm, subcoriaceous, apex acute to subacuminate, the acumen blunt, base cuneate, both surfaces glabrous; lateral veins 12–16 pairs, the basal pair up to 1/6–1/4 the length of the lamina, unbranched, tertiary venation reticulate, partly parallel to lateral veins; petiole 1.3–4.5 cm long, puberulous at base, epidermis flaking off; stipules 0.7–1.1 cm long, puberulous, persistent at the shoot apex, forming an ovoid terminal bud. Figs on short spurs on the older wood, solitary or in pairs, peduncle 0.1–0.2 cm long, glabrous or puberulous, basal bracts 1–1.5 mm long, glabrous or puberulous, persistent; receptacle subglobose, 0.4–0.5 cm diam. when dry, glabrous, apex convex; ostiole 1–1.5 mm diam., the upper ostiolar bracts glabrous; internal hairs present. Staminate flowers near ostiole, sessile; tepals connate, reddish brown; stamen one. Pistillate flowers sessile or pedicellate; tepals 3–4, lanceolate or ovate, free or connate, reddish brown; ovary dark red. Fig. 5-5.

Distribution and Habitat: Philippines. In lowland rain forest at altitude 60–80 m.

Other species in this subsection (see Chantarasuwan et al., 2013, 2014):

Ficus alongensis Gagnep. (Chantarasuwan et al., 2013: 658)
Ficus arnottiana (Miq.) Miq. (Chantarasuwan et al., 2013: 659)
Ficus caulocarpa (Miq.) Miq. (Chantarasuwan et al., 2013: 659)
  Ficus caulocarpa var. *caulocarpa* (Chantarasuwan et al., 2013: 660)
  Ficus caulocarpa var. *dasycarpa* Corner (Chantarasuwan et al., 2013: 660)
Ficus chiangraiensis Chantaras. (Chantarasuwan et al., 2013: 660)
Ficus concinna (Miq.) Miq. (Chantarasuwan et al., 2013: 662)
Ficus cordata Thunb. (Chantarasuwan et al., 2013: 663)
Ficus cornelisiana Chantaras. & Y.Q. Peng (Chantarasuwan et al., 2014: 6)
Ficus cupulata Haines (Chantarasuwan et al., 2013: 665)
Ficus densifolia Miq. (Chantarasuwan et al., 2013: 665)
Ficus geniculata Kurz (Chantarasuwan et al., 2013: 665)
  Ficus geniculata var. *geniculata* (Chantarasuwan et al., 2013: 666)
  Ficus geniculata var. *insignis* (Kurz) C.C.Berg (Chantarasuwan et al., 2013: 666)
Ficus henneana Miq. (Chantarasuwan et al., 2013: 666)
Ficus hookeriana Corner (Chantarasuwan et al., 2013: 667)
Ficus ingens (Miq.) Miq. (Chantarasuwan et al., 2013: 667)
Ficus lecardii Warb. (Chantarasuwan et al., 2013: 668)
Ficus madagascariensis C.C.Berg (Chantarasuwan et al., 2013: 669)
Ficus middletonii Chantaras. (Chantarasuwan et al., 2013: 669)
Ficus orthoneura H.Lév. & Vaniot (Chantarasuwan et al., 2013: 671)
Ficus prasinicarpa Elmer ex C.C.Berg (Chantarasuwan et al., 2013: 671)
Ficus prolixa G.Forst. (Chantarasuwan et al., 2013: 672)
Ficus pseudoconcinna Chantaras. (Chantarasuwan et al., 2013: 672)
Ficus religiosa L. (Chantarasuwan et al., 2013: 673)
Ficus salicifolia Vahl (Chantarasuwan et al., 2013: 673)
Ficus saxophila Blume (Chantarasuwan et al., 2013: 675)
  Ficus saxophila subsp. *saxophila* (Chantarasuwan et al., 2013: 675)
  Ficus saxophila subsp. *cardiophylla* (Merr.) C.C.Berg (Chantarasuwan et al., 2013: 676)
Ficus subpisocarpa Gagnep. (Chantarasuwan et al., 2013: 676)
  Ficus subpisocarpa subsp. *subpisocarpa* (Chantarasuwan et al., 2013: 676)
  Ficus subpisocarpa subsp. *pubipoda* C.C.Berg (Chantarasuwan et al., 2013: 676)
Ficus superba (Miq.) Miq. (Chantarasuwan et al., 2013: 677)
Ficus tjakela Burm.f. (Chantarasuwan et al., 2013: 677)
Ficus verruculosa Warb. (Chantarasuwan et al., 2013: 678)

***Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. subsect. *Conosycea* (Miq) C.C. Berg**, Blumea 49: 465. 2004 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner, Gard. Bull. Singapore 17: 371. 1960 ≡ *Urostigma* Gasp. subg. *Conosycea* Miq., Fl. Ind. Bat. 1,2: 349. 1859 — LECTOTYPE (designated by Corner, 1959): *Ficus annulata* Blume.

= *Urostigma* Gasp. sect. *Valida* Miq., Fl Ind. Bat. 1,2: 334. 1859 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. ser. *Validae* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 285. 1867; Corner, Gard. Bull. Singapore 17: 272. 1960 — LECTOTYPE (designated by Corner, 1959): *Urostigma valida* (Blume) Miq. [= *Ficus annulata* Blume].

= *Ficus* L. sect. *Stilpnophyllum* Endl. subsect. *Sessiliflorae* Sata, Contr. Hort. Inst. Taihoku Imp. Univ. 32: 179, 190, 375, 376. 1944 — TYPE: unknown.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner, Gard. Bull. Singpore 17: 372. 1960 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner ser. *Drupaceae* Corner subser. *Drupaceae* Corner, Gard. Bull. Singapore 17: 372. 1960 — TYPE: *Ficus drupacea* Thunb.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner subser. *Indicae* Corner, Gard. Bull. Singapore 17: 372. 1960 ≡ Perula Raf., Sylv. Tellur.: 59.1838, non Schreb. 1791 — TYPE: *Ficus benghalensis* L.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner subser. *Zygotricheae* Corner, Gard. Bull. Singapore 17: 372. 1960 — TYPE: *Ficus consociata* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner subser. *Crassirameae* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus crassiramea* Miq.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus sundaica* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Dubiae* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus dubia* Wall. ex King

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Glaberrimae* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus glaberrima* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Subvalidae* (Miq.) Corner, Gard. Bull. Singapore 17: 373. 1960 ≡ *Urostigma* Gasp. sect. *Subvalida* Miq., Fl. Ind. Bat. 1,2: 339. 1859 — TYPE: *Ficus sundaica* Blume

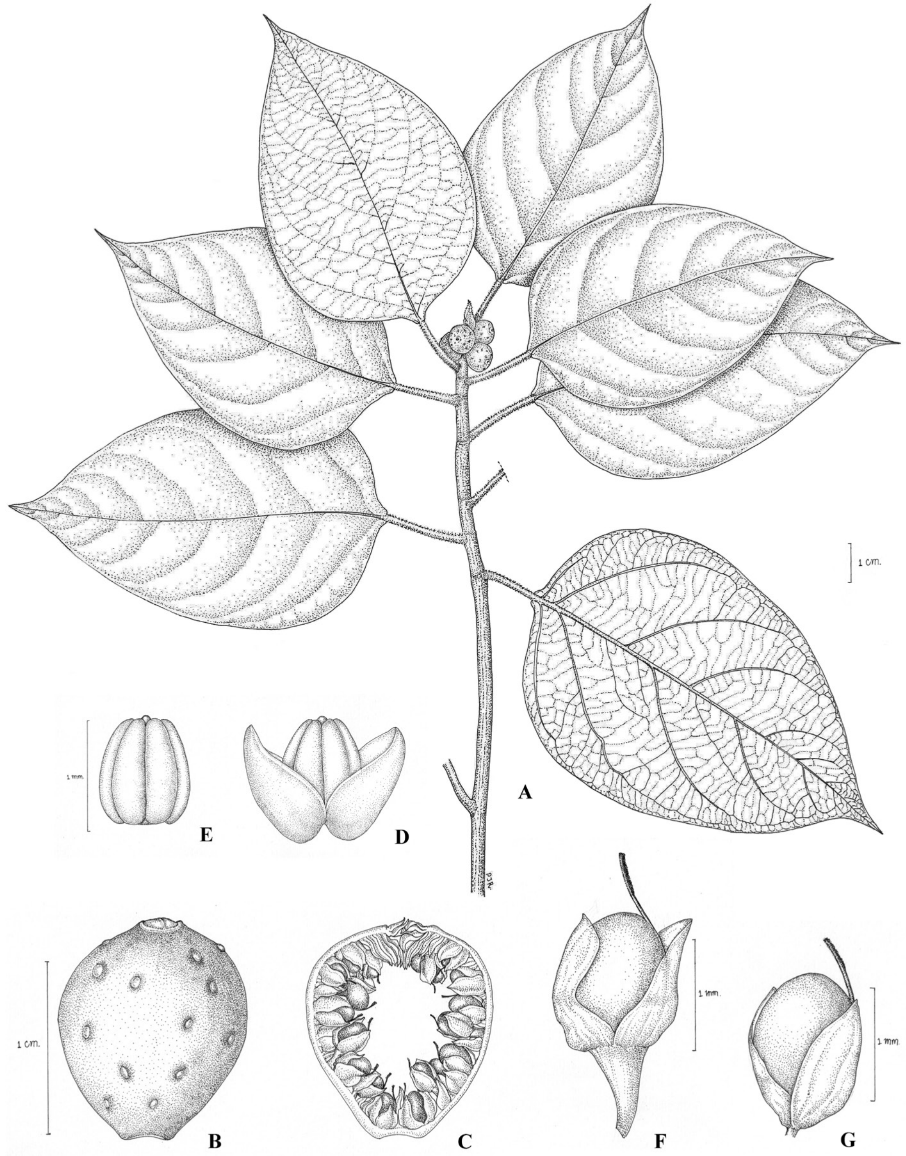

FIGURE 5-6. *Ficus pubipetiola* Chantaras. A: Twig with leaves and figs. B: Fig. C: Fig in longitudinal section. D: Staminate flower. E: Anther. F and G: Pistillate flowers.-Drawing: Pajaree Inthachup, 2014.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Perforatae* Corner, Gard. Bull. Singapore 17: 374. 1960 — TYPE: *Ficus pisocarpa* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Benjamina* (Miq.) Corner, Gard. Bull. Singapore 17: 374. 1960 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. ser. *Benjamineae* Miq. Ann. Mus Bot. Lugduno–Batavi 3: 287. 1867 — TYPE: *Ficus benjamina* L.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Benjamina* (Miq.) Corner ser. *Callophylleae* Corner, Gard. Bull. Singapore 17: 374. 1960 — TYPE: *Ficus callophylla* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Leucogyne* Corner, Gard. Bull. Singapore 17: 371. 1960 — TYPE: *Ficus rumphii* Blume

Trees, mostly evergreen, without intermittent growth to rarely intermittent growth with 2 or 3 short internodes forming a transition zone. Leaves spirally arranged, not articulate; epidermis multiple, enlarged lithocysts at both sides of lamina; petiole relatively thick and short. Figs solitary or in pairs axillary, or just below the leaves, more frequently sessile than pedunculate; receptacle often longer than wide; basal bracts 3(2), small to large, often unequal in size or shape, mostly persistent; ostiole closed, with the upper ostiolar bracts overlapping, or open, with the upper ostiolar bracts not or partly imbricate, the 3 upper ostiolar bracts often unequal in size, sometimes only 2 clearly visible; internal hairs mostly absent; staminate flowers dispersed; tepals mostly red(dish) brown; ovary white or partly reddish, sometimes entirely reddish.

***Ficus amplissima* J.E.Sm.** in Rees, Cycl. 14: n. 68. 1810, non Miq. 1867; Corner, Gard. Bull. Singapore 18: 84. 1961; 21: 11. 1965; K.M.Matthew, Fl. Tam. Carnatic 3: 1515. 1983 ≡ *Tsjela* Rheede, Hort. Mal. 3: 85, t. 63. 1682, nom. inval. ≡ *Ficus tsiela* Roxb., Hort. Bengal.: 66. 1826, nom. superfl.; Fl. Ind. 3: 549. 1832; King in Hook.f., Fl. Brit. India 5: 515. 1888. ≡ *Ficus tsjela* Roxb. ex Buch.–Ham., Tr. Linn. Soc. 15: 149. 1826, nom. superfl.; King, Ann. Roy. Bot. Gard. (Culcutta) 1: t.74. 1887 ≡ *Ficus indica* auct. non L.: L., Sp. Pl. 2: 1060. 1753; Vahl. Enum. Pl., ed. 2: 195. 1806; Willd., Sp. Pl., ed. 4, 4(2): 1146. 1806.—TYPE: Rheede (1682) t. 63, based on *Tsjela* Rheed.

= *Urostigma pseudobenjamineum* Miq., London J. Bot. 6: 566. 1847 ≡ *Ficus pseudobenjaminea* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867—TYPE: INDIA. Luddaloor, *Wight s.n. in herb. Rupel* (holotype: K).

= *Urostigma pseudotsiela* Miq., London J. Bot. 6: 566. 1847. ≡ *Ficus pseudotsiela* (Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: t. 74. 1887—TYPE: *Wight*. in Herb. Hook. (not found yet, information based on Corner 1965).

***Ficus rumphii* Blume**, Bijdr. Fl. Ned. Ind. 9: 437. 1825; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867; King, Ann. Roy. Bot. Gard. (Calcutta) 1: 54, t. 67B. 1887; Gagnep. in Lecomte, Fl. Indo–Chine 5: 768. 1928; Corner, Wayside Trees 1: 687. 1940; Gard. Bull. Singapore 21: 11. 1965; C.C.Berg and Corner in Nooteb., Fl. Males. Ser. 1, 17 (2): 609. 2005 ≡ *Urostigma rumphii* (Blume) Miq. in Zoll., Syst. Verz. 2: 90. 1854; Fl. Ind. Bat. 1, 2: 322. 1859 — TYPE: INDONESIA. Java, *Reinwardt 1121* (holotype: L; isotype: P).

= [*Ficus populiformis* Schott ex Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867, nom.nud.]

= *Ficus religiosa* L. var. ß "*Arbor conciliorum* etc." Lam., Encycl. 2, 2: 493. 1788. nom. illig.–*Ficus cordifolia* Roxb., Fl. Ind. (Carey ed.) 3: 548. 1832 ≡*Urostigma cordifolium* (Roxb.) Miq., London J. Bot. 6: 564. 1847 ≡ *Ficus conciliorum* Oken, Allg. Naturgesch.3: 1561. 1841, nom. superfl. — TYPE: based on Rumphius: *Arbor conciliorum* Rumph., Herb. Amboin. 3: t.91, 92. 1743.

= *Ficus damit* Gagnep., Notul. Syst. (Paris) 4: 88. 1927; in Lecomte, Fl. Indo–Chine 5: 812, f.93. 1928 — TYPE: VIETNAM. Quang–tri, Lao–bao, *Poilane 1337* (holotype: P).

Ficus pubipetiola Chantaras., sp. nov. — TYPE : THAILAND, Lopburi, Tha Wung, Wat Khao Samorkhorn, 18 September 2010, *Chantarasuwan 180910-2*, (holotype : THNHM, isotype : L).

Leaf lamina ovate, 4–9 by 6.5–12 cm , subcoriaceous, apex (sub)acuminate, pubescent on midrib and primary veins on lower surface, petiole 1.1–2.5 cm long, pubescent. Figs axillary, sessile.

Small trees, up to 7 m tall. Branches drying grey-brown, without intermittent growth. Leafy twigs 2–4 mm thick, pubescent, epidermis flaking off. Leaves spirally arranged, not articulate; lamina ovate, 4–9 by 6.5–12 cm, subcoriaceous, apex (sub)acuminate, the acumen sharp, base broadly cuneate or sub-attenuate, rarely sub-cordate, upper surface glabrous except pubescent on midrib, lower surface glabrous except pubescent on midrib and primary veins; lateral veins 5–9 pairs, furcated away from margin, the basal pair up to ¼–2/5th the length of the lamina, branched, tertiary venation reticulate; petiole 1.1–2.5 cm long, pubescent, epidermis persistent. Stipules 0.8–1.7 cm long, brown pubescent, persistent at tip of twig. Figs axillary, solitary or in pairs, sessile; basal bracts 3, 1–2 mm long, glabrous, persistent, receptacle obovate, 0.8–1.1 cm diam. when dry, glabrous, apex convex, ostiole 2–2.5 mm diam., upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers dispersed, sessile to pedicellate; tepals 3, ovate to broad-lanceolate, free, red-brown; stamen one. Pistillate flowers sessile to pedicellate, sometimes with a bract at base of pedicel; tepals 3, ovate or broadly lanceolate, free, red–brown; ovary white (or pale yellow). Fig. 5-6.

Distribution and Habitat: Thailand, on limestone in dwarf community, at elevation of c. 30 m. Figs in September–November.

Other species in this subsection are:

Ficus acamptophylla (Miq.) Miq. (Berg & Corner, 2005: 622)
Ficus altissima Blume (Berg & Corner, 2005: 625)
Ficus annulata Blume (Berg & Corner, 2005: 625)
Ficus archboldiana Summerh. (Berg & Corner, 2005: 627)
Ficus belete Merr. (Berg & Corner, 2005: 628)
Ficus benghalensis L. (Berg & Corner, 2005: 630)
Ficus benjamina L. (Berg & Corner, 2005: 631)
Ficus binnendijkii (Miq.) Miq. (Berg & Corner, 2005: 633)
Ficus borneensis Kochummen (Berg & Corner, 2005: 634)
Ficus bracteata (Wall. ex Miq.) Miq. (Berg & Corner, 2005: 635)
Ficus callophylla Blume (Berg & Corner, 2005: 637)
Ficus chrysolepis Miq. (Berg & Corner, 2005: 640)
Ficus chrysolepis subsp. *chrysolepis* (Berg & Corner, 2005: 626, 640)
Ficus chrysolepis subsp. *novoguineensis* (Corner) C.C. Berg (Berg & Corner, 2005: 626, 641)
Ficus consociata Blume (Berg & Corner, 2005: 641)
Ficus cordatula Merr. (Berg & Corner, 2005: 642)
Ficus corneri Kochummen (Berg & Corner, 2005: 643)
Ficus costata Aiton (Corner, 1981: 246)
Ficus crassiramea (Miq.) Miq. (Berg & Corner, 2005: 643)
Ficus crassiramea subsp. *crassiramea* (Berg & Corner, 2005: 644)
Ficus crassiramea subsp. *stupenda* (Miq.) C.C. Berg (Berg & Corner, 2005: 647)
Ficus cucurbitina King (Berg & Corner, 2005: 647)
Ficus curtipes Corner (Berg & Corner, 2005: 638, 648)
Ficus dalhousiae Miq. (Corner, 1965: 12)
Ficus delosyce Corner (Berg & Corner, 2005: 649)
Ficus depressa Blume (Berg & Corner, 2005: 650)
Ficus drupacea Thunb. (Berg & Corner, 2005: 651)
Ficus dubia Wall. ex King (Berg & Corner, 2005: 653)
Ficus fergusoni (King) Worthington (Corner, 1981: 253)
Ficus forstenii Miq. (Berg & Corner, 2005: 654)
Ficus glaberrima Blumea (Berg et al., 2011: 625)
Ficus glaberrima subsp. *glaberrima* (Berg et al., 2011: 625)
Ficus glaberrima subsp. *siamensis* (Corner) C.C. Berg (Berg et al., 2011: 625)
Ficus globosa Blume (Berge & Corner, 2005: 626, 657)
Ficus humbertii C.C. Berg (Berg & Wiebes, 1992)
Ficus involucrata Blume (Berg & Corner, 2005: 658)
Ficus juglandiformis King (Berg & Corner, 2005: 659)
Ficus kerkhovenii Valeton (Berg & Corner, 2005: 659)
Ficus kochummeniana C.C. Berg (Berg & Corner, 2005: 661)
Ficus kurzii King (Berg & Corner, 2005: 662)

Ficus lawesii King (Berg & Corner, 2005: 655, 663)
Ficus lowii King (Berg & Corner, 2005: 664)
Ficus maclellendii King (Berg & Corner, 2005: 665)
Ficus menabeensis Perrier (Berg & Wiebes, 1992: 95)
Ficus microcarpa L.f. (Berg & Corner, 2005: 624, 666)
Ficus microsyce Ridl. (Berg & Corner, 2005: 623, 670)
Ficus miqueliana C.C. Berg (Berg & Corner, 2005: 617)
Ficus mollis Vahl (Corner, 1981: 249)
Ficus pallescens (Weiblen) C.C. Berg (Berg & Corner, 2005: 671)
Ficus paracamptophylla Corner (Berg & Corner, 2005: 672)
Ficus patellata Corner (Berg & Corner, 2005: 673)
Ficus pellucidopunctata Griff. (Berg & Corner, 2005: 674)
Ficus pisocarpa Blume (Berg & Corner, 2005: 674)
Ficus pubilimba Merr. (Berg & Corner, 2005: 676)
Ficus retusa L. (Berg & Corner, 2005: 676)
Ficus rigo F.M. Bailey (Berg & Corner, 2005: 677)
Ficus soepadmoi Kochummen (Berg & Corner, 2005: 678)
Ficus spathulifolia Corner (Berg & Corner, 2005: 678)
Ficus stricta (Miq.) Miq. (Berg & Corner, 2005: 679)
Ficus subcordata Blume (Berg & Corner, 2005: 669, 680)
Ficus subgelderi Corner (Berg & Corner, 2005: 681)
Ficus sumatrana (Miq.) Miq. (Berg & Corner, 2005: 682)
Ficus sundaica Blume (Berg & Corner, 2005: 684)
Ficus talbotii King (= *F. calcicola* Corner) (Berg et al., 2011: 647)
Ficus tristaniifolia Corner (Berg & Corner, 2005: 669, 686)
Ficus xylophylla (Wall. ex Miq.) Miq. (Berg & Corner, 2005: 687)

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APPENDIX 1 Species, voucher specimen, and Gen Bank information for sequence data reported in the study: sequence per entry: Species; Taxon code; Voucher; Source and Geographic regions; GenBank accession (ITS, ETS, G3pdh, ncpGS)

Ficus alongensis Gagnep.; *alongensis* 1; Steward and Cheo 1187 (P); China, Shaanxi, Chang An; KJ845962, KJ845902, KJ846015, -

Ficus alongensis Gagnep.; *alongensis* 2; R.C. Ching 1917 (P); China; KJ845963, KJ845903, - , -

Ficus arnottiana (Miq.) Miq.; *arnottiana* 1; A.H.M. Jayasuriya 1293 (L); Sri Lanka, Anuradhapura, Ritigala Strict Natural reserve; - , KJ845879, - , -

Ficus arnottiana (Miq.) Miq.; *arnottiana* 2; 2038(no collector name) (L); India, Mangalor; - , KJ845880, - , -

Ficus caulocarpa (Miq.) Miq.; *caulocarpa* 1; C.E. Ridsdale SMHI 323 (L); Philippines, Taytay municipality, Lake Manguao; KJ845953, - , - , -

Ficus caulocarpa (Miq.) Miq.; *caulocarpa* 2; Chantarasuwan 261111-1 (L); Thailand, Trang, Nayong; KJ845954, KJ845894, KJ846009, -

Ficus caulocarpa (Miq.) Miq.; *caulocarpa* 3; Chantarasuwan 071010-2 (L); Thailand, Nakhon Si Thammarat, Noppitam; KJ845955, KJ845895, KJ846010, -

Ficus concinna (Miq.) Miq.; *concinna* 1; Chantarasuwan 071010-1 (L); Thailand, Nakhon Si Thammarat, Thasala; KJ845989, KJ845928, KJ846035, -

Ficus concinna (Miq.) Miq.; *concinna* 2; Chantarasuwan 140910-3 (L); Thailand, Ratchaburi, Chombung; KJ845990, KJ845929, KJ846036, -

Ficus concinna (Miq.) Miq.; *concinna* 3; Chantarasuwan 120910-5 (L); Thailand, Rayong, Pe; KJ845991, KJ845930, KJ846037, KJ846071

Ficus concinna (Miq.) Miq.; *concinna* 4; Chantarasuwan 051010-4 (L); Thailand, Prachuap Khiri Khan, Kuiburi; KJ845992, KJ845931, KJ846038, KJ846072

Ficus cordata Thunb.; *cordata* 1; Dinter 275 (WAG); Namibia;KJ845973, KJ845912, KJ846020, -

Ficus cordata Thunb.; *cordata* 2; Seydel 1555 (WAG); Namibia, Erongo, Okongawa; KJ845974, 845913, KJ846021, -

Ficus cordata Thunb.; *cordata* 3; Theson 3363 (WAG); Namibia; KJ845975, KJ845914, KJ846022, KJ846063

Ficus densifolia Miq.; *densifolia* 1; Baider CB2421 (L); Mauritius; KJ845983, KJ845922, KJ846030, KJ846068

Ficus densifolia Miq.; *densifolia* 2; Baider CB2422 (L); Mauritius; KJ845984, KJ845923, KJ846031, KJ846069

Ficus densifolia Miq.; *densifolia* 3; M02 (CEFE-CNRS); Mauritius; KJ845985, KJ845924, KJ846032, -

Ficus densifolia Miq.; *densifolia* 4; M01 (CEFE-CNRS); Mauritius; KJ845986, KJ845925, KJ846033, KJ846070

Ficus geniculata Kurz var. *geniculata; geniculata* 1; Chantarasuwan 150910-1 (L); Thailand, Kanchanaburi, Thong Pha Phum, Lintin; KJ845940, KJ845882, KJ845999, KJ846044

Ficus geniculata Kurz var. *geniculata; geniculata* 2; Chantarasuwan 210910-1 (L); Thailand, Lamphun, Muang; KJ845941, KJ845883, KJ846000, KJ846045

Ficus geniculata Kurz var. *geniculata; geniculata* 3; Chantarasuwan 301111-1 (L); Thailand, Chiang Rai, Muang, Pongsali; KJ845942, KJ845884, - , KJ846046

Ficus geniculata Kurz var. *insignis* (Kurz) C.C.Berg; geniculate-insignis; Parker 1144 (L); Australia, Northern Territory, Darwin; KJ845943, KJ845885, KJ846001, KJ846047

Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg; *glaberrima-siamensis* 1; Chantarasuwan 110910-2 (L); Thailand, Sa Kaeo, Khao Chakan; KJ845996, KJ845935, KJ846041, KJ846076

Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg; *glaberrima-siamensis* 2; Chantarasuwan 110910-3 (L); Thailand, Sa Kaeo, Khao Chakan; KJ845997, KJ845936, KJ846042, KJ846077

Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg; *glaberrima-siamensis* 3; Chantarasuwan 180910-3 (L); Thailand, Lop Buri, Thawung; KJ845998, KJ845937, KJ846043, -

Ficus henneana Miq.; *henneana* 1; J.R. Maconochie 2208 (L); Australia, Arnhem Land, Elcho Isl.; KJ845967, - , KJ846016, KJ846058

Ficus henneana Miq.; *henneana* 2; B. Hyland 8086 (L); Australia, Queensland, Atherton; KJ845968, KJ845907, - , KJ846059

Ficus hookeriana Corner; *hookeriana*; Hooker & T.Thomson 120 (L); India, Sikkim; KJ845988, KJ845927, - , -

F*icus ingens* (Miq.) Miq.; *ingens* 1; BG 03 (L); Ivory Coast; KJ845964, KJ845904, - , KJ846056

Ficus ingens (Miq.) Miq.; *ingens* 2; Correia 3777 (WAG); Mozambique; KJ845965, KJ845905, - , -

Ficus ingens (Miq.) Miq.; *ingens* 3; Jongkind 4317 (WAG); Ivory Coast; KJ845966, KJ845906, - , KJ846057

Ficus lecardii Warb.; *lecardii* 1; Harris 2136 (WAG); Central African Republic; KJ845971, KJ845910, KJ846018, KJ846061

Ficus lecardii Warb.; *lecardii* 2; Letouzey 6949 (WAG); Cameroon; KJ845972, KJ845911, KJ846019, KJ846062

Ficus madagascariensis C.C.Berg; *madagascariensis* ; P.R. Montagnac 72 (WAG); Madagascar, without locality; KJ845956, KJ845896, - , KJ846053

Ficus middletonii Chantaras.; *middletonii* ; Chantarasuwan 051010-2 (L); Thailand, Prachuap Khiri Khan, Kuiburi; KJ845952, KJ845893, KJ846008, KJ846052

Ficus orthoneura H.Lév. & Vaniot; *orthoneura* 1; Chantarasuwan 231111-1 (L); Thailand, Tak, Phobpra; KJ845987, KJ845926, KJ846034, -

Ficus prasinicarpa Elmer ex C.C.Berg; *prasinicarpa* 1; Ridsdale 434 (L); Philippines; KJ845947, -, -, -

Ficus prasinicarpa Elmer ex C.C.Berg; *prasinicarpa* 2; Nagari 7309 (L); Papua New Guinea; KJ845948, KJ845889, - , -

Ficus prolixa G. Forst.; *prolixa* 1; Gillett 2206 (L); Marquesas; KJ845949, KJ845890, KJ846005, KJ846051

Ficus prolixa G. Forst.; *prolixa* 2; Fosberg 25302 (L); Guam; KJ845950, KJ845891, KJ846006, -

Ficus pseudoconcinna Chantaras.; *pseudoconcinna* ; Soenarko 355 (L); Indonesia,Sulawesi; KJ845946, KJ845888, KJ846004, KJ846050

Ficus religiosa L.; *religiosa* 1; BG 04(L); unknown; KJ845980, KJ845919, KJ846027, KJ846066

Ficus religiosa L.; *religiosa* 2; Chantarasuwan 110910-4 (L); Thailand, Sa Kaeo, Khao Chakan; KJ845981, KJ845920, KJ846028, -

Ficus religiosa L.; *religiosa* 3; Chantarasuwan 150910-2 (L); Thailand, Kanchanaburi, Thong Pha Phum, Lintin; KJ845982, KJ845921, KJ846029, KJ846067

Ficus cf. rumphii; rumphii cf.; Chantarasuwan 180910-2 (L); Thailand, Lop Buri, Thawung; KJ845995, KJ845934, - , KJ846075

Ficus rumphii Blume; *rumphii* 1; Chantarasuwan 120910-4 (L); Thailand, Rayong, Pe; KJ845993, KJ845932, KJ846039, KJ846073
Ficus rumphii Blume; *rumphii* 2; Chantarasuwan 140910-1 (L); Thailand, Ratchaburi, Chombung; KJ845994, KJ845933, KJ846040, KJ846074
Ficus salicifolia Vahl; *salicifolia* 1; Humbert s.n. (WAG); South Africa; KJ845976, KJ845915, KJ846023, KJ846064
Ficus salicifolia Vahl; *salicifolia* 2; Bornmüller 646 (WAG); Saudi Arabia; KJ845977, KJ845916, KJ846024, -
Ficus subpisocarpa Gagnep. subsp. *pubipoda* C.C. Berg; subpisocarpa- pubipoda 1; Chantarasuwan 110910-1 (L); Thailand, Chachoengsao, Panom Sarakham; KJ845969, KJ845908, - , -
Ficus subpisocarpa Gagnep. subsp. *pubipoda* C.C. Berg; subpisocarpa- pubipoda 2; Chantarasuwan 011211-1 (L); Thailand, Chachoengsao, Panom Sarakham; KJ845970, KJ845909, KJ846017, KJ846060
Ficus superba (Miq.) Miq.; *superba* 1; C. Friedberg 138 (L); Indonesia, Timor central; KJ845944, KJ845886, KJ846002, KJ846048
Ficus superba (Miq.) Miq.; *superba* 2; Chantarasuwan 120910-2 (L); Thailand, Rayong, Kleang; KJ845945, KJ845887, KJ846003, KJ846049
Ficus tsjakela Burm.f.; *tsjakela*; Kostermans 27682 (L); Sri Lanka, Botanics Garden Peradeniya; KJ845951, KJ845892, KJ846007, -
Ficus verruculosa Warb.; *verruculosa* 1; Radcliff-Smith 5982 (WAG); Malawi; KJ845978, KJ845917, KJ846025, -
Ficus verruculosa Warb.; *verruculosa* 2; Adjakidje 2779 (WAG); Benin; KJ845979, KJ845917, KJ846026, KJ846065
Ficus virens Aiton var. *glabella* (Blume) Corner; *virens-glabella 1*; Chantarasuwan 071010-3 (L); Thailand, Nakhon Si Thammarat, Noppitam; KJ845960, KJ845900, KJ846013, KJ846055
Ficus virens Aiton var. *glabella* (Blume) Corner; *virens-glabella 2*; Chantarasuwan 071010-4 (L); Thailand, Nakhon Si Thammarat, Noppitam; KJ845961, KJ845901, KJ846014, -
Ficus virens Aiton var. *virens; virens 1*; P. Martensz AE 257 (L); Australia, Northern Territory; KJ845957, KJ845897, KJ846011, KJ846054
Ficus virens Aiton var. *virens; virens* 2; E. Jacobson 2191 (L); Indonesia ,Sumatra; KJ845958, KJ845898, KJ846012, -
Ficus virens Aiton var. *virens; virens* 3; G. Leach UPNG 3747 (L); Papua New Guinea, Central Province; KJ845959, KJ845899, - , -
Ficus virens Aiton var. *virens; virens 4*; L.H. Cramer 4670 (L); Sri Lanka, North-Western province, Puttalam, Talawila; KJ845938, KJ845881, - , -
Ficus virens Aiton var. *virens; virens 5*; Preyadasaman 5 (L); India, Coimbatore; KJ845939, - , - , -

APPENDIX 2. List of morphological and leaf anatomical characters used in the phylogenetic analysis.

1. Habit: (1) shrub; (2) tree. 2. Aerial roots: (1) present; (2) absent. 3. Intermittent growth: (1) present; (2) absent. 4. Leaf articulation: (1) present; (2) absent. 5. Indumentum of leafy twig: (1) glabrous to puberulous; (2) tomentose to villous. 6. Periderm of leafy twig: (1) persistent; (2) flaking off. 7. Leaf persistence: (1) deciduous; (2) evergreen. 8. Position of broadest part of leaf: (1) base; (2) middle; (3) apex. 9. Relative presence of cordate leaves: (1) cordate leaves dominant (>50%) (2) cordate leaves not dominant (<50%). 10. Caudate leaf apex: (1) present; (2) absent. 11. Relative width of lamina compared to length: (1) broad (> ¼); (2) narrow (< ¼). 12. Relative length of basal pair of nerves: (1) ≤ 1/3 of lamina; (2) > 1/3 of lamina. 13. Number of lateral veins: (1) 4-9; (2) ≥10. 14. Branching of lateral veins: (1) present; (2) absent. 15. Branching of basal veins: (1) present; (2) absent. 16. Tertiary venation: (1) partly parallel with primary veins; (2) reticulate. 17. Waxy glands: (1) at base of midrib; (2) in axil of lateral veins. 18. Relative petiole length: (1) < ¼ of leaf length; (2) > ¼ of leaf length. 19. Epidermis of petiole: (1) persistent; (2) flaking off. 20. Indumentum of petiole: (1) glabrous; (2) puberulous. 21. Length of stipules: (1) < 1 cm long; (2) ≥ 1 cm long. 22. Stipular bracts: (1) forming broadly ovoid terminal bud; (2) forming ovoid terminal bud. 23. Epidermis of stipule: (1) persistent; (2) flaking off. 24. Indumentum of stipule: (1) glabrous to puberulous; (2) tomentose to villous. 25. Persistence of stipule: (1) persistent; (2) caducous. 26. Ramiflorous figs: (1) with spur; (2) without spur. 27. Grouping of figs: (1) 1 or 2; (2) 3 to 8. 28. Indumentum of figs: (1) glabrous to puberulous; (2) tomentose to villous. 29. Fig peduncle: (1) present; (2) absent. 30. Number of basal bracts: (1) 2; (2) 3. 31. Persistence of basal bracts: (1) persistent; (2) caducous. 32. Degree of covering of fig by basal bracts: (1) only base of fig; (2) up to middle of fig. 33. Fig size: (1) 0.4–1 cm diam. when dry; (2) > 1 cm diam. when dry. 34. Fig form: (1) ovate to subglobose; (2) obovate to subpyriform; (3) oblong. 35. Colour of fig at maturity: (1) orange-red; (2) black; (3) green. 36. Apex of fig: (1) convex; (2) flat; (3) concave. 37. Size of ostiole: (1) 1–3 mm diam.; (2) > 3 mm diam. 38. Indumentum of ostiolar bracts: (1) glabrous; (2) puberulous. 39. Internal hairs of fig: (1) present; (2) absent. 40. Position on staminate flowers: (1) near ostiole; (2) dispersed. 41. Number of stamens: (1) 1; (2) 2. 42. Colour of ovary: (1) white; (2) red-brown. 43. Tepal connectivity: (1) free; (2) connate. 44. Epidermis: (1) simple; (2) multiple. 45. Number of radiating epidermal cells around lithocysts: (1) 5–8; (2) 9–16. 46. Cuticular ridge abaxially: (1) present; (2) absent. 47. Occurrence of enlarged lithocysts: (1) only abaxially; (2) adaxially or abundantly adaxially and a few abaxially. 48. Crystarque cells: (1) present; (2) absent. 49. Epidermal lithocysts: (1) present; (2) absent. 50. Palisade layers: (1) single; (2) multiple (2 and more). 51. Marginal sclerenchyma: (1) present; (2) absent. 52. Vascular bundles in midrib; (1) separate bundles; (2) 2 opposing arcs to closed cylinder. 53. Pith bundles in midrib: (1) present; (2) absent. 54. Pith bundles in petiole: (1) present; (2) absent. 55. Bundle sheaths: (1) vertically transcurrent; (2) circular, not transcurrent. 56. Silicified cells in mesophyll: (1) present; (2) absent. 57. Silicified cells in epidermis: (1) present; (2) absent. 58. Glandular hairs at petiole: (1) present; (2) absent. 59. Glandular hairs at lamina: (1) present; (2) absent. 60. Stomata: (1) level to epidermis; (2) sunken. 61. Giant stomata: (1) present; (2) absent. 62. Inner stomatal ledge: (1) present; (2) absent. 63. Thickness of cuticle on adaxial lamina: (1) ≤ 1 μm; (2) > 1 μm 64. Ratio of prismatic and druse crystal in midrib: (1) prismatic > druse; (2) druse > prismatic. 65. Subepidermal sclerified layer in petiole: (1) present; (2) absent. 66. Subepidermal sclerified layer in midrib: (1) present; (2) absent.

APPENDIX 3. Data matrix of morphological(1-43) and leaf anatomical(44-66) characters scored for the phylogenetic analyses and character reconstruction. Polymorphisms are indicated by all states presented by a comma, and inapplicable or unknown characters by "-" . Details of characters and states are also listed below.

APPENDIX 3. Data matrix of morphological(1-43) and leaf anatomical(44-66) characters scored for the phylogenetic analyses and character reconstruction. Polymorphisms are indicated by all states presented by a comma, and inapplicable or unknown characters by "-" . Details of characters and states are also listed below.

Taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
F. alongensis 1	2	2	1	1	1	1	1	1	2	2	1	1,2	1	1	1	2	1	2	1	1	1	2
F. alongensis 2	2	2	1	1	1	1	1	1	2	2	1	1,2	1	1	1	2	1	2	1	1	1	2
F. altissima	2	1	2	2	1	1	1	1	2	2	1	1	1	1	1	2	1	2	1	1	2	2
F. americana	2	1	2	2	1	1	2	2,3	2	2	1	1	2	2	2	1	1	2	1	1	1	2
F. arnottiana 1	2	2	1	1	1	1,2	1	1	1	1	1	2	1	2	1	2	1	1	1	1,2	1	2
F. arnottiana 2	2	2	1	1	1	1,2	1	1	1	1	1	2	1	2	1	2	1	1	1	1,2	1	2
F. aurea	2	1	2	2	1	1	2	1	2	2	1	1,2	1	2	2	2	1	2	1	1	2	2
F. benjamina	2	1	2	2	1	2	2	1	2	2	1	1	2	2	2	1	1	2	1	1	1	2
F. brachypoda	2	2	2	2	1	1	2	1	2	2	1	1	2	2	2	1	1	1	1	1,2	1	2
F. bubu	2	1	2	2	1	2	2	1,2	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. caulocarpa 1	2	2	1	1	1	1	1	2	2	2	1,2	1	2	2	2	2	1	1	1	1	1	2
F. caulocarpa 2	2	2	1	1	1	1	1	2	2	2	1,2	1	2	2	2	2	1	1	1	1	1	2
F. caulocarpa 3	2	2	1	1	1	1	1	2	2	2	1,2	1	2	2	2	2	1	1	1	1	1	2
F. concinna 1	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. concinna 2	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. concinna 3	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. concinna 4	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. cordata 1	2	2	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	1	1	1	1	2
F. cordata 2	2	2	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	1	1	1	1	2
F. cordata 3	2	2	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	1	1	1	1	2
F. densifolia 1	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. densifolia 2	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. densifolia 3	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. densifolia 4	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. geniculata 1	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. geniculata 2	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. geniculata 3	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. geniculata_insignis	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	1	2	1	1	2	1,2	1	2
F. glaberrima_ siamensis 1	2	1	2	2	1	1	2	1	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. glaberrima_ siamensis 2	2	1	2	2	1	1	2	1	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. glaberrima_ siamensis 3	2	1	2	2	1	1	2	1	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. henneana 1	2	2	1	1	1	1	1	2	2	2	1	1	1,2	1	2	2	1	1	1	1	1	2
F. henneana 2	2	2	1	1	1	1	1	2	2	2	1	1	1,2	1	2	2	1	1	1	1	1	2
F. hookeriana 1	2	2	1	2	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	1	1
F. hookeriana 2	2	2	1	2	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	1	1
F. ingens 1	2	2	1	2	2	1	1	1	2	2	1	1,2	1	1	1	2	1	1	1	1	1	2
F. ingens 2	2	2	1	2	2	1	1	1	2	2	1	1,2	1	1	1	2	1	1	1	1	1	2
F. ingens 3	2	2	1	2	2	1	1	1	2	2	1	1,2	1	1	1	2	1	1	1	1	1	2
F. lecardii 1	2	2	1	2	1	1	1	1	2	2	1	1	1	2	2	2	1	1	1	1,2	1	2
F. lecardii 2	2	2	1	2	1	1	1	1	2	2	1	1	1	2	2	2	1	1	1	1,2	1	2
F. madagascariensis	1,2	2	1	2	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. maxima	2	2	2	2	1	2	2	1	2	2	1	1	1	1	2	2	2	2	2	1	2	2
F. menabeensis	2	1	2	2	1	2	2	1	2	2	1	1	1	2	2	2	1	2	1	2	1	2
F. middletonii	2	2	1	1	1	1	1	1	2	2	1	1	1	1	1	2	1	1	1	1,2	1	2
F. orthoneura 1	1	2	1	2	1	1	1	2	2	2	1	1	2	1	2	2	1	1	1	1	1	1
F. orthoneura 2	1	2	1	2	1	1	1	2	2	2	1	1	2	1	2	2	1	1	1	1	1	1
F. orthoneura 3	1	2	1	2	1	1	1	2	2	2	1	1	2	1	2	2	1	1	1	1	1	1
F. pleurocarpa	2	2	2	2	2	1	2	1	2	2	1	1	2	2	2	1	1	2	1	2	2	2
F. prasinicarpa 1	2	2	1	1	1	2	1	1	2	2	1	1,2	1	2	1	2	1	1	1	1	1	2
F. prasinicarpa 2	2	2	1	1	1	2	1	1	2	2	1	1,2	1	2	1	2	1	1	1	1	1	2
F. prolixa 1	2	2	1	1	1	1	1	1	2	2	1	1,2	1	2	1	2	1	1	1,2	1,2	1	2
F. prolixa 2	2	2	1	1	1	1	1	1	2	2	1	1,2	1	2	1	2	1	1	1,2	1,2	1	2
F. pseudoconcinna	2	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	1	1	1	1	1	2
F. religiosa 1	2	2	1	1	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1	1	1	1	2
F. religiosa 2	2	2	1	1	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1	1	1	1	2
F. religiosa 3	2	2	1	1	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1	1	1	1	2
F. rumphii 1	2	2	1	2	1	2	1	1	2	2	1	2	1	1	1	2	1	1	1	1	2	2
F. rumphii 2	2	2	1	2	1	2	1	1	2	2	1	2	1	1	1	2	1	1	1	1	2	2
F. rumphii cf.	2	2	2	2	1	2	1	1	2	2	1	2	1	1	1	2	1	2	1	2	1	2
F. salicifolia 1	2	2	1	2	1	1	1	1	2	2	2	1	2	2	2	2	1	1	1	1,2	1	2
F. salicifolia 2	2	2	1	2	1	1	1	1	2	2	2	1	2	2	2	2	1	1	1	1,2	1	2
F. subpisocarpa_ pubipoda 1	2	2	1	1	1	2	1	2	2	2	1	1	1	2	2	2	1	1	2	2	1	1
F. subpisocarpa_ pubipoda 2	2	2	1	1	1	2	1	2	2	2	1	1	1	2	2	2	1	1	2	2	1	1
F. superba 1	2	2	1	1	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	2	1
F. superba 2	2	2	1	1	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	2	1
F. tonduzii	2	2	2	2	1	1	2	1	2	2	1	1	1	1	2	2	2	1	2	1	2	2
F. tsjakela	2	2	1	1	1	1	1	1	2	2	1	1	2	2	2	2	1	1	1	1	1	2
F. verruculosa 1	1	2	1	2	1,2	1	2	1,2	2	2	1	1,2	2	2	2	2	1	2	1	1,2	1	2
F. verruculosa 2	1	2	1	2	1,2	1	2	1,2	2	2	1	1,2	2	2	2	2	1	2	1	1,2	1	2
F. virens 1	2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1
F. virens 2	2	2	1	1	1	1	1	1	2	2	1	1	1,2	1	1	2	1	1	1	1	1	1
F. virens 3	2	2	1	1	1	1	1	1	2	2	1	1	1,2	1	1	2	1	1	1	1	1	1
F. virens 4	2	2	1	1	1	2	1	1	2	2	1	1	1,2	2	2	1	1	1	1	1	2	2
F. virens 5	2	2	1	1	1	2	1	1	2	2	1	1	1,2	2	2	1	1	1	1	1	2	2
F. virens_glabella 1	2	2	1	1	1	1	1	3	2	2	1	1	1,2	2	2	2	1	1	1	1	1	1
F. virens_glabella 2	2	2	1	1	1	1	1	3	2	2	1	1	1,2	2	2	2	1	1	1	1	1	1

Taxon/character	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
F. alongensis 1	1	1	2	2	1	1	1	2	1	1	1	1	-	1	1	1	2	1	1	2	1,2	1
F. alongensis 2	1	1	2	2	1	1	1	2	1	1	1	1	-	1	1	1	2	1	1	2	1,2	1
F. altissima	1	1	2	2	1	1	2	1,2	1	1	2	1	1	1	1	1	2	2	1	2	1	-
F. americana	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	2	1	-	1	-
F. arnottiana 1	1	1	2	1	2	1	1	2	1	1	1	1	-	1	1	1	2	2	1	2	2	2
F. arnottiana 2	1	1	2	1	2	1	1	2	1	1	1	1	-	1	1	1	2	2	1	2	2	2
F. aurea	1	1	1	2	1	1	1,2	1	1	2	1	1	1	1	1	1	-	2	1	2	1	-
F. benjamina	1	1	2	2	1	1	2	2	1	1	1	1	1	1	1	1	1	2	1	2	1	-

F. brachypoda	1	1	1,2	2	1	1	1	2	2	1	2	3	1	1	1	1	2	2	1	2	1	-
F. bubu	1	1	2	1	2	1	1	2	1	1	2	1	1	3	1	1	2	2	1	2	1	-
F. caulocarpa 1	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1,2	1
F. caulocarpa 2	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1,2	1
F. caulocarpa 3	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1,2	1
F. concinna 1	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. concinna 2	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. concinna 3	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. concinna 4	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. cordata 1	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1,2	2	1	1	2	1	1
F. cordata 2	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1,2	2	1	1	2	1	1
F. cordata 3	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1,2	2	1	1	2	1	1
F. densifolia 1	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. densifolia 2	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. densifolia 3	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. densifolia 4	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. geniculata 1	1	1	1	1	2	1	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. geniculata 2	2	2	1	1	1	1	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata 3	2	2	1	1	1	1	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata_insignis	1	2	1	1	2	2	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. glaberrima_ siamensis 1	1	1	2	2	1	1	1	2	2	1	1	1	1	1	1	1	2	2	1	2	1,2	2
F. glaberrima_ siamensis 2	1	1	2	2	1	1	1	2	2	1	1	1	1	1	1	1	2	2	1	2	1,2	2
F. glaberrima_ siamensis 3	1	1	2	2	1	1	1	2	2	1	1	1	1	1	1	1	2	2	1	2	1,2	2
F. henneana 1	1	1	2	2	1	1	1	2	2	1	2	1	2	1	2	1	2	1	1	2	1	1
F. henneana 2	1	1	2	2	1	1	1	2	2	1	2	1	2	1	2	1	2	1	1	2	1	1
F. hookeriana 1	1	1	1	2	1	1	2	-	1	2	2	1	-	2	2	1	2	2	1	2	1	2
F. hookeriana 2	1	1	1	2	1	1	2	-	1	2	2	1	-	2	2	1	2	2	1	2	1	2
F. ingens 1	1	1	2	2	1	1	1	2	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1
F. ingens 2	1	1	2	2	1	1	1	2	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1
F. ingens 3	1	1	2	2	1	1	1	2	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1
F. lecardii 1	1	1	2	2	1	1	1	2	1	1	1	1	1	1	1	1,2	1	1	1	2	1	1
F. lecardii 2	1	1	2	2	1	1	1	2	1	1	1	1	1	1	1	1,2	1	1	1	2	1	1
F. madagascariensis	1	1	1	2	1	1	2	2	1	1	1	1	-	1	1	1	2	1	1	2	1	1
F. maxima	1	1	1	2	1	1	1	2	1	1	2	1	-	1	1	2	2	2	2	2	1	-
F. menabeensis	1	1	2	2	1	1	2	2	1	1	1	1	1	1	1	1	-	2	1	1	1	-
F. middletonii	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1
F. orthoneura 1	1	1	1	1	1	1	1	2	1	1	1,2	1	-	1	1,2	1	2	2	1	2	1	2
F. orthoneura 2	1	1	1	1	1	1	1	2	1	1	1,2	1	-	1	1,2	1	2	2	1	2	1	2
F. orthoneura 3	1	1	1	1	1	1	1	2	1	1	1,2	1	-	1	1,2	1	2	2	1	2	1	2
F. pleurocarpa	1	2	1	2	1	1	1	2	1	1	2	1	1	1	1	1	2	2	1	2	1	-
F. prasinicarpa 1	1	1	2	1	1	1	1	2	1	1	1	1,2	2	1	1	1	2	1	1	2	1	1
F. prasinicarpa 2	1	1	2	1	1	1	1	2	1	1	1	1,2	2	1	1	1	2	1	1	2	1	1
F. prolixa 1	1	1	1	1	1	1	1	2	1	1	1	1,2	2	1	1	1	1	2	1	2	1,2	1
F. prolixa 2	1	1	1	1	1	1	1	2	1	1	1	1,2	2	1	1	1	1	2	1	2	1,2	1
F. pseudoconcinna	1	1	1	2	1	1	1	2	1	1	1	1	2	1	1	1	2	1	1	2	1	1
F. religiosa 1	1	1	1,2	2	1	1	2	2	1	2	1	1	2	1	1	1	2	1	1	2	1	1

F. religiosa 2	1	1	1,2	2	1	1	2	2	1	2	1	1	2	1	1	1	2	1	1	2	1	1
F. religiosa 3	1	1	1,2	2	1	1	2	2	1	2	1	1	2	1	1	1	2	1	1	2	1	1
F. rumphii 1	1	1	1	2	1	1	2	1,2	1	1	1	2	2	1	1	1	2	2	1	1	1	2
F. rumphii 2	1	1	1	2	1	1	2	1,2	1	1	1	2	2	1	1	1	2	2	1	1	1	2
F. rumphii cf.	1	1	1	2	1	1	2	2	1	1	1	2	2	1	1	1	2	2	1	1	1	2
F. salicifolia 1	1	1	1	1	1	1	1	2	1	1	1,2	1	2	1	1	1,2	1	1	1	2	1	1
F. salicifolia 2	1	1	1	1	1	1	1	2	1	1	1,2	1	2	1	1	1,2	1	1	1	2	1	1
F. subpisocarpa_ pubipoda 1	1	1	1	1	2	1	1	2	2	1	1,2	1,2	2	1	1	1	1	1	1	2	2	1
F. subpisocarpa_ pubipoda 2	1	1	1	1	2	1	1	2	2	1	1,2	1,2	2	1	1	1	1	1	1	2	2	1
F. superba 1	1	2	1	1	2	1	1	2	2	1	2	2	2	1	1	1	2	1	1	2	1,2	1
F. superba 2	1	2	1	1	2	1	1	2	2	1	2	2	2	1	1	1	2	1	1	2	1,2	1
F. tonduzii	1	1	1	2	1	1	1	2	1	1	2	1	-	1	1	1	2	2	2	2	1	-
F. tsjakela	1	1	1	1	2	1	2	2	1	1	1	1	-	1	1	1	2	1	1	2	1	1
F. verruculosa 1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2	1	1	2	1	1
F. verruculosa 2	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2	1	1	2	1	1
F. virens 1	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. virens 2	1	1	2	1	1	1	1,2	2	1	1	1,2	1	2	1	1	2	1	1	1	2	1	1
F. virens 3	1	1	2	1	1	1	1,2	2	1	1	1,2	1	2	1	1	2	1	1	1	2	1	1
F. virens 4	1	1	2	2	1	1	2	2	1	1	1	2	1	2	1	1	2	2	1	1	1	2
F. virens 5	1	1	2	2	1	1	2	2	1	1	1	2	1	2	1	1	2	2	1	1	1	2
F. virens_glabella 1	2	1	1	1	2	1	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. virens_glabella 2	2	1	1	1	2	1	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1

Taxon/character	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**
F. alongensis 1	2	2	1	1	2	1	1	1	2	2	1	2	2	1	2	1	2	2	2	1	1	1
F. alongensis 2	2	2	1	1	2	1	1	1	2	2	1	2	2	1	2	1	2	2	2	1	1	1
F. altissima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. americana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. arnottiana 1	1	2	2	2	2	2	1,2	2	1	1	1	2	2	2	2	1	2	1	1	2	2	2
F. arnottiana 2	1	2	2	2	2	2	1,2	2	1	1	1	2	2	2	2	1	2	1	1	2	2	2
F. aurea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. benjamina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. brachypoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. bubu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. caulocarpa 1	2	2	1	1,2	2	2	1	2	1	1	1	1	2	1	2	1	2	2	2	1	1	1
F. caulocarpa 2	2	2	1	1,2	2	2	1	2	1	1	1	1	2	1	2	1	2	2	2	1	1	1
F. caulocarpa 3	2	2	1	1,2	2	2	1	2	1	1	1	1	2	1	2	1	2	2	2	1	1	1
F. concinna 1	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. concinna 2	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. concinna 3	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. concinna 4	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. cordata 1	2	2	1	1	1,2	2	2	2	1	1	2	1,2	2	2	2	2	2	2	1	1	1	1
F. cordata 2	2	2	1	1	1,2	2	2	2	1	1	2	1,2	2	2	2	2	2	2	1	1	1	1
F. cordata 3	2	2	1	1	1,2	2	2	2	1	1	2	1,2	2	2	2	2	2	2	1	1	1	1
F. densifolia 1	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1
F. densifolia 2	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1
F. densifolia 3	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1

F. densifolia 4	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1
F. geniculata 1	2	2	1	1	1	2	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata 2	2	2	1	1	1	2	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata 3	2	2	1	1	1	2	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata_insignis	2	2	1	1	2	2	1	2	1	1	1	2	2	1	2	1	1	2	1	1	1	1
F. glaberrima_ siamensis 1	1	2	2	2	2	1	1	2	1	1	1	2	2	2	2	1	1	2	1,2	2	2	2
F. glaberrima_ siamensis 2	1	2	2	2	2	1	1	2	1	1	1	2	2	2	2	1	1	2	1,2	2	2	2
F. glaberrima_ siamensis 3	1	2	2	2	2	1	1	2	1	1	1	2	2	2	2	1	1	2	1,2	2	2	2
F. henneana 1	2	2	1	2	1	2	1	2	1	1	1	2	2	2	2	1	2	2	1	1	2	1
F. henneana 2	2	2	1	2	1	2	1	2	1	1	1	2	2	2	2	1	2	2	1	1	2	1
F. hookeriana 1	1	1	1	1,2	1	1,2	2	2	1	1	1	2	2	2	2	1	2	2	2	1	2	1
F. hookeriana 2	1	1	1	1,2	1	1,2	2	2	1	1	1	2	2	2	2	1	2	2	2	1	2	1
F. ingens 1	2	2	1	1	1	2	1	2	1	1	1	1,2	2	1,2	1,2	1	2	2	1	1	1	1
F. ingens 2	2	2	1	1	1	2	1	2	1	1	1	1,2	2	1,2	1,2	1	2	2	1	1	1	1
F. ingens 3	2	2	1	1	1	2	1	2	1	1	1	1,2	2	1,2	1,2	1	2	2	1	1	1	1
F. lecardii 1	1	2	1	2	1	1	2	2	1	1	1	2	2	2	2	2	1	2	1	1	2	1
F. lecardii 2	1	2	1	2	1	1	2	2	1	1	1	2	2	2	2	2	1	2	1	1	2	1
F. madagascariensis	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. maxima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. menabeensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. middletonii	2	2	1	2	2	2	1	2	1	1	1	2	2	1	1	1	2	1,2	1	1	1	1
F. orthoneura 1	1	1	1	2	2	1,2	1	1	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. orthoneura 2	1	1	1	2	2	1,2	1	1	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. orthoneura 3	1	1	1	2	2	1,2	1	1	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. pleurocarpa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. prasinicarpa 1	1	2	1	1,2	1,2	1	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. prasinicarpa 2	1	2	1	1,2	1,2	1	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. prolixa 1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	1,2	1	2	1	2	1,2	1	1	1	1
F. prolixa 2	2	2	1	1,2	1,2	1	1	2	1	1	1	1	1,2	1	2	1	2	1,2	1	1	1	1
F. pseudoconcinna	1	2	1	1	1,2	1	1	2	1	1	1	1	1	2	2	1	2	2	2	1	1	1
F. religiosa 1	2	2	1	1	1,2	2	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	1
F. religiosa 2	2	2	1	1	1,2	2	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	1
F. religiosa 3	2	2	1	1	1,2	2	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	1
F. rumphii 1	1	2	2	2	2	2	1	2	1	1	1	2	2	1	2	1	1	2	2	2	2	2
F. rumphii 2	1	2	2	2	2	2	1	2	1	1	1	2	2	1	2	1	1	2	2	2	2	2
F. rumphii cf.	1	2	2	2	2	2	1	2	1	1	1	1	2	1	1	1	2	2	2	2	2	2
F. salicifolia 1	1	2	1	2	1	2	1	2	1,2	1	1	2	2	1	2	2	1	1	1	1	2	2
F. salicifolia 2	1	2	1	2	1	2	1	2	1,2	1	1	2	2	1	2	2	1	1	1	1	2	2
F. subpisocarpa_ pubipoda 1	1	2	1	1	1	1	1	2	1	1	1	2	2	1	2	1	2	1	1	1	1	1
F. subpisocarpa_ pubipoda 2	1	2	1	1	1	1	1	2	1	1	1	2	2	1	2	1	2	1	1	1	1	1
F. superba 1	1	2	1	1	2	1	1	2	1	1	1	2	2	2	2	1	2	2	1	1	1	1
F. superba 2	1	2	1	1	2	1	1	2	1	1	1	2	2	2	2	1	2	2	1	1	1	1
F. tonduzii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. tsjakela	1	1	1	1,2	1,2	2	2	2	1	1	2	1,2	2	2	2	2	1	2	2	1	1	1

F. verruculosa 1	1	2	1	1,2	1,2	1	2	2	1,2	1	1	1	1	2	2	1,2	2	2	1	1	2	2
F. verruculosa 2	1	2	1	1,2	1,2	1	2	2	1,2	1	1	1	1	2	2	1,2	2	2	1	1	2	2
F. virens 1	2	2	1	1	1	2	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. virens 2	2	2	1	1	1	2	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. virens 3	2	2	1	1	1	2	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. virens 4	1	2	2	2	2	2	1	2	1	1	1	1,2	1,2	2	2	2	1	2	2	2	2	1
F. virens 5	1	2	2	2	2	2	1	2	1	1	1	1,2	1,2	2	2	2	1	2	2	2	2	1
F. virens_glabella 1	2	2	1	1	1	2	1	2	1	1	1	2	1	2	2	1	2	2	2	1	1	1
F. virens_glabella 2	2	2	1	1	1	2	1	2	1	1	1	2	1	2	2	1	2	2	2	1	1	1

Chapter 6

Ficus cornelisiana, a new species of *Ficus* subsection *Urostigma* (Moraceae) from the Sino-himalayan

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Abstract

A small fig tree has been misidenfied as *Ficus orthoneura* for a long time. However, morphologically it is distinct from *F. orthoneura* and *F. hookeriana*. Typical are the ellipsoid, puberulous receptacle and caducous basal bracts. Leaf anatomy shows a multiple epidermis with the cells in the inner layer much larger than in the outer layer and thus both layers resemble an epidermis with a separate hypodermis. The abaxial cuticle is strongly sculptured, the palisade layer shows some long subdivided cells, and enlarged lithocysts are only present abaxially. Because of these differences we hereby describe it as a new species, named in honour of Cornelis (Cees) Berg: *Ficus cornelisiana*.

Keywords – China, *Ficus*, Moraceae, new species, Vietnam.

Introduction

During the last 10 years a fig tree developed in Xishuangbanna Tropical Botanical Garden (XTBG, China) on a beautiful limestone rock purchased in Hanoi (Vietnam). The origin of the plant is uncertain, it can be an accidental introduction from Vietnam or it may be native in Kunming. Presently, the tree is on display in XTBG.

The plant was originally identified as *F. orthoneura* H. Lév. & Vaniot (Léveillé, 1907). However, it also resembled *F. hookeriana* Corner (1959). The plant was compared with both species as described in Chantarasuwan et al. (2013). Also, leaf anatomy (Chantarasuwan et al., submitted) was used to identify the XTBG plant.

Morphology showed that the specimen deviates distinctly from *F. hookeriana* and *F. orthoneura* (Table 6-1), while leaf anatomy showed some resembling characters with *F. hookeriana* and *F. orthoneura*, especially in the multiple epidermis with the cells in the second layer much larger than in the outer layer and in the abaxial cuticula that is strongly sculptured. On the other hand, the specimen lacks sclerenchyma caps in the midrib and petiole, and in that is clearly distinct from *F. hookeriana* and *F. orthoneura*. However, this difference may have been induced by the good treatment in the garden, where it is not subjected to drought stress that normally results in the formation of sclerenchyma.

Because of the differences, the specimen merits distinction as a new species. The new epithet *cornelisiana* honours the late Prof. Cornelis C. Berg, the worldwide *Ficus* expert.

Leaf anatomical methods

For leaf anatomy, dry leaves were rehydrated by boiling in water for a few minutes and were then stored in 50% alcohol. Cross sections were made with a Reichert slide microtome from three parts: 1) the middle of the lamina including the midrib, 2) a part of the lamina with the margin, and 3) three zones of the petiole: base, middle, and top near the lamina. Sixteen pieces were collected from each part. Free hand paradermal sections were taken from the adaxial and abaxial leaf surfaces. Half of the sections and paradermal sections were bleached and stained with safranin/haematoxylin. All sections were dehydrated and mounted in Euparal. Cuticular macerations were made by placing a leaf sample in a 1:1 mixture of hydrogen peroxide (30%) and acetic acid (99-100%) at 60°C overnight. The cuticle was cleaned the following day and placed in a mixture of 0.5% Sudan IV in 70% alcohol at 40°C for 2-3 h and mounted in glycerin jelly.

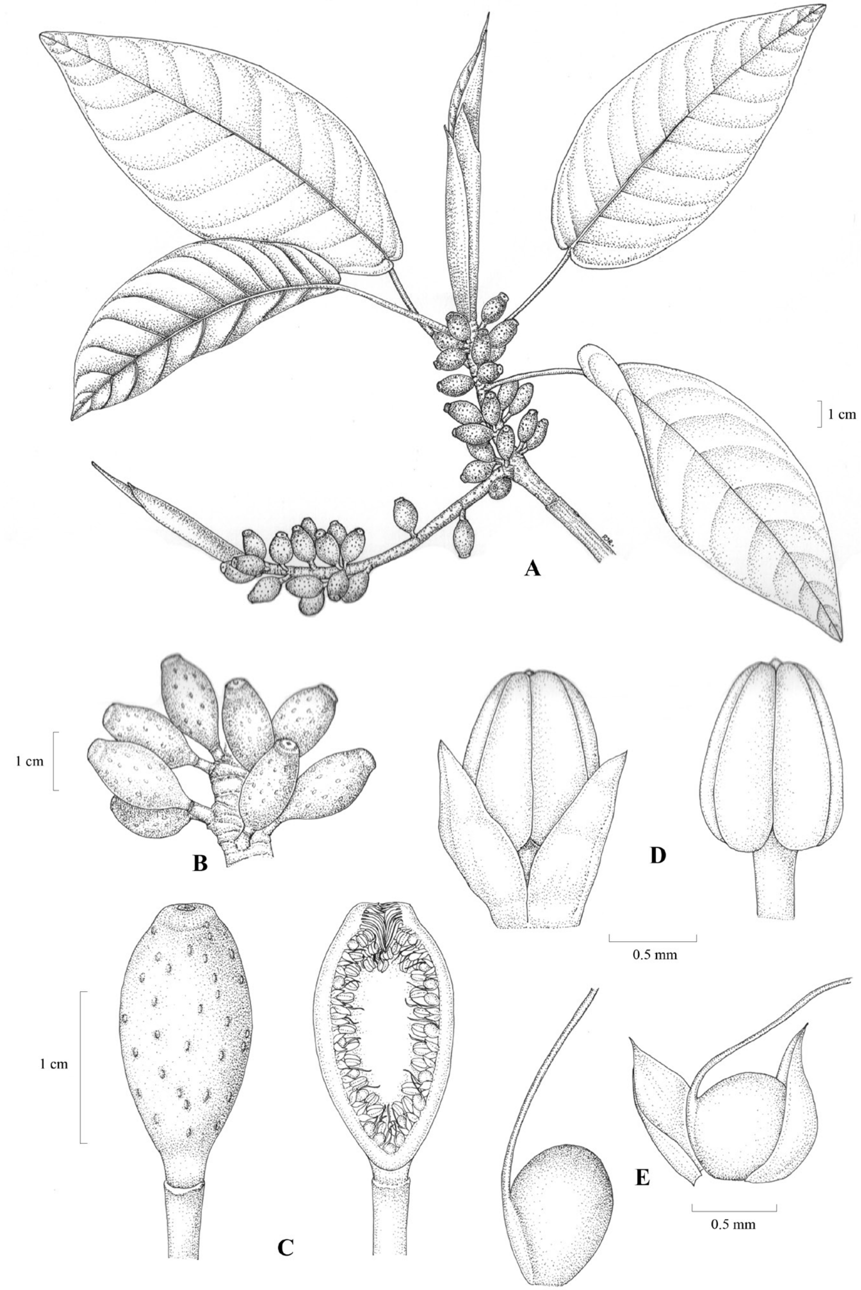

FIGURE 6-1 : *Ficus cornelisiana* Chantaras. & Y.Q. Peng. A. Twigs with leaves and figs. B. Figs. C. Fig in longitudinal section. D. Staminate flowers with and without tepals. E. Pistillate flowers with and without tepals. [*Yan–Qiong Peng s.n.* (L)]. Drawing: Pajaree Inthachup, 2013.

FIGURE 6-2 : Living part of *Ficus cornelisiana* Chantaras. & Y.Q. Peng. A. Twig with leaves and figs. B. Twigs with young leaves and figs. C. Fig in longitudinal section, note the caducous basal bracts.). All photographs by Yan–Qiong Peng.

Table 6-1 Comparison of morphological characters of *F. cornelisiana*, *F. orthoneura*, and *F. hookeriana*.

Characters	*F. cornelisiana*	*F. orthoneura*	*F. hookeriana*
Receptacle form	ellipsoid	subglobose	subglobose
Peduncle	1–3 mm long	2–5 mm long	sessile
Receptacle stipe	1–3 mm long	absent	absent
Receptacle indumentum	brown puberulous	glabrous	glabrous
Basal bracts of receptacle	3, free, caducous	3, free, persistent	3, connate into a cup, persistent

Ficus cornelisiana Chantaras. & Y.Q. Peng, sp. nov.–Fig. 6-1, 6-2.

Leaves (sub)cordate. Figs stipitate, receptacle ellipsoid, minutely brown puberulous; internal hairs absent. Staminate flowers dispersed, numerous. – Type: *Yan–Qiong Peng s.n.*, (holo: XTBG; iso: L), China, Yunnan, Kunming, Xishuangbanna Tropical Botanical Garden (cultivated), 23 June 2006.

Small tree, up to 5 m tall; branches drying brown or grey brown; leafy twigs 0.8–1 cm thick, glabrous, periderm persistent. *Stipules* 0.4–0.5 cm long, persistent, minutely puberulous to glabrous and up to 7 cm long in the open shoot. *Leaves* not articulate; petiole 3.5–5 cm long, glabrous, epidermis persistent; lamina elliptic to obovate, 13–15 by 5.5–7 cm, (sub)coriaceous, base (sub)cordate, apex obtuse or subacute, the acumen blunt, both surfaces glabrous; lateral veins 12 or 13 pairs, usually furcate away from the margin, the basal pairs up to 1/4–1/3 the length of the lamina, mostly branched, tertiary venation reticulate. *Figs* axillary or just below the leaves, solitary or in pairs, peduncle 1–3 mm long, puberulous; basal bracts 3, caducuous; receptacle ellipsoid, 0.8–1 cm diam when dry, with stipe 1–3 mm long, surface usually wrinkled when dry, brown puberulous, black at maturity, apex flat to convex; ostiole 2.5–3 mm diam, upper ostiolar bracts brown puberulous; internal hairs absent. *Staminate flowers* dispersed, numerous, sessile; tepals 3 (or 4), free, reddish brown. *Pistillate flowers* sessile; tepals (2 or) 3, ovate to elliptic, free, reddish brown; ovary red-brown, without or with stipe.

Distribution– Only known from the type, cultivated in XTBG, of Sino-himalayan origin (either endemic in Yunnan or in northern Vietnam, the place where the rock originated on which the plant is growing).

Note– The abundant, dispersed staminate flowers suggest passive pollination.

Leaf anatomy

Material studied: type (see above) – Fig. 6-3.

In surface view: Indumentum abaxially of glandular hairs with 1-celled heads. Cuticle smooth adaxially, strongly ridged abaxially. Anticlinal walls straight. Radiating epidermal cells around lithocysts 5–8 abaxially. Stomata 18.5–25 by 12.5–18.5 μm; giant stomata 25–28 by 18.5–22 μm.

In transverse section: Cuticle about 2 μm thick above lamina, above midrib and margin 5–8 μm thick. Epidermis multi-layered adaxially, cells in outer layer smaller than in inner layer; abaxially outer periclinal epidermal wall and cuticle strongly ridged resulting in seemingly papillate appearance in sectional view. Stomata level with epidermis, only outer cuticular ledges present. Enlarged lithocysts abaxially. Mesophyll dorsiventral. Palisade 1- to partly 2-layered. Midrib composed of a cylinder of separate to partially merged bundles to two opposing arcs without fibre caps; subepidermal ground tissue not sclerified.

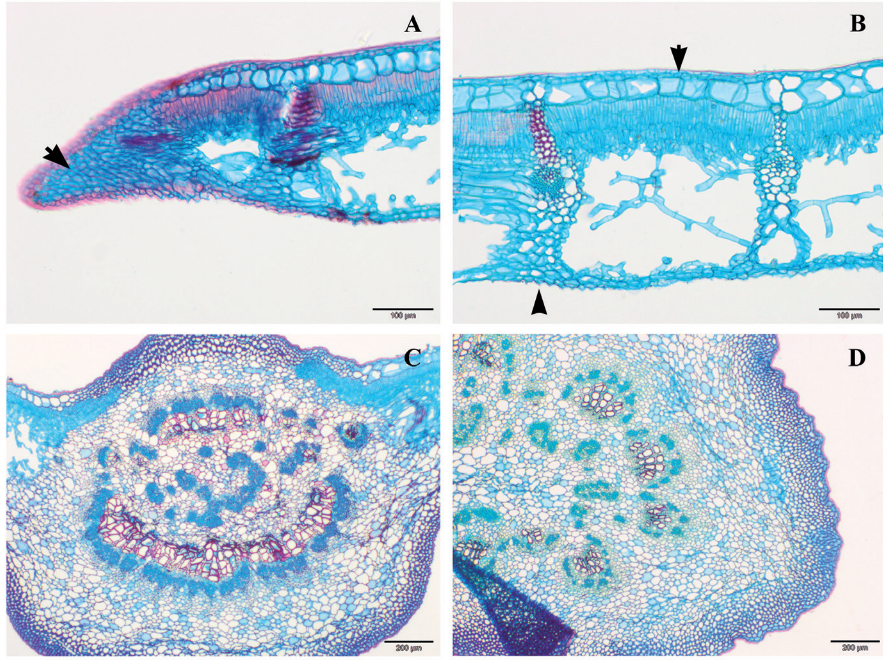

FIGURE 6-3 : Cross section of the lamina of *F. cornelisiana* Chantaras. & Y.Q. Peng. A. Leaf margin without marginal sclerenchyma (arrow). B. The lamina showing a multiple epidermis with the cells in the second layer much larger than in the outer layer (arrow) and abaxial cuticula strongly sculptured (arrow head). C. Midrib composed of a cylinder of separate to partially merged bundles in two opposing arcs without fibre caps. D. Petiole with cylinder of separate bundles, without sclereid caps [from *Yan–Qiong Peng s.n.* (L.)].). All photographs by B. Chantarasuwan.

Petiole with cylinder of separate bundles, without sclereid caps; peripheral ground tissue not sclerified. Pith bundles present in midrib and petiole. Veins vertically transcurrent; minor veins embedded in mesophyll. Sclerenchyma strands in margin absent. Druse crystals present in mesophyll, phloem parenchyma of midrib and petiole; prismatic crystals present in palisade, periphery of the bundle sheaths around the veins, and in the parenchyma of midrib and petiole.

Acknowledgements

The first author wishes to thank the Royal Thai Government on behalf of the Ministry of Science and Technology for a scholarship and he also likes to acknowledge the support from the Thailand National Science Museum, both enabled him to study for a Ph.D. in Leiden, the Netherlands. We are grateful to Dr. Steve Compton, University of Leeds, to pass on a sample of the new species to Leiden and Pajaree Inthachup, Bangkok Herbarium (BK), for the beautiful drawing.

Chapter 7

Historical Biogeography of *Ficus* subsection *Urostigma* (Moraceae): Palaeotropical Intercontinental Disjunctions revisited

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Abstract

Aim: The historical biogeography of *Ficus* subsect. *Urostigma* is analysed with the aid of a dated phylogeny to investigate the spatio-temporal diversification patterns in Asia and to see which hypotheses could best explain the various Palaeotropical Intercontinental Disjunctions (PIDs).

Location: Tropics and subtropics worldwide with an emphasis on Africa, Madagascar and Asia up to Australia.

Methods: Estimates of divergence times of subsect. *Urostigma* were obtained using a Baysian relaxed clock analysis via the program BEAST using three calibration points. The output of beast was used to analyse the historical biogeographic patterns via the program rasp (S-DIVA option). The results were compared with existing geological knowledge.

Results: The taxon probably originated in Madagascar or Madagascar and India, and dispersed once (or twice) to Africa and once to Asia. From Asia dispersal finally covered Southeast Asia mainland, Malesia, Australia, Micronesia and the island chains in the West Pacific. Wallace's Line throught central Malesia was only crossed by widespread species, of which few sister species are endemic east of Wallace's Line. One (ancestral) species dispersed back from Asia to Africa.

Main conclusions: The combination of dates and area optimisations for the ancestral nodes of *Ficus* subsect. *Urostigma* show that the first PID could best be explained by species rafting on India to Asia, after which the majority of species evolved in Asia up to Australia. The second PID probably involved dispersal via south Asia and Arabia to Africa in the early Miocene before the worldwide climate cooled down and areas became drier. Dispersal over Wallace's Line in Malesia is mainly by widespread species from which only a few local endemics in east Malesia and Australia developed. The multiple samples per species indicated that especially African species developed quite early, 17-18 Ma, while the Malesian species are younger, usually less than 7 Ma.

Keywords: Africa, ancestral area reconstruction, Asia, dispersal, *Ficus* subsect. *Urostigma*, historical biogeography, Palaeotropical disjunction, vicariance.

Introduction

Ficus L. subsection *Urostigma* (Gasp.) Endl. is a group of figs that are mainly trees, many of which are hemi-epiphytic and they generally show intermittent growth and possess few aerial roots. The leaves are often deciduous, spirally arranged, and (sub)articulate (some African and Madagascan species lack the articulation). The inflorescences are borne below the leaves or on the spurs of older branches and the synconia (figs) change colour from white via pink and purple to finally black (Berg & Wiebes, 1992; Berg & Corner, 2005). The group was recently revised by Chantarasuwan et al. (2013) and phylogenetic analyses (Weiblen, 2000; Jousselin et al., 2003; Machado et al., 2005; Rønsted et al., 2005, 2008; Xu et al., 2011, Chantarasuwan et al., ms) showed that its composition had to be slightly altered. *Ficus amplissima* J.E.Sm. and *F. rumphii* Blume, placed by Berg (2004) in subsect. *Urostigma*, appeared to be part of subsect. *Conosycea* (Miq.) C.C.Berg. Chantarasuwan et al. (ms.) made this change.

Subsect. *Urostigma* in its present circumscription (Chantarasuwan et al., ms) is found in tropical Africa, Madagacascar and ranges in Asia from India to Japan and troughout the southern part of the Malay Archipelago to Australia and the west Pacific (Fig. 7-1). Most species are found in Asia, but a few are present in Africa or on Madagascar. These species are partly at the base of the cladogram, but also split off higher up in the cladogram. This means that dispersal between Asia and Africa happened several times, and probably via different pathways. Sirichamorn et al. (2014) gave a nice overview of four different theories explaining the disjunct distribution between Africa and Asia, the so-called Palaeotropical intercontinental disjunctions (PID): (1) Gondwanan taxa rifted on India from Africa (and Madagascar) to Southeast Asia ('Out of India' hypothesis; McKenna, 1973; Morley, 1998; Conti et al., 2002); (2) dispersal occurred via boreotropical forests during the Palaeocene and Eocene ('boreotropical' hypothesis; Wolfe, 1975; Morley, 2000, 2007); (3) long-distance dispersal (e.g., Li et al., 2009; Warren et al., 2010); and (4) overland dispersal between Asia and Africa via Arabia and south Asia during the first warm half of the Eocene (e.g., Zhou et al., 2012). A dated phylogeny of *F.* subsect. *Urostigma* will contribute to this discussion. The hypotheses are exclusive, also in time, thus several may apply to subsect. *Urostigma*. Continuing contributions to this discussion will show which hypotheses best explain the most common patterns. The dataset of subsect. *Urostigma* is rather unique for this purpose, 27 out of 31 species are included and often several samples per species.

The aims of the study are to date the phylogeny of *F.* subsect. *Urostigma*, to see how old some of the species are, to analyse the historical biogeography, and to see how the patterns found contribute to the discussions of PIDs and general Asian biogeography patterns.

Material and methods

Taxon sampling, DNA markers
The same taxa, with usually multiple samples per species (2-4 samples), and the same four genetic markers were used as in the phylogenetic analysis of Chantarasuwan et al. (ms). Three nuclear markers were used (ETS, 481 basepairs, G3dh, 779 bp, ITS, 815 bp) and one chloroplast marker (ncpGS, 599 bp). Also the same evolutionary models were applied, HKY+G except GTR+G for ETS. An overview of the samples and genbank accession numbers can be found in Chantarasuwan et al. (ms).

Dating
Calibration points were obtained from Xu et al. (2011, their table 7-2) and the dating was performed within a Bayesian framework with the program BEAST v.1.8.0 (Drummond & Rambaut, 2007; Drummond et al., 2012, 2013). BEAUTi (part of the BEAST package) was used to create the input file with the following settings: – four groups were defined: Alltaxa (mean age 86.67 Ma, corresponds with node 1, Genus *Ficus* in Table 7-2 of Xu et al., 2012), Ingroup (excl. *F. maxima* Mill., *F. tonduziii* Standl.; mean age 79.23 Ma = node 3 Other clades excluding section *Pharmacosycea* in Table 7-2 of Xu et al., 2012), subsect. *Urostigma* (mean age 35.53 Ma,= node 15 section *Urostigma* in Table 7-2 of Xu et al., 2012), section *Conosycea* (no age); – Yule process speciation, - an exponential relaxed clock, – random starting tree; – ucld prior set to uniform and those of Alltaxa, Ingroup, *Urostigma* also set to uniform (no indication exists about any distribution type of the ages for these groups: Ho, 2007), with as upper and lower bounds for Alltaxa = 136.83-60.00 Ma, Ingroup = 130.12-50.59 Ma, *Urostigma* = 60.54-18.13 Ma. All other priors were left to default. The analysis was run twice for a 100 million generations.

The results were tested for Effective Sampling Sizes (ESS values > 200) with TRACER v.1.6 (Rambaut & Drummond, 2009). TREEANNOTATOR (part of BEAST package) was used to find the Maximum Clade Credibility (MCC) tree and this cladogram was visualised with FIGTREE v.1.4.0 (Rambaut, 2009).

Ancestral area reconstruction
Twelve areas (Fig. 7-1) were discriminated based on the presence of endemic species (areas A, B, C, E, H, J, L) or areas of overlap in the various configurations of the distributions (D, F, G, I, K). Table 7-1 gives an overview of the distributions of all sampled species.

Parsimony-based Statistical Dispersal-Vicariance Analysis (S-DIVA) was used for the historical biogeographic analyses, which is based on dispersal-Vicariance Analysis (DIVA; Ronquist, 1997) and implemented in RASP v.2.0b (Yu et al., 2010, 2013). Every 1000th tree saved from the 100 million trees generated with BEAST were used as input tree, of which 10,000 were discarded as burn-in. The remaining cladograms were evaluated against the

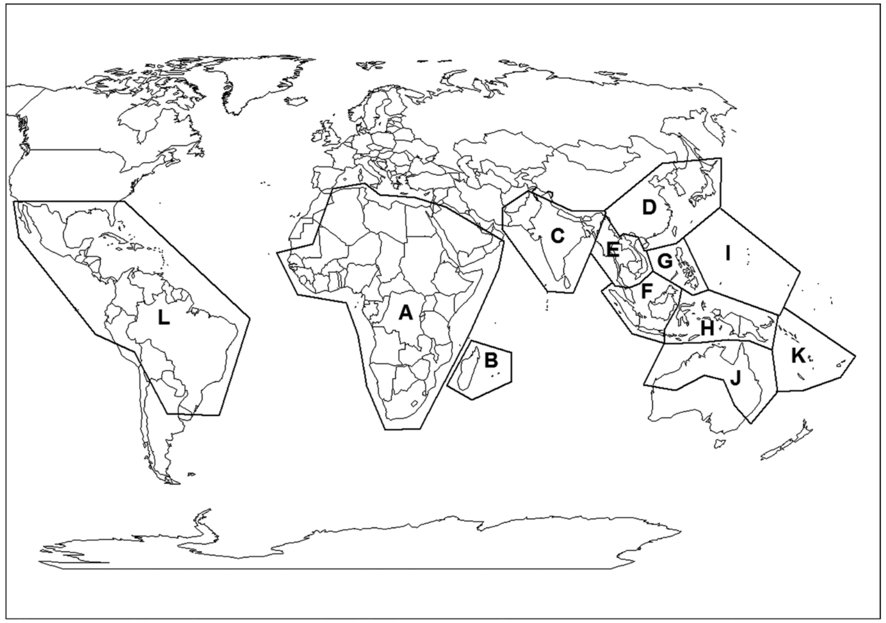

FIGURE7-1. Phytogeographic areas (Table 7-1) as used in the historical biogeographic analysis. A = Africa; B = Madagascar and surrounding islands; C = 'Greater' India; D = China, Japan; E = Southeast Asia; F = west Malesia; G = the Philippines; H = east Malesia; I = Micronesia; J = Australia; K = West Pacific.

MCC tree by S-DIVA. Variable numbers of areas, ranging from 2-6, were optimised per node; higher numbers took too much computing time.

Results

The dated phylogeny can be found in Fig. 7-1, the historical biogeographic analysis is shown in Fig. 7-3.

Probably subsection *Urostigma* originated between 61.2 (95% Highest Posterior Density interval [HPD]: 75.7-50.6; node 149 Fig. 7-3, Table 7-2) Ma, the stem node, and 51 (60.6-40.3; node 148 Fig. 7-3, Table 7-2) Ma, the crown node of the *Urostigma* clade. The first species to split of was *F. madagascariensis* C.C.Berg [c. 51 (60.6-40.3 Ma; node 148)], followed by *F. densifolia* Miq. [between 42.2 (72.5-30; node 147) and 8.5 (17.1-3.1) Ma; node 92]. Both species occur on Madagascar (area B; Fig. 7-1). Next, species (*F. cordata* Thunb., *F. lecardii* Warb., *F. verruculosa* Warb.) develop in Africa between 39.6 (50.7-28.8; node 146) Ma and 33.1 (46.1-18.8; node 145) Ma, followed by the first developments in Asia (*F. religiosa* L., *F. tsjakela* Burm. F. and '*F. pseudocaulocarpa*' Chantaras.) between 36.6 (50.7-28.8; node 139) and 28.3 (42.9-13.2; node 138) Ma (areas C, D, E, and later also G; Fig. 7-1),

Table 7-1. Phytogeographic areas and the distributions of the sampled species.

Phytogeographic areas	
A = Africa	
B = Mascarines	
C = India s.l.: Pakistan, India, Sri Lanka, Nepal, Bhutan, Bangladesh	
D = China, Japan	
E = Southeast Asia (Myanmar, Thailand, Laos, Cambodia, Vietnam)	
F = West Malesia (Malay Peninsula, Sumatra, Borneo, Java)	
G = Philippines	
H = East Malesia: Sulawesi, Lesser Sunda Islands, Moluccas, New Guinea	
I = Micronesia	
J = Australia	
K = West Pacific	
L = America	
Species	**Distribution**
Ficus alongensis Gagnep.	DE
Ficus altissima Blume	CDEFGH
Ficus americana Aubl.	L
Ficus arnottiana (Miq.) Miq.	C
Ficus aurea Nutt.	L
Ficus benjamina L.	CDEFGHJK
Ficus brachypoda (Miq.) Miq.	J
Ficus bubu Warb.	A
Ficus caulocarpa (Miq.) Miq.	CDEFH
Ficus concinna (Miq.) Miq.	CDEFG
Ficus cordata Thunb.	A
Ficus densifolia Miq.	B
Ficus glabella Blume	EFGHJ
Ficus geniculata Kurz	CDE
Ficus geniculata Kurz var. *insignis* (Kurz) C.C.Berg	CEJ
Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg	EF
Ficus henneana Miq.	J
Ficus hookeriana Corner	CDE
Ficus ingens (Miq.) Miq.	A
Ficus lecardii Warb.	A
Ficus madagascariensis C.C.Berg	B
Ficus maxima Mill.	L
Ficus menabeensis H.Perrier	B
Ficus middletonii Chantaras.	CE
Ficus orthoneura H.Lév. & Vaniot	DE
Ficus pleurocarpa F.Muell.	J
Ficus prasinicarpa Elmer	GHK
Ficus prolixa G.Forst.	IK
'Ficus pseudocaulocarpa' Chantaras. (name still to be published)	G
Ficus pseudoconcinna Chantaras.	H
'Ficus pubipetiola' Chantaras. (name still to be published)	E
Ficus religiosa L.	CDE
Ficus rumphii Blume	CEFH
Ficus salicifolia Vahl	A
Ficus subpisocarpa Gagnep. subsp. *pubipoda* C.C.Berg	EF
Ficus superba Miq.	EFH
Ficus tonduzii Standl.	L
Ficus verruculosa Warb.	A
Ficus tsjakela Burm.f.	C
Ficus virens Aiton	CDEFGHIJ
Ficus wightiana (Miq.) Benth.	C

Table 7-2. Nodes (Figs. 2, 3) and their mean, earliest and youngest ages as estimated by the BEAST analysis of four molecular markers and three calibration points. In the last column the most likely S-DIVA optimisations for 2-6 areas per node.

Node	Mean age	Earliest	Youngest	S-DIVA optimisation(s)
77	6.65	13.11	1.94	E
78	12.37	20.81	5.65	E
79	20.2	31.18	11.1	BE
80	18.66	31.08	8.24	E
81	26.66	39.26	16.17	E
82	0.84	3.02	0	E
83	5.64	12.97	1.33	E
84	32.42	46.48	20.32	E
85	8.78	17.53	2.62	L
86	18.24	31.42	8.21	AL
87	10.86	24.65	2.22	J
88	34.53	49.67	20.21	2 areas: AJ; 3,4: AJL, JI, AJ; 5,6: AJL, AJ
89	43.87	59.15	29.47	2 areas: AE; 3: AEJ, EJL; 4-6: AEJL, AEJ
90	3.13	7.82	0.45	B
91	2.91	7.19	0.44	B
92	8.51	17.05	3.12	B
93	18.42	30.9	7.18	A
94	3.83	10.5	0.43	E
95	3.18	8.46	0.4	C
96	5.18	10.68	1.42	C
97	10.62	18.41	4.46	C
98	10.62	18.02	4.46	C
99	3.28	6.39	1.06	C
100	4.84	8.5	2.05	C
101	6.1	10.18	2.72	C
102	11.27	17.35	6.32	C
103	5.74	10.99	1.51	K, I
104	5.04	9.64	1.44	C
105	8.55	14.16	3.88	CI
106	14.65	21.27	8.94	C
107	1.57	4.63	0.07	E
108	3.09	9.54	0.27	CE
109	17.55	24.82	10.92	C
110	20.74	29	13.2	C
111	25.14	34.8	16.67	CE
112	2.16	5.58	0.24	J

Table 7-2. Continued

113	7.41	14.54	2.41	CJ
114	12.1	21.45	5.15	C
115	15.55	26.35	6.9	2-6: all containing CG, CH, CK.
116	28.55	38.57	19.16	C
117	10.07	17.53	4.55	
118	4.61	10.16	1.05	E
119	15.39	23.97	8.38	E
120	4.77	11.66	0.72	H
121	19.1	28.56	11.13	EH
122	0.77	5.58	0.0	A
123	9.91	16.93	4.65	A
124	7.93	16.76	1.76	E
125	15.39	24.44	7.82	AE
126	19.41	29.27	10.93	E
127	26.33	32.7	13.9	E
128	1.00	4.53	0.0	E
129	10.58	20.15	3.93	E
130	8.73	18.25	1.77	E
131	17.15	30.82	8.23	E
132	26.33	36.02	17.57	E
133	31.36	41.59	21.8	CE
134	33.21	43.83	23.3	AC
135	3.61	8.62	0.64	C
136	7.68	16.34	2.3	C
137	1.96	7.44	0.02	CG
138	28.34	42.92	13.24	C
139	36.55	50.68	28.8	C
140	2.22	6.38	0.22	A
141	17.85	29.29	8.39	A
142	26.45	39.31	14.25	A
143	11.46	21.22	4.16	A
144	17.28	29.21	8.05	A
145	33.08	46.09	18.81	A
146	39.58	50.68	28.8	A
147	42.22	72.54	30.0	AB
148	51.31	60.59	40.3	B
149	61.17	75.71	50.59	2: A; 3,4: many, all B and usually A; 5: ABEJL, ABEJ; 6: ABEFJ, ABEFJL, ABEJ, ABEJL
150	0.93	4.82	0.0	L
151	69.92	92.61	60.0	2: EL; 3: AEL; 4:AEJL; 5:ABEJL; 6: ABEFJL, ABEJL

while *F. salicifolia* Vahl develops again in Africa [area A, Fig. 7-1; between 33.2 (43.8-23.3; node 134) and 18.4 (30.9-7.2; node 93) Ma]. All further developments are in Asia, with one later return to Africa [*F. ingens* (Miq.) Miq., between 15.4 (24.4-7.8; node 125) and 9.9 (16.9-4.7; node 123) Ma]. One Asian clade [*F. subpisocarpa* Gagnep. var. *pubipoda* C.C.Berg up to *F. wightiana* (Miq.) Benth.] mainly occurs in Greater India (Area C, Fig. 7-1) and the other clade (*F. alongensis* Gagnep. to *F. hookeriana* Corner including the African *F. ingens*) in Southeast Asia (Area E, Fig. 7-1). One of the interesting dispersal barriers in Asia is Wallace's Line (Wallace, 1859; van Welzen et al., 2011), running from east of the Philippines, between Borneo and Sulawesi and between Bali and Lombok. *Ficus* subsection *Urostigma* crosses this line with several widespread species [*F. caulocarpa* (Miq.) Miq., *F. geniculata* Kurz var. *insignis* (Kurz) C.C.Berg, *F. glabella* Blume, *F. prasinicarpa* Elmer ex C.C. Berg, *F. superba* (Miq.)Miq., and *F. virens* Aiton]. The mainly Greater Indian clade (area C, Fig. 7-1; clade *F. subpisocarpa-F. wightiana*) has two species occurring east of Wallace's Line, *F. prolixa* G.Forst. [Micronesia and W. Pacific, areas I & K; dispersal between 8.6 (14.2-3.9; node 105) and 5.7 (11-1.5; node 103) Ma] and *F. henneana* Miq. [Australia, area J; dispersal between 7.4 (14.5-2.4; node 113) and 2.2 (5.6-0.24; node 112) Ma]. The mainly Southeast Asian clade (area E, Fig. 7-1; clade *F. alongensis–F. hookeriana*) has one species east of Wallace's Line, *F. pseudoconcinna* Chantaras. [E Malay Archipelago, area H; dispersal between 19.1 (28.6-11.1; node 121) Ma and present].

Discussion

Species ages

Usually several samples per species were used in the analyses. The dating (Fig. 7-2) shows that the species often developed quite early. The crown nodes of the African species with multiple samples, *F. cordata*, *F. lecardii* and *F. salicifolia*, are all between 20 and 13 Ma (Lower to middle Miocene), only the crown node of *F. verruculosa* is much younger (but its stem nodedates from the same period). The Asian species have crown nodes of c. 10 Ma to much younger, just like the Madagascan *F. densifolia*. Samonds et al. (2012) show that from 20 Ma onwards it becomes difficult for floating and swimming animals to reach Madagascar from Africa, because of changing winds and water currents, which might mean that the opposite, dispersal from Madagascar to Africa, may have been facilitated. In Asia, the eastern part of Malesia (Malay Archipelago; Raes & van Welzen, 2009), attached to west Malesia and emerged above sea level during especially the last 10 Ma (Hall, 2002, 2009, 2012), which may have catalysed speciation in *Ficus*.

S-DIVA optimisations

Five different S-DIVA analyses were run with a variable number of areas to be optimised per internal node ranging from two to six areas. Generally, the optimisations gave the same results for all nodes, the most likely of these are shown in Table 7-2 and Fig. 7-3. Only five nodes had (slightly) different optimisations, the result of allowing more areas per node: node 88, 89, 115,

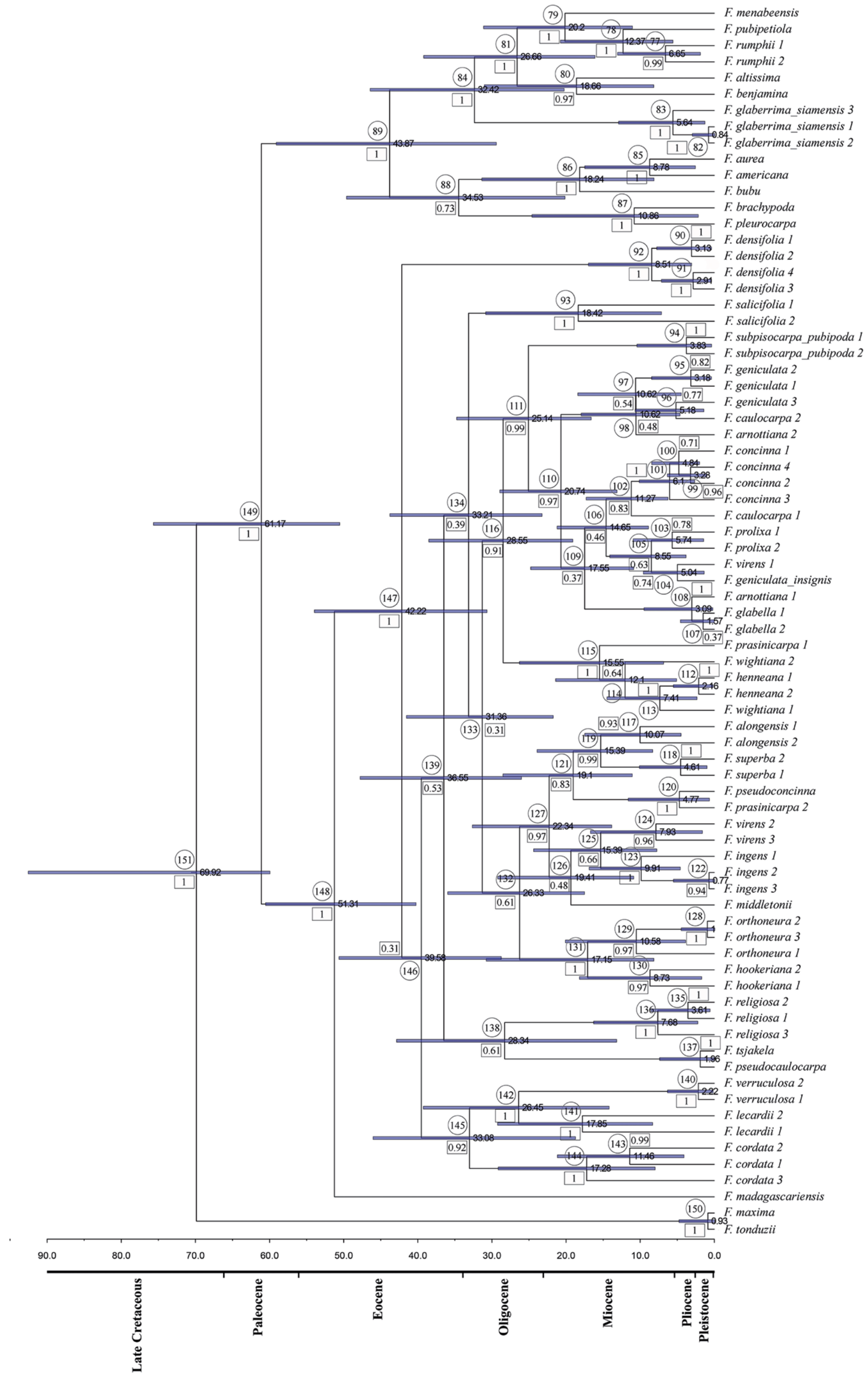

FIGURE7-2. Dated phylogeny. The numbers per node are the node number (in circles), the posterior probabilities (in square boxes) and the mean age of the nodes, the bars indicate the 95% Highest Posterior Density interval [HPD] (mean ages and HPD also summarised in Table 7-2).

149, 151 (Table 7-2, Fig. 7-3). Table 7-2 shows some of the possibilities for these nodes, in Fig. 7-3 a 'mean' area (the area in common) is shown. The optimisations of 149 and 151 can be ignored, these are the basal nodes and probably do not represent realistic ancestral areas, because of the insufficient sampling of the outgroups. The latter also applies to node 88 and 89, the outgroups are only partly represented. The variable node 115 (CH shown in Fig. 7-3) has, like nodes 105 (CI), 113 (CJ), 125 (AE), 134 (AC), an unlikely, disjunct optimisation. These are the result of the parsimony method used in DIVA (Ronquist, 1997), with no penalty for vicariance and sympatric speciation, and a penalty of 1 for dispersal and extinction. This results in internal nodes with wide distributions (like the nodes above), which can then be followed by vicariance in higher nodes.

Scenario

The first species that split off (*F. madagascariensis* and *F. densifolia*) occur on Madagascar (Fig. 7-3). The optimatisations of the basal internal nodes (Fig. 7-3: nodes 151, 149, 148, 147) show Madagascar (area B, Fig. 7-1) or Madagascar in combination with Africa (area A) and/or other areas. The latter form unrealistic ancestral areas, because South America, area L, and Australia, area J, had already split from Africa, starting c. 165 Ma, with a broad gap between Africa and South America at c. 135 Ma (Moyersoen, 2006; Samonds et al., 2012). This is much older than the age of the stem node of subsect. *Urostigma*, node 149, 61.2 (75.7-51) Ma (Fig. 7-2; Table 7-2). The breakup between Africa and the Madagascar- India-Seychelles complex (c. 130 Ma; Samonds et al., 2012) and the subsequent breaking up of the latter plate (c. 87.6 ± 0.6 Ma; Storey et al., 1995; Samonds et al., 2012) also predate the estimated age of origin of subsect. *Urostigma*. Thus, which distributions did the basal species and ancestors of subsect. *Urostigma* have? Most likely, the first species occurred on Madagascar (still present are *F. madagascariensis* and *F. densifolia*). From Madagascar there must have been dispersal to Africa as the clade *F. verruculosa–F.cordata* is African and slightly later, higher in the cladogram, *F. salicifolia* is also African. It is unclear if this was a single dispersal event or two events. The support for nodes 134 and 146 is low (posterior probabilities 039 and 0.31, respectively), thus *F. salicifolia* may have been part of the *F. verruculosa–F. cordata* clade. The latter (thus a single event) is more likely, because the wind and water currents favoured dispersal from Africa to Madagascar (Samonds et al., 2012). The figs of subsect. *Urostigma* are small, thus bird dispersal is likely and birds are relatively independent of wind directions.

How did subsect. *Urostigma* reach Asia? Two possibilities exist. The optimisation for node 134 (Fig. 7-3) is Africa-India (areas A, C), with an age 33.2 (43.8-23.3) Ma. India collided with Asia c. 35 Ma (Samonds et al., 2012). One possibility is dispersal from Africa via Arabia to India and then Asia. However, the connection Africa-Arabia-west Asia is younger, connection were the Meswa Bridge, c. 23.5 Ma, and the Gomphoterium Bridge, c. 18 Ma (Rögl, 1999). The optimisation of node 134 is caused by the position of

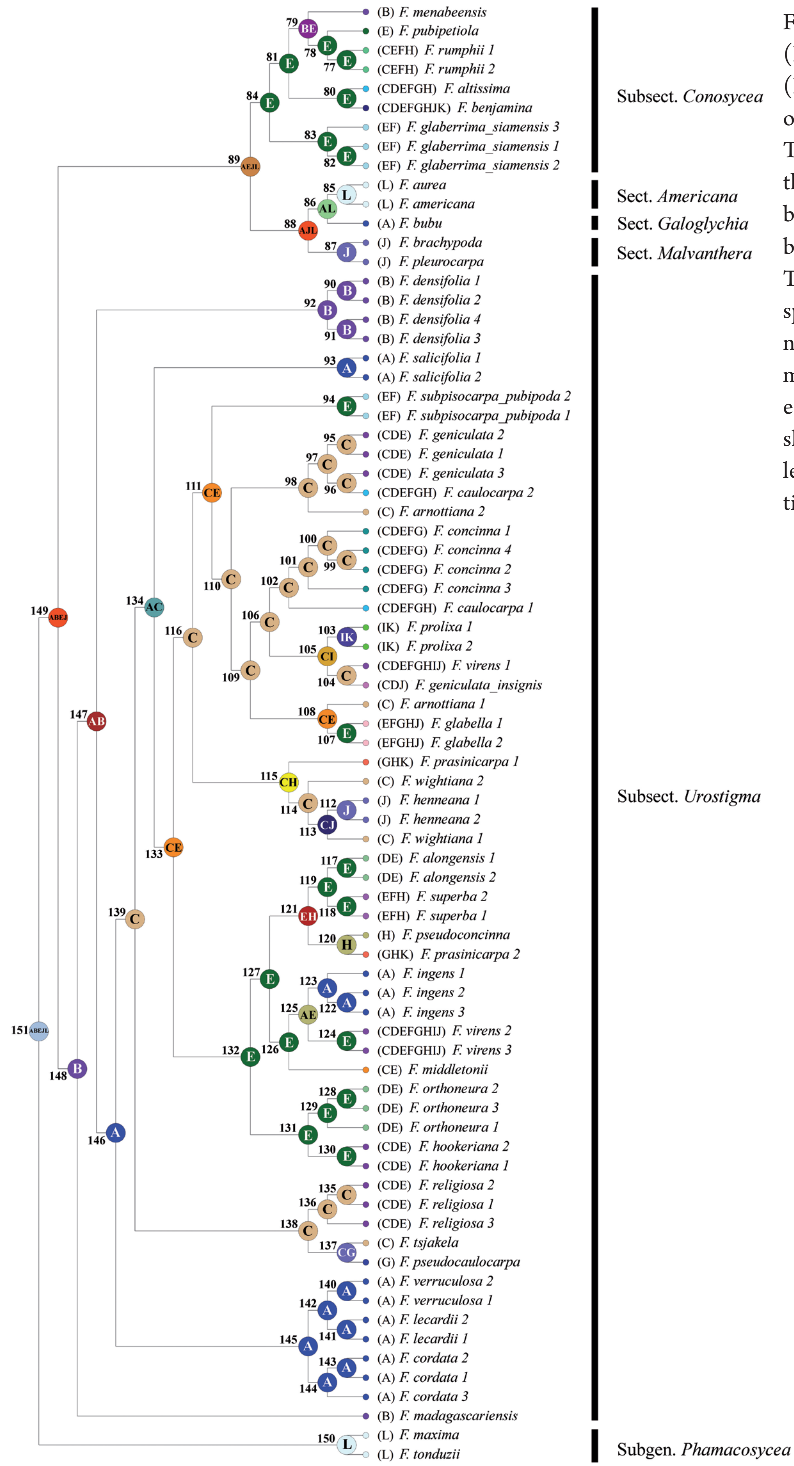

FIGURE 7-3. Phylogeny (Fig. 7-2) with the area (Fig. 7-1, Table 7-1) optimisations per node. The distributions of the species is indicated between brackets before the species names. The numbers corresponds with the node numbers. Only the optimisations with the highest probabilities are shown and the branch lengths do not indicate time as in Fig. 7-2.

F. salacifolia, and as already indicated above, a possibility with low likelihood. The other, more likely alternative of reaching Asia, is rifting with India. Briggs (1989) indicates that India, while moving to Asia, may have had a rather constant interchange of biodiversity with Africa and Asia, because it does not really harbour a typical, endemic flora and fauna. This is substantiated by Ali & Aitchison (2008), who show in various hypotheses dispersal, back and forth, between India and Madagascar, India and Africa and India and Asia. Ancestral species may already have been present on India next to Madagascar, or they dispersed from Madagascar to India after these two terranes had already split. After reaching Asia, the clade *F. religiosa*–*F. pseudoacaulocarpa* developed in mainly India, followed by two developments, one clade (*F. subpisocarpa*–*F. wightiana*) also mainly developed in India (area C, Fig. 7-1, but with many widespread species and an Australian endemic, see below) and the other clade (*F. alongensis F. hookeriana*) developed especially in southeast Asia (area E, Fig. 7-1, also with many widespread and east Malesian taxa). Spreading over Malesia is mainly by widespread species, all from west to east.

Wallace's line

Several species occur east of Wallace's line, and could only have reached their distributions by dispersal, either by themselves or via ancestral species. In the Southeast Asian clade *F. henneana* (node 112, Fig. 7-3) is endemic in Australia (area J, Fig. 7-1) with as sister species *F. wightiana* from India (area C; nodes 113, 114), together they are sister to *F. prasinicarpa 1* (node 115), found in the Philippines, east Malesia, and the west Pacific (areas G, H, K). It is difficult to explain the presence in Australian from a Southeast Asian origin (area C), which is more or less the optimisation for the internal nodes 113,114, 115. However, compared with the distribution of *F. prasinicarpa*, which occurs in adjacent areas, the dispersal to Australia is easy to explain and it occurred in a period (less than 20 Ma) that exchange between west Malesia and Australia was possible (van Welzen et al., 2014). *Ficus pseudoconcinna* Chantaras. is another species that occurs only east of Wallace's Line (east Malesia, area H, node 120), and its distribution overlaps with the closely related *F. prasinicarpa 2* (which crosses Wallace's Line), similar with *F. prolixa* (Micronesia, west Pacific, areas I, K, node 103), which partly overlaps with the distribution of its sister group consisting of the species *F. virens 1* and *F. geniculata* var. *insignis*.

Palaeotropical Intercontinental Disjunctions

The first PID is the dispersal from Africa/Madagascar to Asia, explained above as rifting on India ('Out of India' hypotheses, see Introduction). There is one more dispersal between Asia and Africa, from Asia to Africa. *Ficus ingens* (Miq.) Miq. is an African species and its sister species is *F. virens 2/3*, which occurs from India (area C) to Australia (area J). Their crown node (node 125) has as age 15.4 (24.4-7.8) Ma and the stem node (node 126) 19.4 (29.3-10.9) Ma. These ages are too young for the 'Out of Africa' hypothesis and the Boreal Forest hypothesis. Considering the fact that *F. ingens* occurs in the northern parts of India, the most likely hypothesis is dispersal via south Asia and Arabia to Africa. This is comparible with the genera Macaranga Thouars and Mallotus Lour. (Euphorbiaceae; van Welzen et al., 2014), which even earlier dispersed from Asia to Africa (c. 23 Ma) when the Arabian land bridges were still forming (Rögl, 1999). The dispersal of *Ficus* to Africa occurred when the Miocene climate was still warm and humid, before the Middle Miocene Climatic Optimum (c. 17-15 Ma; Zachos et al., 2001). Then forests were more extensive and conditions along the coastal areas favoured dispersal. The PIDs found for the legumes in Sirichamorn et al. (2014) also dispersed along the Asian-Arabian coast, these species are mangrove related.

Climate

During the different epochs that subsect. *Urostigma* existed the climate changed several times drastically from warm and wet to colder and drier. Moreover, the various contemporary species also inhabit a large variety of climates and soils. Seemingly, the figs can tolerate various climates, especially the widespread species. Most species occur in areas with a yearly dry monsoon (Chantarasuwan et al., 2013), adaptation to which may have helped survival. Areas like most of Africa, Madagascar, India, Southeast Asia, the Philippines, east Malesia, Australia, etc. have a dry spell during part of the year. In Malesia, most species occur in the southern part, areas with often a severe dry season (central and eastern Java, Lesser Sunda Islands; Chantarasuwan et al., 2013). In areas with a dry season, and usually deciduous trees, figs may form the last available food supply for animals like orang-utans (Sugardjito et al., 1987).

Dating

Xu et al. (2011) used fossil *Ficus achenes* (Collinson, 1989) of c. 60 Ma as calibration point and an artificial constraint on the root of 190 Ma (Lower Jurassic; otherwise the program BEAST did not work), even though the oldest known Angiosperm fossils were 130 Ma (Lower Cretaceous). Still, these apparently poor calibration points worked out quite well. Our data and scenario support (do not contradict) the dates found by Xu et al. (2011) and coincide with the various tectonic hypotheses.

Conclusions

The combination of dates and area optimisations for the ancestral nodes of *Ficus* subsect. *Urostigma* show that it likely originated in Madagascar and dispersed once or twice to Africa and rafted on India to Asia. In Asia many species became widespread, sometimes ranging from India to Micronesia and Australia, thus crossing Wallace's Line. Only few species are endemic to areas east of Wallace's Line. One reversed dispersal from Asia to Africa occurred in the early Miocene, probably along south Asia and Arabia.

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Chapter 8

Which species of *Ficus* subsection *Urostigma* in Thailand are used as food, ornamental plants or sacred trees?

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Abstract

During field trips in Thailand, October 2010 and November 2011, samples of *Ficus* subsection *Urostigma* were collected for a taxonomic project, at the same time information on the uses proved to be an additional profit. The uses of eight species were recorded, at least five species are food plants, especially in northern Thailand, six are (also) ornamental plants widely growing in every region, and seven species are sacred trees, present everywhere in the country.

Introduction

Ficus subsect. *Urostigma* (Gasp.) C.C.Berg contains 27 species, of which 5 species are from continental Africa, Madagascar, and the Arab Peninsula and 22 species are found in Asia, Australia and the West Pacific (Berg and Corner, 2005). Twelve species were recorded for Thailand, which are all deciduous plants, and most are essentially hemi-epiphytic, without abundant aerial roots, though some species may be terrestrial. *Ficus orthoneura* H.Lév. & Vaniot is the only shrub within this subsection that is present in Thailand. The trees show intermittent growth, the leaves are always spirally arranged, the margin is always entire and the venation is basically pinnate and brochidodromous. The leaves are articulate in most species. Stipules are often conspicuous as part of the terminal bud cover. They show differences in length, even on the same plant, usually quite long, thin and caducous on the open shoots, and shorter, usually not longer than 2 cm, persistent and thicker on the closed shoots. The figs are often borne below the leaves, sometimes in the leaf axils, and in some species on spurs on the older wood. They occur solitary or in pairs, to up to 8 figs together on the spurs. The staminate flowers of all species in Thailand occur near the ostiole (opening). The ovaries of the pistillate flowers are red-brown.

Mankind uses *Ficus* species already for a long time. *Ficus carica* L. is one of the famous species; it is cultivated for more than 5000 years (Goor, 1965), and its products are sold worldwide even today. *Ficus* and the Asian people have a long standing relation, because *F. religiosa* L. is a sacred tree within Buddhism and Hinduism for already more than 2500 years. At least 16 species are used in India as food (Ambasta, 1986), 10 species are known for their edible fruits (Verheij and Coronel, 1991) and 11 species are used as vegetables (Siemonsma and Piluek, 1993) in SE Asia. Many species are medicinal plants, 16 species are used in India in traditional medicine (Ambasta, 1986), and 26 species are used for medicinal reasons or as poison in SE Asia (de Padua et al., 1999). Other species of *Ficus* are valuable for various products, e.g., the inner bark of *F. altissima* Blume is suitable for the production of paper, and the wood of *F. benghalensis* L., *F. glomerata* Roxb., and *F. retusa* L. is used for furniture (Ambasta, 1986). The latex from *F. elastic* Roxb. ex Hornem. contains rubber, which can be applied as natural rubber (Boer and Ella, 2000). The leaves of many species are fodder to cattle.

Ficus has a strong tradition in all levels of Thai society. Seventeen species are reported as food in Thailand, many species provide medicine or are related to religion (Eiadthong, 2004). *Ficus racemosa* L. is one of the famous fig species in Thai culture, it is the symbolic tree of Chumphon province, and its wood is very important in royal rituals, because the throne used during the royal coronation was made from its wood.

Similar to other groups of *Ficus*, species of *F.* subsect. *Urostigma* are also used by humans for a long time. The legend of Buddhist recount of a sacred fig tree which was important more than 2550 years ago, when Gautama Buddha got enlightenment under this Bodhi tree in Bodh Gaya, India; *Ficus religiosa* L. is the scientific name for this species.

Another species, *F. arnottiana* (Miq.) Miq., is a well-known medicinal plant used in Indian traditional medicine to treat several ailments (Gregory et al., 2009). And finally, young leaves of *F. superba* Miq. are eaten cooked as a vegetable in SA Asia (Siemonsma and Piluek, 1993).

In this study we like to investigate if more species of *Ficus* subsection *Urostigma* are used and how they are used.

METHODOLOGY

The studies were executed in the provinces of Chiang Mai and Chiang Rai in northern Thailand, Bangkok and Pathum Thani in the central part, Chachoengsao and Rayong in the south-eastern, Krabi and Nakhon Si Thammarat in the peninsular part of Thailand. Three main topics were studied: food, ornamental and religious use. Information on the use as food were recorded by interviewing the people in each area, e.g., 21persons in Chiang Mai, 17 persons in Chiang Rai, 9 persons in Chachoengsao, 13 persons in Rayong, 28 persons in Nakhon Si Thammarat, and 7 persons in Krabi; no persons were interviewed in Bangkok and Pathum Thani. The use as religious or ornamental plants was observed directly during the trip.

RESULTS

Eight species from a total of twelve Thai species of the subsection are utilized, five species as food, seven as sacred tree, and six as ornamental plant.

Food Trees

Many species of *Ficus* subsect. *Urostigma* are used as food. The parts eaten are the fruits and leaves. De Padua et al. (1999) reported that the fruits and tender leaf buds of *F. religiosa* are edible. The young syconium (fig) of *F. virens* Aiton and young leaves of *F. superba*, *F. subpisocarpa* Gagnep., and *F. virens* are used as vegetables (Eiadthong, 2004).

Five species are used as food in the north, two species in the southeast and only one in the south. The Thai name “Phak Huead Deang” used in the north relates to three species, *F. geniculata* Kurz var. *geniculata*, *F. virens* var. *glabella* (Blume) Corner, and *F. caulocarpa* (Miq.) Miq.

Ficus superba: The species inhabits areas close to the sea in the south-eastern and peninsular. The Thai name is “Leab”. The people in Rayong and Nakhon Si Thammarat use it as food. Young shoots (and leaves) are cooked as curry or boiled with coconut milk and served with chili paste(Fig. 8-1). The plants are usually collected in the wild.

FIGURE 8-1. A dish of *Ficus superba* shoots with coconut milk, a native menu from Kleang, Rayong province. Photographs by B. Chantarasuwan.

FIGURE 8-2. A sacred tree, *Ficus superba*, in Kleang, Rayong province. Photographs by B. Chantarasuwan.

Ficus subpisocarpa: The species is distributed all over Thailand. Its name is also "Leab", which shows the usual confusion with *F. superba*, especially in the coastal areas where both *F. superba* and *F. subpisocarpa* co-occur. However, this does not present a big problem for the utilization as similar parts are used for comparable dishes. Young shoots (and leaves) are cooked or eaten in the northern and south-eastern. In the northern, the species is cooked as a curry or used in a salad and the use in the south-eastern is similar to that of *F. superba*.

Ficus geniculata var. *geniculata*: It is found in all parts of Thailand, usually in plantations in the northern part. The young shoots (and leaves) are red. The Thai name is "Phak Huead Deang" and it is cooked as a curry or used as a salad.

Ficus geniculata var. *insignis* (Kurz) C.C.Berg: Also distributed in all parts of Thailand, but most common in the northern, where it is also used in plantations. Young shoots (and leaves) are pale green. The name is "Phak Huead Khow" and it is also cooked as a curry or used as a salad like subsp. geniculata.

Ficus virens var. *glabella*: distributed in all parts of Thailand. Commonly used in plantations in the northern part and often misidentified as *F. geniculata* var. *geniculata*. Young shoots (and leaves) are red, like *F. geniculata* var. *geniculata*, and it is also called "Phak Huead Daeng". It is used in curries or salads, just like *F. geniculata* var. *geniculata*.

Ficus caulocarpa: Distributed in all parts of Thailand. In the northern part this species grows together with and closely resembles *F. geniculata* and *F. virens*, and, therefore, it is usually misidentified as *F. geniculata* var. *geniculata*. Again, also called "Phak Huead Daeng", because young shoots (and leaves) are also red. Its cooking process is similar to that of *F. geniculata*.

Religious or Sacred Trees

Ficus religiosa is a well-known sacred tree in Thai culture. It usually grows near Buddhist temples. People in the northern part believe that this tree is holy; every year, when the traditional Thai new year is present, they have a ritual during which they parade with poles and place it uphold the tree, expecting to prop the Buddhism and support in life in return. Furthermore, it is also the symbolic tree of the province Prachin Buri. Not all trees of *F. religiosa* are automatically sacred trees. If sacred, then the tree should originally have been a cutting of the Mahabodhi Tree in the Sri Mahabodhi Temple in Bodh Gaya, or it should have grown large and been used in religious rituals or royal ceremonies. For other species, only big *Ficus* trees are accepted as sacred trees and the seedlings or saplings are not regarded sacred.

Sacred trees in Thailand are easy to recognize, because of the evident use of colourful cloths wrapped around the trunks, or there are flowering garlands hanging from the stems, or small shrines are placed close to the tree, and the trees may sometimes also have some gnomes around them.

FIGURE 8-3. *Ficus geniculata* var. *geniculata* growing in home area for shading and shoot picking in Ban Tham village, Chiang Dao, Chiang Mai province. Photographs by B. Chantarasuwan.

The mature trees of seven species of *Ficus* subcect. *Urostigma* are regarded sacred in Thailand. The most popular is *F. religiosa*, which mostly grows near Buddhist temples, but Thai people commonly misidentify *F. rumphii* Blume as *F. religiosa* and also believe it to be related to Buddhism. Still, big sized specimens of *F. rumphii* are regarded sacred just like other colossal *Ficus* trees. The sacred tree species found are *F. superba*(Fig. 8-2), *F. subpisocarpa*, *F. geniculata* var. *geniculata*, *F. virens* var. *virens*, *F. virens* var. *glabella*, *F. caulocarpa*, and *F. concinna* (Miq.) Miq.

Ornamental Plants

In spite of the fact that all species of *Ficus* subsect. *Urostigma* in Thailand are deciduous trees some species are also popular as ornamental. They are mostly cultivated in recreational parks or public places. Six species are especially popular ornamental plants.

Ficus religiosa is not only a sacred tree but also an ornamental that is commonly planted near monasteries or in official places. *Ficus concinna* is generally found in recreational parks or public places, many are present in the Dusit Zoo in Bangkok, where its fruits are favorite among frugivorous birds, which makes the species a favourite landmark for bird watchers. Both subspecies of *F. geniculata* (Fig. 8-3), and *F. virens* var. *glabella*, and *F. caulocarpa* are mainly planted in domestic areas in the northern part. Even when principally planted as food tree they are also used by many people as shade trees or as an ornamental plants.

One shrub species, *F. orthoneura* inhabits limestone mountains. We found it growing in a pot in Phatum Thani.

Conclusions

Eight out of twelve species of *Ficus* subsect. *Urostigma* in Thailand are used by the Thai people. In the northern part people know exactly how to use the shoots (and young leaves) for food. However, we never found the fruits to be eaten.

In all regions of Thailand species of the subsection are used as ornamental plant or as sacred, religious tree. Especially, *F. religiosa* is very popular as sacred tree, but it is also used as an ornamental plant.

The useful species *F. geniculata* var. *geniculata*, *F. geniculata* var. *insignis*, *F. virens* var. *glabella* and *F. caulocarpa* are valuable in all three uses that we evaluated (food, religious, ornamental).

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acknowledge the support from the Thailand National Science Museum, both enabled him to study for a Ph.D. in Leiden, the Netherlands.

Summary & Conclusion

Summary and Conclusions

Ficus subsect. *Urostigma* is a taxonomically notorious group, because of the very variable morphological characters, the wide range of distributions, its unsatisfactory systematic classification, and its problematic circumscription when compared with other subsections. Moreover, *Ficus amplissima* and *F. rumphii* were misplaced by Berg (2004), and this also had its impact on the morphological characters typical for the group. Therefore, the aims of thesis are: 1) To solve the problem of the classification, 2) To study the history, as well evolutionary as biogeographically, and 3) To establish the subsection's economic value.

Five research methods were used: Morphological characters, leaf anatomy, pollen morphology, molecular phylogeny, and historical biogeography. Seven topics are the result: 1) A revision was made based on morphology in which 27 species are recognized, but which also showed that morphology alone cannot solve all problems because of variation within the species. 2) Leaf anatomy displayed less variation in characters and anatomical characters proved to be useful for the classification of *Ficus*, especially in combination with morphology. 3) Pollen morphology appeared to be similar for all species and the characters can merely be used for generic recognition. 4) A new classification for subsection *Urostigma* is proposed in which the circumscription of the subsection and the species is the result of combining molecular phylogenetic information with morphology and leaf anatomy. 5) *Ficus cornelisiana*, a new species from Sino-Himalayan, was reported based on morphological and leaf anatomical evidence. 6) The historical biogeography was studied by using molecular dating and ancestral area reconstruction. 7) The use of some Thai species within subsect. *Urostigma* is reported, six of them are used as food, as ornamental, or the uses are related to religion or sacred purposes.

Which species can we morphologically distinguish in *Ficus* subsect. *Urostigma*? What are their diagnostic morphological characters? What is the extend of morphological overlap between the species?

Based on morphology, 27 species of *Ficus* subsection *Urostigma* were described in the revision of Chantarasuwan et al. (2013, see chapter 2). *Ficus cornelisiana* was later added as a new species based on morphology and leaf anatomy (Chantarasuwan et al., 2014, see chapter 6). A new classification based on morphology, leaf anatomy, and a molecular phylogeny (chapter 5) resulted in the reinstatement of *F. glabella* and *F. wigthiana* as species and the description of a new species, *F. pseudocaulocarpa*, distinct from *F. caulocarpa*. Thus in total 31 species are recognised as part of subsect. *Urostigma*. Morphologically the subsection is distinct by the presence of intermittent (seasonal) growth, shedding of the leaves during the dry season, articulated leaves in Asian-Australian species, figs below the leaves and/or on spurs on the older branches, and staminate flowers mostly near the opening (ostiole) of the fig. However, none of these characters is always present or unique for the subsection. *Ficus verruculosa* is evergreen, while *F. religiosa* does not shed its leaves when growing conditions are everwet. Figs below the leaves or on are spur are also present in other sections such as Sect. *Americana* (e.g., *F. americana*), sect. *Galoglychia* (e.g., *F. bubu*). Staminate flowers near the ostiole is a rather good character, but some species of subsect. *Urostigma* show dispersed staminate flowers (*F. cornelisiana*, *F. densifolia*, *F. hookeriana*, *F. orthoneura*, and *F. prolixa*), while *F. arnottiana* shows staminate flowers mainly around the ostiole, but also a few dispersed when there are abundant staminate flowers. Dispersed staminate flowers are typical for other sections of subgen. *Urostigma*. The variation within species can be high, easily causing misidentifications if only morphology is used to recognise species. Hence morphology has to be combined with other characters.

Do the species of *Ficus* subsect. *Urostigma* differ in leaf anatomy? Does the leaf anatomy provide proper diagnostics for the recognition of species? Will leaf anatomy strengthen or improve morphological species circumscriptions?

The main leaf anatomical characters of *Ficus* subsection *Urostigma* (Moraceae) for the subsection recognition (Chantarasuwan et al., 2014, see chapter 3) are: The epidermis is mostly single-layered, but sometimes a multiple layer is present. The multiple epidermis comes in two forms: 1) The outer and inner epidermal cells are similar in shape and only gradually increasen in size from the periphery to the deeper layers (*F. arnottiana*, *F. wightiana*) or 2) the cells in the inner layer are much larger than those in the outer layer and both layers resemble an epidermis with a separate hypodermis (*F. cornelisiana*, *F. hookeriana* and *F. orthoneura*). "Enlarged lithocysts" mostly appear on the abaxial side of the lamina, except in *F. arnottiana*, which shows abundant enlarged lithocysts adaxially and very few abaxially. The anatomical variation within species is limited when compared with morphology. However, some species are not clearly identifiable with only leaf anatomy (*F. ingens* vs. *F. virens*, *F. prasinicarpa* vs. *F. pseudoconcinna*). Nevertheless, leaf anatomy in combination with morphology provides conclusive characters for species recognition.

Does pollen morphology show the same functionality as leaf anatomy in the characterisation of species?

The pollen morphology of the species within *Ficus* subsection *Urostigma* (Moraceae) (Chantarasuwan et al., 2014, see chapter 4) is largely similar to that of other sections. The main characters are: The grains are very small to small, mostly 2–porate with an ellipsoid or gibbous shape, or they are sometimes 3–porate and rarely 4–porate and then quadrangular in polar view. The pores are circular and 1.2–4.7 μm diam. The exine is less than 1 μm thick, and the ornamentation is nearly always scabrate. The pollen morphology does not provide good characters to diagnose species or even the subsections.

What is the most likely phylogeny of *F.* subsect. *Urostigma*? How do the two species in section *Leucogyne, F. amplissima* and *F. rumphii*, fit in? How is *Ficus* subsect. *Urostigma* related to other subsections and sections within *Ficus* subgenus *Urostigma*?

The controversial classification of two species, *F. amplissima* and *F. rumphii*, forming former sect. *Leucogyne*, has been clarified. Based on morphology, leaf anatomy, and molecular phylogeny [chapter 5, but see also Rønsted et al. (2005, 2008), Cruaud et al. (2012)], evidence is presented to classify the two species in subsection Conosycea. The phylogenetic results also show *Ficus* subsect. *Urostigma* to be more close related with the dioecious figs (subgenera *Ficus*, *Sycidium*, *Sycomorus* and *Synoecia*) than with other members within subgen. *Urostigma* (sect. *Americana*, subsect. *Conosycea*, sect. *Galoglychia*, and sect. *Stilpnopyllum*). Morphological character states shared with other groups are the result of parallel evolution or reversals (homoplasy).

How can the phylogenetic results be translated into a classification? Are clades recognisable with the aid of morphology, leaf anatomy, and/or pollen morphology? How can we explain the evolutionary trends in morphology, leaf anatomy, and pollen morphology?

Changes in the environment (climate, geology) result in variability, homoplasy in characters and speciation. The variability and homoplasy in characters can obscure the phylogeny of a group. Molecular data, because of their multitude of characters, then help to reconstruct a phylogeny, and when combined with morphology and anatomy, clades in the phylogeny also become recognisable. The phylogeny clearly demonstrated the high levels of homoplasy in the morphology, not only within subsection *Urostigma*, but also among members of the various infrageneric groups. The phylogeny also helped to unravel or indicate cryptic species. Convergence in characters made it impossible to first separate *F. pseudocaulocarpa* and *F. caulocarpa*, because they were morphologically quite similar, but the molecular data clearly separated both entities in the phylogeny, which resulted in the description of a new species, *F. pseudocaulocarpa*.

Where and when did the major diversification events occur in the evolution of *Ficus* subsect. *Urostigma*? Which scenario results from the historical biogeography of the species? How can we explain the disjunction between the African and Asian-Australian species?

The origin of the subsection was probably on Madagascar at the end of the Paleocene or early-Eocene. Birds may be the main dispersal agent in the distribution of the figs from Madagascar to Africa in the Eocene. Probably the subsection reached Asia by rafting on India, because India has the first origin of the Asia species (*F. religiosa F. tsjakela* and *F. pseudocaulocarpa* mainly developed in India). All other species dispersed from India and widespread species even crossed Wallace's Line and even reached Micronesia and Australia (e.g., *F. glabella*, *F. geniculata* var. *insignis*, *F. virens*). *Ficus ingens*, an African species in the Asian clades, probably returned to Africa before the middle Miocene, when the Arabian land bridges were formed (Rögl, 1999) and when the climate was still warm and humid (Zachos et al., 2001).

Which species of *Ficus* subsect. *Urostigma* are used by man and for which purposes?

Species of *Ficus* subsect. *Urostigma* are commonly used as food and/or medicine around the world. In Thailand, the young syconium (fig) and young leaves of five species are used as food. *Ficus superba*, growing inshore, is consumed by people living in the south-eastern and peninsular part of Thailand; *F. caulocarpa*, *F. geniculata*, *F. glabella* and *F. subpisocarpa* are grown in home areas in the northern part for food. Seven species are utilised as sacred trees, *F. religiosa* is the most famous sacred tree in Hinduism and Buddhism. Six species are employed as ornamental plants.

Future studies

The taxonomic part of *Ficus* subsect. *Urostigma* is now clear, but some molecular work is still needed to prove the relationships of *F. cupulata* and *F. chiangraiensis*. The problematic variation within *F. virens* was only partly dissolved here, but more molecular data are needed to unravel this complex of cryptic species. Leaf anatomy appeared to be very suitable for species recognition in combination with morphology. Studying the leaf anatomy of other infrageneric groups of *Ficus* will also increase the taxonomic identification of their species. The functional ecology of the *Ficus* species was not studied. Figs are often very important as food tree for animals, quite often helping them to survive through the dry season (Berg & Corner, 2005; Berg et al., 2011; Shanahan et al., 2001; Harrison et al., 2012). The effect of deforestation and a changing climate on the species, its predators and its ecosystem should be studied to provide information for durable wildlife conservation.

Samenvatting en Conclusies

Samenvatting en Conclusies

Ficus subsectie *Urostigma* is taxonomisch een beruchte groep door de zeer variabele, morfologische kenmerken, de zeer verschillende verspreidingen, en zijn onbevredigende classificatie en omschrijving, vooral in vergelijking met andere subsecties. Bovendien waren *Ficus amplissima* en *F. rumphii* door Berg (2004) misplaatst in deze groep en dat had ook zijn weerslag op de morfologische kenmerken, die typisch voor de groep zijn.

De doelstellingen van dit proefschrift zijn daarom: 1) Het oplossen van het classificatie probleem, 2) De historie bestuderen, zowel evolutionair als biogeografisch, 3) De economische waarde van de subsectie vast stellen.

Vijf onderzoeksmethoden zijn gebruikt: Morfologische kenmerken, bladanatomie, pollen morfologie, moleculaire fylogenie en historische biogeografie. Zeven onderwerpen zijn het resultaat: 1) Er is een revisie gemaakt op basis van morfologie, waarin uiteindelijk 27 soorten onderscheiden zijn, maar waarin ook aangetoond werd, dat morfologie alleen niet afdoende is om alle problemen op te lossen door de variatie binnen de soorten. 2) Bladanatomie laat minder variatie in kenmerken zien en anatomische kenmerken blijken zeer bruikbaar te zijn bij de classificatie van de soorten, vooral in combinatie met morfologie. 3) Pollen morfologie bleek bij alle soorten hetzelfde te zijn en de kenmerken zijn alleen bruikbaar voor geslachtsherkenning. 4). Er wordt een nieuwe classificatie voor subsectie *Urostigma* voorgesteld, waarbij de omschrijvingen van de subsectie en de soorten het resultaat zijn van een combinatie van moleculaire fylogenie, morfologie en blad anatomie. 5) *Ficus cornelisiana*, een nieuwe soort uit het Sino-Himalaya gebied, wordt beschreven op basis van morfologisch en blad anatomisch bewijs. 6) De historische biogeografie is bestudeerd door gebruik te maken van moleculaire datering en de reconstructie van vooroudergebieden. 7) Het gebruik van sommige Thaise soorten uit subsectie *Urostigma* wordt beschreven. Zes soorten worden gebruikt als voedsel, als sierplanten, of ze worden voor religieuze en sacrale doeleinden gebruikt.

Welke soorten kunnen we morfologisch onderscheiden in *Ficus* subsectie *Urostigma*? Wat zijn hun diagnostisch morfologische kenmerken? Hoe groot is de morfologische overlap tussen de soorten?

Op basis van morfologie werden 27 soorten in *Ficus* subsectie *Urostigma* beschreven in de revisie door Chantarasuwan et al. (2013, zie hoofdstuk 2). *Ficus cornelisiana* is later toegevoegd als nieuwe soort (Chantarasuwan et al., 2014, zie hoofdstuk 6). Een nieuwe classificatie gebaseerd op morfologie, blad anatomie en een moleculaire fylogenie (hoofdstuk 5) resulteerde in het opnieuw erkennen van *F. glabella* en *F. wightiana* als soorten en de beschrijving van een nieuwe soort, *F. pseudocaulocarpa*, onderscheidbaar van *F. caulocarpa*. Dus in totaal worden 31 soorten erkend als behorend tot subsectie *Urostigma*.

Morfologisch is de subsectie herkenbaar aan intermitterende (seizoens)groei, het afvallen van bladeren gedurende het droge seizoen, articulerende bladeren in Azië en Australië, vijgen onder de bladeren en/of op sporen (brachyblasten) op de oudere takken, en de mannelijke bloemen die zich meestal rond de opening (ostiole) van de vijg bevinden. Echter, al deze kenmerken zijn nooit altijd aanwezig of uniek voor de subsectie. *Ficus verruculosa* is niet blad verliezend, terwijl *F. religiosa* zijn bladeren niet laat vallen als het in een altijd nat klimaat groeit. Het kenmerk vijgen onder de bladeren of op een spoor is ook aanwezig in andere secties, zoals Sectie *Americana* (b.v. *F. americana*), sectie *Galoglychia* (b.v. *F. bubu*). Mannelijke bloemen rond de ostiole is een redelijk goed kenmerk, maar sommige soorten uit subsectie *Urostigma* hebben verspreide mannelijke bloemen (*F. cornelisiana*, *F. densifolia*, *F. hookeriana*, *F. orthoneura* en *F. prolixa*), terwijl *F. arnottiana* gewoonlijk mannelijke bloemen rond de ostiole heeft, maar soms ook een paar verspreid als er veel mannelijke bloemen aanwezig zijn. Verspreide mannelijke bloemen is typisch voor andere secties in subgenus *Urostigma*. De variatie binnen de soorten kan hoog zijn, wat gemakkelijk tot misidentificaties leidt als alleen morfologie gebruikt wordt om de soorten te herkennen. Daartoe moeten morfologische kenmerken dus aangevuld worden met andere kenmerken.

Verschillen de soorten van *Ficus* subsectie *Urostigma* in bladanatomie? Voorziet bladanatomie in goede diagnostische kenmerken voor soortherkenning? Versterkt bladanatomie de morfologische soortsomschrijvingen?

De belangrijkste blad anatomische kenmerken van *Ficus* subsectie *Urostigma* (Moraceae), die geschikt zijn voor soortherkenning, zijn (Chantarasuwan et al., zie hoofdstuk 3): De epidermis bestaat meestal uit één laag, maar soms is deze meerlagig. De meerlagige epidermis is in twee vormen aanwezig: 1) De cellen in de buitenste en binnenste epidermale lagen zijn gelijk van vorm, maar worden geleidelijk groter naar binnen toe (*F. arnottiana*, *F. wightiana*), of 2) de cellen in de binnenste laag zijn veel groter dan die in de buitenste laag en beide lagen lijken op een epidermis en een separate hypodermis (*F. cornelisiana*, *F. hookeriana* en *F. orthoneura*). "Vergrote lithocysten" zijn meestal aanwezig aan de abaxiale zijde van de bladschijf, behalve in *F. arnottiana*, die vooral adaxiaal vergrote lithocysten heeft en slechts een paar abaxiaal. De anatomische variatie binnen de soorten is gering in vergelijking met de morfologie. Echter, sommige soorten kunnen met behulp van blad anatomie niet eenduidig geïdentificeerd worden (*F. ingens* versus *F. virens*, *F. prasinicarpa* versus *F. pseudoconcinna*). Niettegenstaande, bladanatomie in combinatie met morfologie levert afdoende kenmerken voor soortherkenning.

Laat het stuifmeel dezelfde functionaliteit zien als bladanatomie bij characterisering van soorten?

De pollen morfologie van de soorten in *Ficus* subsectie *Urostigma* (Moraceae) (Chantarasuwan et al., 2014, zie hoofdstuk 4) is grotendeels gelijk aan dat van de andere secties. The belangrijkste kenmerken zijn: De korrels zijn erg klein tot klein, meestal 2-poraat met een ellipsoïde tot gibbose vorm, of ze zijn soms 3-poraat en zelden 4-poraat en dan vierhoekig in polair aanzicht. De poriën (openingen) zijn rond en 1.2-4.7 µm diam. De exine is minder dan 1 µm dik en de ornamentatie is bijna altijd scabreus. De pollen morfologie bevat geen kenmerken, die geschikt zijn voor het herkennen van soorten of zelfs maar subsecties.

Wat is de meest waarschijnlijke fylogenie voor *F.* subsectie *Urostigma*? Hoe kunnen de twee soorten in sectie, *F. amplissima* en *F. rumphii*, ingepast worden? Hoe verhoudt *Ficus* subsectie *Urostigma* zich tot de andere subsecties en secties in *Ficus* subgenus *Urostigma*?

De controversiële classificatie van twee soorten, *F. amplissima* en *F. rumphii*, samen vroeger sectie *Leucogyne* vormend, is opgelost. Gebaseerd op morfologie, blad anatomie, en de moleculaire fylogenie [hoofdstuk 5, maar zie ook Rønsted et al. (2005, 2008), Cruaud et al. (2012)], is bewijs geleverd dat de twee soorten in subsectie Conosycea ingedeeld moeten worden. De fylogenetische resultaten laten ook zien dat *Ficus* subsectie *Urostigma* meer verwant is aan de tweehuizige vijgen (subgenera *Ficus*, S*ycidium*, *Sycomorus* en *Synoecia*) dan aan de ander leden van subgenus *Urostigma* (sectie Americana, subsectie *Conosycea*, sectie *Galoghycia* en sectie *Stilpnophyllum*). Morfologische kenmerktoestanden die gedeeld worden met andere groepen zijn vooral het resultaat van parallelle evolutie of reversies (homoplasie).

Hoe kunnen de fylogenetische resultaten vertaald worden in een classificatie? Zijn de clades herkenbaar met behulp van morfologie, bladanatomie en/of pollen morfologie? Hoe kunnen we de evolutionaire trends in morfologie, bladanatomie en pollen morfologie verklaren?

Veranderingen in de omgeving (klimaat, geologie) resulteren in variabiliteit, homoplasie in kenmerken en speciatie. De variabiliteit en homoplasie in kenmerken kunnen de fylogenie van een groep verhullen. Moleculaire gegevens, omdat ze een veelheid aan kenmerken bevatten, kunnen dan helpen de fylogenie te reconstrueren, en wanneer ze gecombineerd worden met morfologie en anatomie worden clades in de fylogenie ook herkenbaar. De fylogenie liet duidelijk de hoge niveaus van homoplasie in de morfologie zien, niet alleen in subsectie *Urostigma*, maar ook bij de soorten uit andere infragenerische groepen. De fylogenie hielp om een aantal cryptische soorten te ontrafelen of aan te duiden. Convergentie in kenmerken maakte het aanvankelijk onmogelijk om *F. pseudocaulocarpa* van *F. caulocarpa* te onderscheiden, omdat ze morfologisch zo gelijk waren. De moleculaire gegevens scheidden beide soorten duidelijk in de fylogenie en dit resulteerde in het beschrijven van *F. pseudocaulocarpa* als nieuwe soort.

Waar en wanneer vonden de belangrijkste diversificatiemomenten plaats in de evolutie van *Ficus* subsectie *Urostigma*? Welk scenario rolt uit de historisch biogeografische studie van de soorten? Hoe kunnen we de disjunctie tussen Afrikaanse en Aziatisch-Australische soorten verklaren?

De subsectie is waarschijnlijk ontstaan op Madagaskar aan het eind van het Paleoceen of het vroege Eoceen. Vogels zijn waarschijnlijk de belangrijkste verspreiders geweest om de vijgen van Madagaskar naar Afrika te brengen in het Eoceen. Mogelijk bereikte de subsectie Azië door mee te drijven op India, de eerste Aziatische soorten ontstonden namelijk in India (*F. religiosa*, *F. tjakela*, en *F. pseudocaulocarpa*). Alle andere soorten verspreidden zich vanuit India en wijdverspreide soorten staken zelfs de Wallace lijn over en bereikten Micronesië en Australië (b.v. *F. glabella*, *F. geniculata* var. *insignis*, *F. virens*). *Ficus ingens*, een Afrikaanse soort middenin de Aziatische clade, keerde mogelijk naar Afrika terug langs de kust voor het midden van het Mioceen, toen de Arabische landbruggen al bestonden (Rögl, 1999) en toen het klimaat nog warm en vochtig was (Zachos et al., 2001).

Welke soorten uit *Ficus* subsectie *Urostigma* zijn door de mens voor verschillende doeleinden gebruikt?

Wereldwijd worden soorten van *Ficus* subsectie *Urostigma* gewoonlijk gebruikt als voedsel en/of medicijnen. In Thailand worden de jonge vijgen en jonge bladeren van vijf soorten gebruikt als voedsel. *Ficus superba*, langs de kust groeiend, wordt door mensen gegeten die in het zuidoosten en het schiereiland gedeelte van Thailand wonen; *F. caulocarpa*, *F. geniculata*, *F. glabella* en *F. subpisocarpa* worden rond huizen in het noorden van Thailand gekweekt als voedsel. Zeven soorten worden gebruikt als heilige bomen. Daarvan is *F. religiosa* de meest beroemde heilige boom in het Hindoeïsme en Boeddhisme. Zes soorten zijn in gebruik als sierplanten.

Toekomstige studies

Het taxonomische deel van *Ficus* subsectie *Urostigma* is nu duidelijk, maar meer moleculair werk is nog nodig om de relaties van *F. cupulata* en *F. chiangraiensis* te verduidelijken. De problematische variatie binnen *F. virens* is hier alleen gedeeltelijk opgelost, maar meer moleculaire gegevens zijn nodig om dit complex van cryptische soorten te ontrafelen. Bladanatomie in combinatie met morfologie bleek zeer geschikt te zijn om soorten te identificeren. Studie van de bladanatomie van andere infragenerische groepen binnen *Ficus* zal leiden tot een verbeterde determinatie van de soorten.

De functionele oecologie van de *Ficus* soorten was niet bestudeerd. Vijgen zijn vaak zeer belangrijk als voedselboom voor dieren, hen vaak helpend het droge seizoen te overleven (Berg & Corner, 2005; Berg et al., 2011; Shanahan et al., 2001; Harrison et al., 2012). Het effect op de vijgen van ontbossing en een veranderend klimaat, hun predatoren en het oecosysteem moeten bestudeerd worden om informatie te vergaren voor een duurzaam behoud van hun biodiversiteit.

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CURRICULUM VITAE

Bhanumas Chantarasuwan was born on 6 August 1971 in Krabi province, Thailand, where he lived in a rural village. His first botanical contacts where initiated by the village elders, who learned him to recognise edible plants in the nearby forest. Bhanumas finished his secondary education at Nuaklongprachabamrung School, Krabi, in 1992, and left for Bangkok to study at the Faculty of Forestry, Kasetsart University. He obtained his Bachelor degree of Sciences (Forestry) in 1996. During his Bachelor study he was drawn into botany by Associate Professor in dendrology Somnuek Phongampai, especially during the two-week dendrological field course in the forest. Next, he had to fulfil his military service in the navy in 1998 and he spent one year in the marine base at Sattahib, Chon Buri. Three years later (2001) he became a permanent staff member in The Thailand National Science museum, where his routine work is surveying plant diversity and collecting plant specimens for the museum. In 2007, he fulfilled his master degree in Forest Biology, also in Kasetsart University. His interest in *Ficus* (Moraceae) was inspired by Mrs. Sumon Masuthon, a lecturer in the Botany Department, a pioneer researcher in the taxonomy of Thai *Ficus*. During a field trip in 2003 Prof.dr. Cornelis C. Berg was the second person who stimulated him to work on *Ficus*. Bhanumas could fulfill his ideal to study *Ficus* when he was granted a scholarship for taxonomic studies by the Ministry of Science and Technology on behalf of the Royal Thai Government, under the responsibility of the Thailand National Science Museum. He started his Ph.D. at the National Herbarium of the Netherlands, Leiden University (now Naturalis Biodiversity Center), under the supervision of Prof.dr. Peter C. van Welzen and Prof. dr. Berg. After his graduation he will continue his career as a staff member of the Thailand National Science Museum, Pathum Thani province, Thailand.

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