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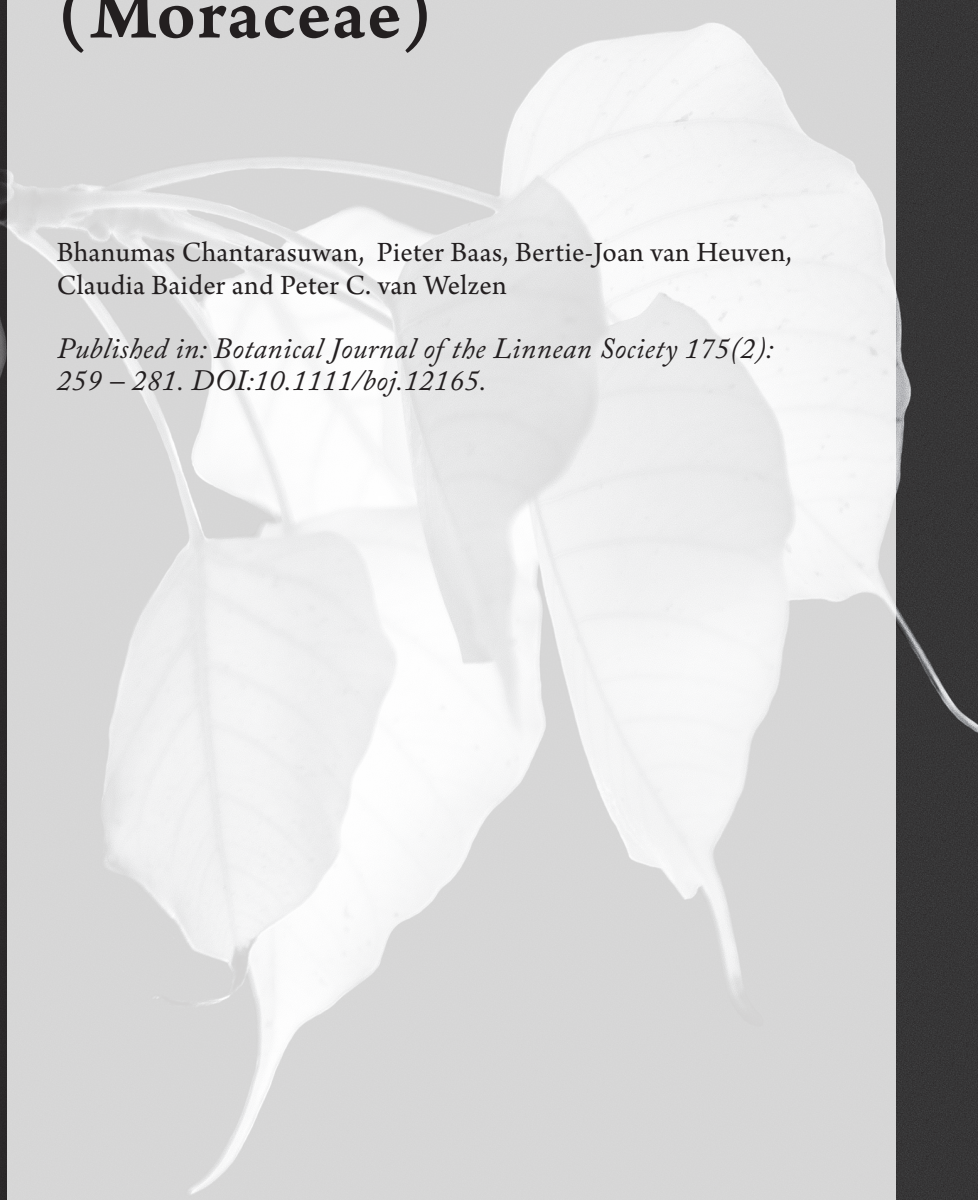


Chapter 3

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

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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

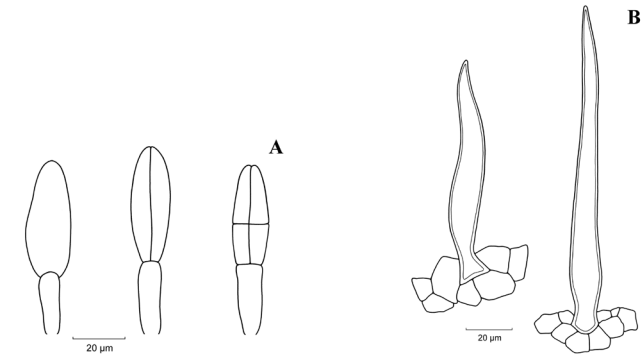


FIGURE 3-1. A. Glandular hairs with 1-, 2- or 4-celled heads, B. Simple hairs. Drawing: Esmée L. C. Winkel, 2013.

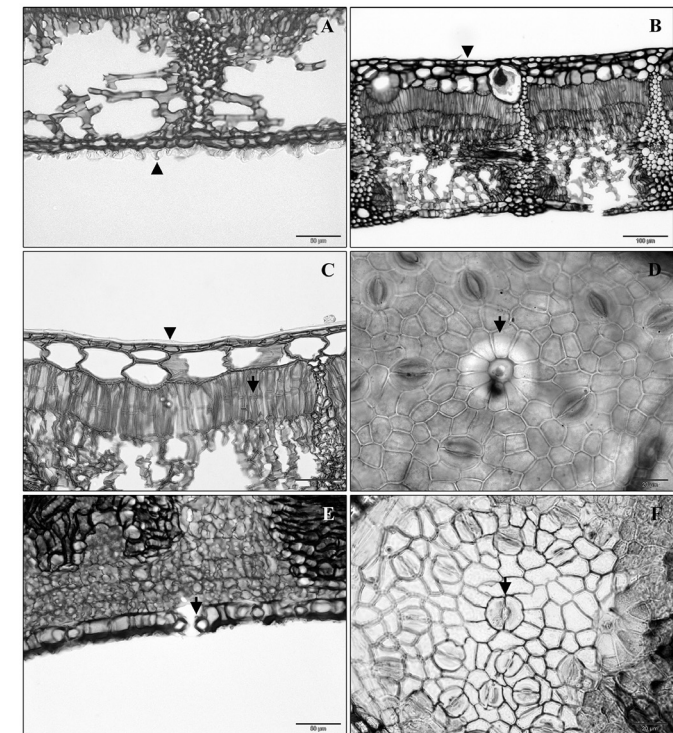


FIGURE 3-2. A. Cuticular ridges (arrowhead) (*F. hookeriana* from Herb. Lugd. Bat. [= L] No 922312770), B. Multiple epidermis (arrowhead) (*F. arnottiana* from Haines 3546), C. Multiple epidermis (arrowhead) and subdivided palisade cells (arrow) (*F. hookeriana* from Herb. Lugd. Bat. [= L] No 922312770), 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

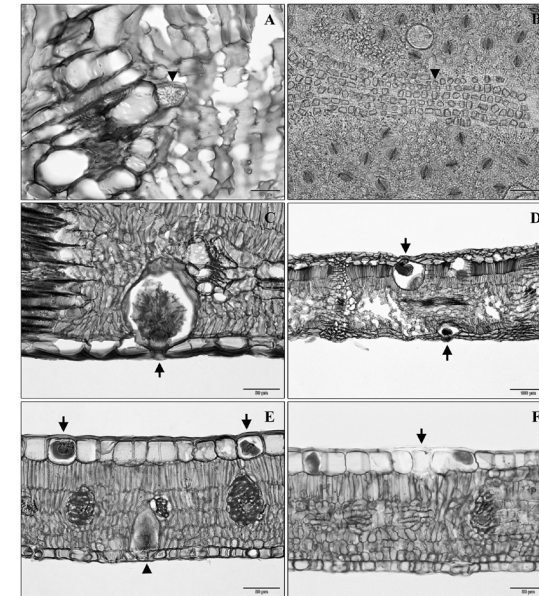


FIGURE 3-3. A. Druse crystal (arrowhead) (*F. salisifolia* from O. Beccari 39), B. Prismatic crystals (arrowhead) (*F. concinna* from B. Chantarasuwan 071010-1), C. Enlarged lithocysts (arrow) (*F. salisifolia* from O. Beccari 39), D. Enlarged lithocysts adaxially and abaxially (arrow) (*F. arnottiana*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

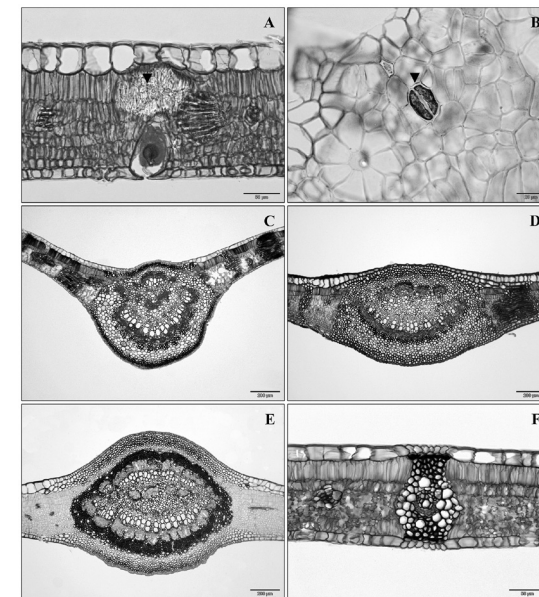


FIGURE 3-4. A. Silicified cells in mesophyll (arrowhead) (*F. religiosa* from B. Chantarasuwan 150910-2), B. Guard cells silicified (arrowhead) (*F. prasinicarpa* from A. J. G. H. Kostermans 1593), C. Midrib vascularization with opposed adaxial and abaxial arcs with central vascular bundles (or phloem 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 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.

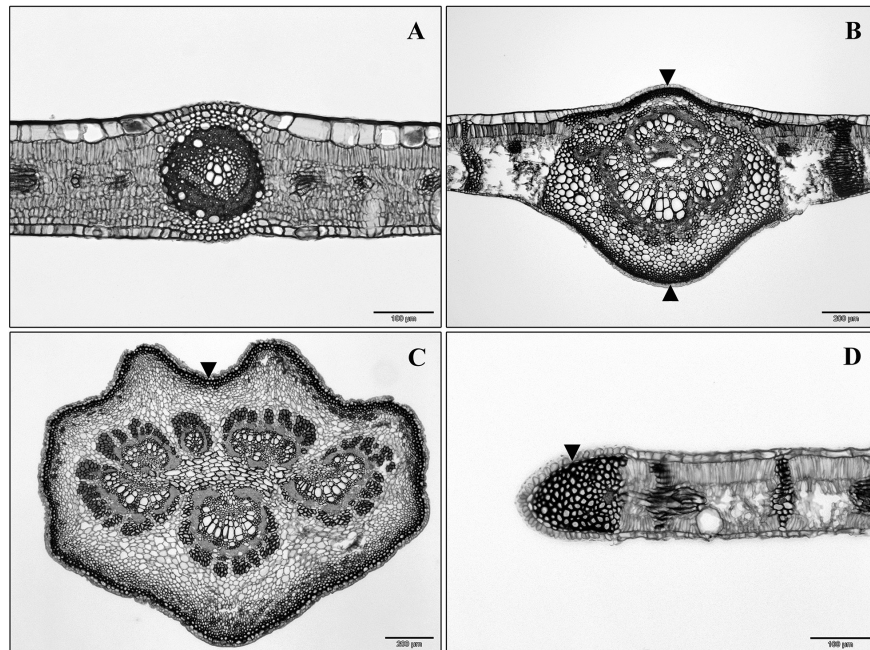


FIGURE 3-5. A. Circular bundle of veins and bundle sheath (*F. religiosa* from B. Chantarasuwan 150910-2), B. Adaxial and abaxial sclerified ground tissue subepidermal in midrib (arrowhead) (*F. geniculata* from B. Chantarasuwan 220910-1). C. Sclerified ground tissue in the petiole (arrowhead) (*F. virens* 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. proluxa*
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 28–38 µm 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 cuticular 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* (Solereeder, 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	Petiole	Bundle sheaths	Mesophyll	Sitified cells	Epidermis	Petiole	Simple hair	lamina	Glandular hairs	Petiole	Lamina	Giant stomata	Inner stomata ledge	Stomatal level	Subepidermal	petiole	Subepidermal	midrib	layer
subsect. <i>Urostigma</i>	S	8-12	-	Ab	+	-	1	+	Sep	-	-	V	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>F. alongensis</i>																													
<i>F. armatiana</i>	M	5-8	-	Ad, Ab	-	-	(1-2)	±	N	+	+	V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(2-3)																													
<i>F. caulocarpa</i>	S	8-12	-	Ab	+,-	-	2	+	N	+	+	V	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>F. chiangraiensis</i>	S	5-8	-	Ab	+	-	2	+	N	+	+	V	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>F. concinna</i>	S	8-12	-	Ab	+	-	3-5	+	N	+	+	V	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>F. cordata</i>	S	8-16	-	Ab	+	+,-	2-5	-	N	+	+	C	+,-	-	-	-	-	-	-	-	-	-	Sun	-	-	-	-	-	-
<i>F. densifolia</i>	S	5-8	-	Ab	-	-	2-5	+	N	-	+	V	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-
<i>F. geniculata</i>	S	8-12	-	Ab	+	+	2	+	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. henneana</i>	S	8-12	-	Ab	-	-	2	+	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-
<i>F. hookeriana</i>	M (2)	5-8	+	Ab	+,-	+	1-2	-	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-
<i>F. iogens</i>	S	8-16	-	Ab	+	+	2-5	+	N	+	+	V	+,-	-	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. lecardii</i>	S	6-9	-	Ab	+,-	+	1	-	N	+	+	V	-	-	-	-	-	-	-	-	-	-	Sun	-	-	-	-	-	-
<i>F. middletonii</i>	S	8-12	-	Ab	+	-	4-5	+	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. orthoneura</i>	M (2)	5-8	+	Ab	-	-	1-2	+	Sep	+	+	V	-	-	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. prasincarpa</i>	S	5-9	-	Ab	+,-	+,-	1	+	N	+	+	V	+	+	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. proluxa</i>	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	Petiole	Bundle sheaths	Mesophyll	Sitified cells	Epidermis	Petiole	Simple hair	lamina	Glandular hairs	Petiole	Lamina	Giant stomata	Inner stomata ledge	Stomatal level	Subepidermal	petiole	Subepidermal	midrib	layer
<i>F. pseudococinnia</i>	S	5-8	-	Ab	+	+,-	1	+	N	+	+	V	+	+	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. religiosa</i>	S	8-12	-	Ab	+	+,-	2-5	+	N, CR	+	+	C	+	+	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. salicifolia</i>	S	5-8	-	Ab	-	+	2	+	N	+,-	+	V	-	-	-	-	-	-	-	-	-	-	Sun	-	-	-	-	-	-
<i>F. saxophila</i>	S	8-12	-	Ab	+	+,-	1-2	-	N, CR	+	+	C	-	-	-	-	-	-	-	-	-	-	L, R, Sun	-	-	-	-	-	-
<i>F. subpiscarpa</i>	S	5-8	-	Ab	+	+	1	+	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
subsp. <i>pubipoda</i>																													
<i>F. superba</i>	S	6-9	-	Ab	+	-	1	+	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
<i>F. tsjakela</i>	S	5-8	+,-	Ab	+,-	+,-	2-5	-	N	+	+	C	+,-	-	-	-	-	-	-	-	-	-	Sun	+	-	-	-	-	-
<i>F. verruculosa</i>	S	6-9	-	Ab	+,-	+,-	1(-2)	-	N	+,-	+	V	+	+	-	-	-	-	-	-	-	-	L, Sun	-	-	-	-	-	-
<i>F. vitens</i>	S	7-12	-	Ab	+	+	4-5	+	N	+	+	V	+	+	-	-	-	-	-	-	-	-	L	+	-	-	-	-	-
sect.	M	5-8	-	Ad	-	-	2	+	N	+	+	V	+,-	-	-	-	-	-	-	-	-	-	Sun	-	-	-	-	-	-
Leucogyne																													
<i>F. amplissima</i>																													
(2-3)																													
<i>F. rumphii</i>	M	5-8	-	Ad	-	-	2	+	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-
(2-3)																													
subsect. Conosycea	M	5-8	-	Ad, Ab	-	-	1	+	N	+	+	V	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-
<i>F. glaberrima</i>																													
(2-3) (-9)																													
subsp. <i>siamensis</i>																													

** 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 translucent, + = present, - = absent, ± = character weakly developed.