THE TAXONOMY OF TERMINALIA (COMBRETACEAE) AND RELATED GENERA

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by

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STATEMENT

The contents of this thesis are based on work conducted by the author in the Department of Botany of the University of Leicester during the period January 1980 to December 1983.

All the work recorded in this thesis is original unless otherwise acknowledged in the text or by references.

Signed ....

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CHAPTER 1

INTRODUCTION

1.1. General description of the family Combretaceae and subtribe Terminaliinae

1.1.1. Combretaceae

The family Combretaceae, to which the genus *Terminalia* belongs, is composed of 18 genera containing about 531 species (Table 1/1). The family is a very natural one, characterized by the compartmented hairs which occur in every genus and in the vast majority of the species (Exell & Stace 1966).

The family is also characterized by its woody habit (usually trees but sometimes shrubs or lianes); petiolate, simple, entire (occasionally minutely serrate or shallowly crenate in *Terminalia*), exstipulate leaves; completely inferior (except in *Strephonema* semi-inferior) and unilocular ovaries, usually with 2 (but up to 12) pendulous ovules; and simple and free (except in *Quisqualis* adnate) style and variable (dry or fleshy, 2-5 winged or ridged or wingless) one-seeded fruits.

The inflorescences are simple axillary spikes (sometimes capitate) or racemes, or axillary or/and terminal panicles. The flowers are usually actinomorphic (rarely slightly zygomorphic); are pentamerous (sometimes tetramerous); are hermaphrodite or andromonoecious (very rarely dioecious); have a receptacle of 2 distinct parts, the lower adnate to and surrounding the ovary (sometimes with adnate bracteoles) and the upper expanded into a cup or funnel-shaped region terminating in 5 or sometimes 4 calyx-lobes; have no corolla or a polypetalous corolla of

Table 1/1. Genera of Combretaceae, their distribution and approximate number of species throughout the world.

genus	America	Africa & Madagascar	Asia incl. New Guinea & the Pacific islands	Australia	Total
<u>Strephonema</u>	0	7	0	0	7
<u>Combretum</u>	33	164	27	0	224
<u>Quisqualis</u>	0	7	9	0	16
<u>Calopyxis</u>	0	22	0	0	2
<u>Meiostemon</u>	0	2	0	0	2
<u>Thiloa</u>	3	0	0	0	3
<u>Guiera</u>	0	1	0	0	1
<u>Calycopteris</u>	0	0	1	0	1
<u>Pteleopsis</u>	0	12	0	0	12
<u>Terminalia</u>	31	65	81	29	201*
<u>Bucida</u>	3	0	0	0	3
<u>Buchenavia</u>	21	0	0	0	21
<u>Anogeissus</u>	0	1	7	0	8
<u>Conocarpus</u>	1	2	1	0	2*
<u>Laguncularia</u>	1	1	0	0	1*
<u>Lumnitzera</u>	0	1	2	2	2*
<u>Macropteranthes</u>	0	0	0	4	4
<u>Dansiea</u> (Byrens ,1981)	0	0	0	1	1
	93	285	128	36	531*

* These figures are less than the sums of the horizontal rows because in <u>Terminalia</u> one species is common to all continents and 2 species common to 2 continents; in <u>Conocarpus</u> 1 species occurs in America & Africa and 1 in Africa & Asia; in <u>Laguncularia</u> the species occurs in America & Africa; and in <u>Lumnitzera</u> 1 species occurs in 3 continents and one in 2 continents.

4-5 petals; and have stamens usually in two whorls of 5 or 4 each (sometimes only one whorl and rarely more than two whorls).

1.1.2. Subtribe Terminaliinae

The family is divided into two subfamilies, Strephonematoideae and Combretoideae (Engler & Diels 1899). The latter includes two tribes, Combreteae and Laguncularieae, of which the former is divided into three subtribes, Combretinae, Pteleopsidinae and Terminaliinae (Exell & Stace 1966). The subtribe Terminaliinae is characterized by having spiral or alternate (rarely subopposite) leaves and no petals, scales or stalk glands (except in *Conocarpus* stalk galnds present).

1.2. Taxonomy of subtribe Terminaliinae

Exell & Stace (1966) included 8 genera in their subtribe Terminaliinae. These genera are *Terminalia*, *Ramatuella*, *Bucida*, *Terminaliopsis*, *Buchenavia*, *Anogeissus*, *Finetia* and *Conocarpus*. The definition and circumscription of the subtribe is still unsettled. The subtribe Pteleopsidinae is now not separable from the subtribe Terminaliinae.

Vollesen (1981) discussed the delimitation of *Pteleopsis* and *Terminalia* and said that the only distinctive character of *Pteleopsis* is the structure of the inflorescence, in which the male flowers are borne at the base of the inflorescence and the bisexual ones at the top. But even this character is sometimes present in *Terminalia*.

Terminaliopsis was united with *Terminalia* by Capuron (1967). *Finetia* was amalgamated with *Anogeissus* by Lecompte (1969) and Scott (1979), and

Ramatuella is relegated to Terminalia section Ramatuella in this work. In fact, unlike the case in subtribe Combretinae, the generic limits of Terminaliinae are not well established. Bucida and Buchenavia, both of which are endemic to America, are distinct genera but they are very closely related to Terminalia. The distinctive character of Bucida is the small wingless fruits with persistent calyx, while that of Buchenavia is the adnate (not versatile) anthers.

Conocarpus, which is unique in the subtribe in having stalked glands on the leaves, and Anogeissus are closely related genera and both differ from Terminalia in possessing fruits in tight cones.

1.3. Economic use

Several members of Combretaceae are of considerable economic importance. In the genus Terminalia, for example, T. superba (its timber is know in the market as 'afara', T. ivorensis ('idigbo'), T. catappa, T. myriocarpa and T. amazonia are important sources of timber for export or for local use. The seeds of T. catappa, which are known as Indian almonds, are very oily and eaten as almonds. T. bentzoë is an important source of one kind of benzoin gum.

Barks, leaves and fruits are used for various local purposes. For example, various medicinal uses are known for the barks and leaves of T. catappa and T. bellirica in India and south-east Asia. Also the barks and leaves are used for making ink (Indian ink), dyeing fibres and tanning leather. The fruits of T. bellirica (commercial myrobalans) are used in medicines for dropsy, haemorrhoids and diarrhoea, and in tanning (Exell 1954).

Several species of the family are grown as ornamentals for their attractive flowers, e.g. Quisqualis indica and Combretum grandiflorum. Other species are grown for shade, e.g. Terminalia catappa, which is now widely cultivated (particularly on beaches) and often naturalized throughout tropical and subtropical regions of the world.

1.4. Distribution

Terminalia is the most widespread genus of the family Combretaceae, containing about 200 species. The genus is distributed throughout the tropics of the old and new worlds, including the islands of the Pacific. Its distribution extends slightly beyond the tropics, reaching Uruguay, southern Africa, and Nepal. The distribution of Terminalia almost represents the distribution of the whole family. Combretum, the largest genus of the family in terms of the number of species, is missing from Australia and the Pacific islands, Lumnitzera is missing from America, and the rest of the genera in the family are confined to one or two continents. Ramatuella, Bucida and Buchenavia, which are very closely related to Terminalia, are endemic to America. Bucida is primarily a a central American genus, extending to S. Florida and the Bahamas, Buchenavia is central and south American, and Ramatuella is confined to Amazonia.

1.5. Ecology

South America, which occupies an area of about 8 million square miles, shows great diversity in both the surface configuration of the land and the climatic conditions. The Brazilian and Guianan highlands are found on the eastern side, the Andes (the world's longest mountain range) extend for about 4000 miles on the western side, and the basins of the Amazon, the Orinoco and the Paraguay-Parana-Palata rivers occupy the central part. Although it is traversed by both the Equator and the Tropic of Capricorn, the climate of tropical South America varies from the hot rainy conditions of the Amazon basin to the cool coastal deserts of Peru. In the southern part the climate is moderate, while in middle latitudes it is cool and rainy, and along the Venzuelan coast hot and dry. But the greatest climatic diversity is found in the Andes.

As the vegetation of any land is usually determined by the surface configuration and the climatic conditions, it is obvious that South America provides a wide range of markedly different habitats. Thus, the ecological adaptation and the habitat requirements of a group of plants should be considered in any taxonomic study. But unfortunately this is virtually impossible unless the area is personally visited or very well documented.

1.6. Previous studies and the aims of this study

There is no complete systematic study of the genus Terminalia available. Most previous works have dealt with regional or continental floras or with a few isolated species. This activity has been mainly concentrated on the Floras of Malaysia (Exell 1954), Africa (Griffiths 1959, Lieben 1968, Wickens 1973, Exell 1978), Madagascar (Capuron 1967, Capuron 1973), New Guinea and Papua (Coode 1969 & 1973) and Australia (Byrnes 1977). Terminalia in South and Central America has previously not been studied in detail, but a number of taxonomists have published works dealing with species of a certain region (Eichler 1867, Exell 1935, 1939 & 1958, Macbride 1941, Standley & Williams 1962, Williams 1962, Exell & Reitz 1967, and Hall & Seymour 1978). But the most important work on American species was that of Eichler (1867), who recognized 21 species of Terminalia.

Since Eichler's monograph many of his species have been reduced to synonymy and a large number of new species have been described. Most American species of Terminalia were originally imperfectly known, because of the sparse material available at that time. Hence most species were based on few specimens, which did not take account of the wide ranges of variation. Thus, a study of all American species of Terminalia, together with that of the closely related genera Ramatuella, Bucida and Buchenavia, was badly needed. Such a study should help to understand the variation within and between the above four genera in the new world, and give us a better understanding of the relationships at specific and sectional levels within the entire genus of Terminalia.

Anatomically only a few species of Terminalia from America have been previously studied. But a number of species from outside America and most species of other genera of the family have been investigated from some aspects (Stace 1965b). In this work the anatomy of Terminalia and its closely related genera Buchenavia, Bucida and Ramatuella shows considerable variation between and within the genera.

Studies on the pollen grains of the Combretaceae have been very few. The pollen grains of Ramatuella, Bucida and Buchenavia have not been investigated before. In this work it is found that Buchenavia has a unique pollen type in the family. Throughout the subtribe Terminaliinae the pollen grains are heterocolporate (except in Buchenavia tricolporate). But there is a significant range of variation in the surface ornamentation.

Therefore the aims of this study were:

1 - to study the taxonomy of the genera Terminalia (in America), Ramatuella, Bucida and Buchenavia in details;

2 - to present a worldwide revision for the genus Terminalia at the sectional level;

3 - to investigate the range of leaf architecture and pollen morphology throughout the family with particular reference to the position of the four American genera of Terminaliinae.

CHAPTER 2

HISTORICAL REVIEW

2.1. Classification of the Combretaceae

It was Robert Brown (1810) who first named the family Combretaceae. He included nine genera, namely *Bucida*, *Terminalia*, *Chuncoa*, *Quisqualis*, *Combretum*, *Cacoucia*, *Laguncularia*, *Getonia* and *Conocarpus*, but he did not attempt to classify them. The name Combretaceae has been conserved against Terminaliaceae J. St. Hil. (1805).

De Candolle (1828) expanded the limit of the family and published the first classification of the whole family, relying mainly on the method of folding of the cotyledons. He divided the family into two tribes; Terminaliées (with spirally convolute cotyledons) and Combretées (with plicate cotyledons). He included some genera of the family Nyssaceae, but he correctly grouped most of the other genera, although his classification has since been much modified.

Don (1832) divided the family into two tribes, as De Candolle did, but emphasized the presence or absence of petals. He transferred the genera *Laguncularia*, *Guiera* and *Poivrea* from the tribe Terminalieae to the tribe Combreteae and relegated *Poivrea* to *Combretum* section *Poivrea*. He kept the genus *Agathisanthes* Bl. (now Nyssaceae) in the tribe Terminalieae.

Endlicher (1836) followed the classification of De Candolle but he transferred *Lumnitzera* from the tribe Combreteae to the tribe Terminalieae. He excluded the genus *Agathisanthes* from the Combretaceae and added *Sphalanthus* Jack (= *Quisqualis*) to the tribe Combreteae.

Bentham (1864) and Bentham & Hooker (1865) changed the concept of the family by including three strange genera *Gyrocarpus* Jacq., *Illigera* Blume, and *Sparattanthelium* Mart. (now put in Gyrocarpaceae or Hernandiaceae).

They divided the family, mainly according to the method of opening of the anthers, into two subfamilies ("subordo"): Combreteae included all the true Combretaceae, and the Gyrocarpae included the other 3 genera now in Hernandiaceae. But the genera *Agathisanthes*, *Ceratostachys* Bl. (Nyassaceae), *Bruguiera* Thouars (Rhizophoraceae) and *Bobua* Dc. (Symplocaceae), which had been included in the family by De Candolle (1828) were excluded.

Eichler (1867), in his treatment of the American members of Combretaceae, followed the De Candolle system, but he elucidated the true relationships of the genera he was dealing with by placing *Terminalia*, *Bucida*, *Buchenavia*, *Ramatuella*, *Conocarpus* and *Laguncularia* in Terminalieae and *Thiloa*, *Combretum* and *Cacoucia* in Combreteae.

Brandis (1893) excluded the Gynocarpeae group, which had been included by Bentham (1864), and provided a key to the genera of Combretaceae.

The most important classification of the family was that of Engler & Diels (1899). They treated *Strephonema* (a genus previously placed in Lythraceae), which possesses a semi-inferior ovary, as a separate subfamily Strephonematoideae and the rest of the genera, which possess a completely inferior ovary, as Combretoideae. The Combretoideae were divided into four tribes: (1) Combreteae, composed of *Calopyxis*, *Combretum*, *Guiera*, *Pteleopsis*, *Quisqualis* and *Thiloa*; (2) Terminalieae containing *Terminalia*, *Buchenavia*, *Bucida*, *Ramatuella*, *Anogeissus* and *Conocarpus*: Calycopterideae, containing the single genus *Calycopteris* (*Getonia*); and (4) Lagunculariеae, containing *Laguncularia*, *Lumnitzera* and *Macropteranthes*.

One of the important contributions of Engler & Diels (1899) was to remove the genera *Laguncularia* and *Lumnitzera* from the tribe Terminalieae and treat them together with the genus *Macropteranthes* as a separate tribe.

Exell (1931) criticized Engler & Diels' classification, saying that the Laguncularieae are a much more distinct group than the other three tribes and merit a different category, and the Combreteae and Terminalieae are very closely related and not separable from each other on any single character. However, he did not formally change the classification.

Stace (1963), who first introduced epidermal characters in the classification of the genera of Combretaceae, discussed the classification presented by Engler & Diels (1899), confirming that their treatment of the genus Strephonema as a separate subfamily was justified. Within the Combretoideae he emphasized that the tribe Laguncularieae is a very distinct one, characterized by having a pair of adnate bracteoles on the lower receptacle, and thus he considered the other three tribes to comprise the single tribe Combreteae. Within this he recognized two subtribes: Combretinae, containing Engler & Diels' tribes Combreteae and Calycopterideae; and Terminaliinae, comprising Engler & Diels' tribe Terminalieae.

Exell & Stace (1966) published the most recent classification of the Combretaceae, based mainly on those of Engler & Diels (1899) and Stace (1963). Their classification differed from that of Stace (1963) in that three subtribes were recognized in the tribe Combreteae: (1) Combretinae, containing seven genera; (2) Pteleopsidinae, containing only Pteleopsis; and (3) Terminaliinae, comprising eight genera (Table 2/1).

The subtribes Pteleopsidinae and Terminaliinae are very closely related and, since the discovery of apetalous species of Pteleopsis in 1968 and 1981, cannot be separated on any single character. Vollesen (1981) has therefore proposed their amalgamation.

It can be seen from the above taxonomic treatments of the Combretaceae that Terminalia has always been placed in the same group (whether tribe or subtribe) as Bucida, Ramatuella, Buchenavia, Anogeissus and Conocarpus. This obviously underlines the close relationships between these genera and Terminalia.

Table 2/1: comparison of major classification of the Combretaceae.

De Candolle 1828	Engler & Diels 1899	Exell & Stace 1966
Tribe Terminalieae	Subfamily Strephonematoideae	Subfamily Strephonematoideae
Bucida	*Strephonema*	*Strephonema*
Agathisanthes	Subfamily Combretoideae	Subfamily Combretoideae
Terminalia	Tribe Combreteae	Tribe Combreteae
Pentaptera	*Guiera*	Subtribe Combretinae
Getonia	*Combretum*	*Combretum*
Chuncoa	*Pteleopsis*	*Quisqualis*
Ramatuella	*Thiloa*	*Calopyxis*
Conocarpus	*Quisqualis*	*Meiostemon*
Poivrea	*Calopyxis*	*Thiloa*
	Tribe Terminalieae	*Guiera*
Tribe Combreteae	*Bucida*	*Calycopteris*
Combretum	*Terminalia*	Subtribe Pteleopsidinae
Cacoucia	*Buchenavia*	*Pteleopsis*
Lumnitzera	*Ramatuella*	Subtribe Terminaliinae
Quisqualis	*Anogeissus*	*Terminalia*
	Conocarpus	*Ramatuella*
	Tribe Calycopterideae	*Terminaliopsis*
	Getonia	*Bucida*
	Tribe Laguncularieae	*Buchenavia*
	Lumnitzera	*Anogeissus*
	Laguncularia	*Finetia*
	Macropteranthes	*Conocarpus*
		Tribe Laguncularieae
		Laguncularia
		Lumnitzera
		Macropteranthes

2.2. Previous treatments of *Terminalia*

Terminalia was named by Linnaeus (1767). The genus received its name from the leaves being crowded at the ends of the branchlets, a character which is common to most species. The name *Terminalia* L. has been conserved against *Adamaram* Adans.

Several genera were published which were later to be reduced to synonyms of *Terminalia*: *Adamaram* and *Panel* (Adanson 1763), *Myrobalanifera* (Houttuyn 1774), *Tanibouca* (Aublet 1775), *Kniphofia* (Scopoli 1777), *Aristotelia* and *Resinaria* (Commerson ex Lamarck 1785), *Chuncoa* (Pavon ex A. L. Juss. 1789), *Badamia*, *Myrobalanus*, and *Catappa* (Gaertner 1790-91), *Gimbernatea* (Ruiz & Pavon 1794), *Fatrea* (Jussieu 1804), *Pentaptera* (Roxburgh 1814), *Vicentia* (Allemao 1844), and *Chicharronia* (Richard 1846).

De Candolle (1828), first to define tribal limits in the Combretaceae, was also the first to construct an infrageneric classification of the genus *Terminalia*. He divided the genus into two sections: *Catappa* (J. Gaertner) DC., comprising ten species with winged or strongly compressed fruits; and *Myrobalanus* (J. Gaertner) DC., comprising ten species with wingless, little compressed fruits. Section *Catappa* was clearly based on the genus *Catappa* J. Gaertner (type: *T. bentzoë*), but De Candolle also included *T. catappa*, the type of the genus *Terminalia*. Among the species included in section *Catappa* were four American species, namely *T. tanibouca* (= *T. dichotoma*), *T. januariensis*, *T. fagifolia* and *T. lanceolata* (= *T. fagifolia*).

He based section *Myrobalanus* on *Myrobalanus* J. Gaertner and *Badamia* J. Gaertner, but he also included *Fatraea* Juss. (as *T. fatraea* DC,) and *Pamea* Aublet (as *T. pamea* DC.).

Because De Candolle (1828) based his sections on the degree of compression and wingedness of the fruits, he sometimes separated closely related species, e.g. *T. catappa* and *T. latifolia*, in different sections.

He recognized 35 species, of which 13 were from America. However, five of these thirteen are not Combretaceae and the remaining 8 are now reduced to 6 species.

Don (1832) followed De Candolle's sections. He placed three American species (T. argentea, T. sericea and T. australis) in section Catappa, and two (T. obovata (now = Buchenavia capitata) and T. adamantium in section Myrobalanus.

Bentham (1864), in dealing with Australian species of Terminalia, followed De Candolle (1828) and recognized the same two sections.

Clarke (1878), in Flora of British India, divided the genus Terminalia into four sections:

Sect. I. Catappa Clarke (fruit not winged, ovoid or subcompressed, sometimes showing 2 or 5 obscure lines or ridges).

Sect. II. Pentaptera (Roxb.) Clarke (Fruit with 5 acute subequal wings).

Sect. III. Chuncoa (Pavon ex Juss.) Clarke (Fruit with 3 very unequal wings).

Sect. IV. unnamed (Fruit large, with 2 very broad wings).

Nomenclaturally, section Catappa of Clarke is not the same as section Catappa of De Candolle because it is not based on Catappa J. Gaertner. Clarke included all species of Myrobalanus (including the type T. bellirica) and 3 other species, of which T. catappa is the type of the genus. Hence the two sections recognized by De Candolle, Don and Bentham were amalgamated by Clarke.

Eichler (1867), in dealing with the Brazilian species, divided the whole genus into seven subgenera depending on the fruit characters and the type of inflorescences:

Subgen. I. Myrobalanus Eichler (comprizing Myrobalanus, Badamia and Fatraea). Fruits wingless or with 4-5 angles; inflorescence spicate. It does not occur in America.

Subgen. II. *Catappa* Eichler (including *Pamea* and part of section *Catappa* of De Candolle). Fruits with 2 lateral narrow wings. In this subgenus he included *T. catappa*, *T. tanibouca*, *T. lucida* and *T. australis*.
Subgen. III. *Diptera* Eichler (including some of *Catappa* DC.). Fruits 2-winged; inflorescence spicate. This contained *T. punctata* (= *T. eichleriana*), *T. fagifolia*, *T. argentea*, *T. modesta*, *T. biscutella*, *T. guyanensis*; *T. januariensis*; *T. macroptera* and *T. phaeocarpa*.
Subgen. IV. *Chuncoa* Eichler (comprising *Chuncoa* and *Gimbernatea*). Fruits with 2-5 wings of which are laterally spreading. This included *T. actinophylla*, *T. oblonga*, *T. glabrescence*, *T. brasiliensis* and *T. obovata*.
Subgen. V. *Vicentia* Eichler (based on the genus *Vicentia*). Fruits with 3-5 subequal wings; inflorescences paniculate. This contains the single species *T. acuminata*.
Subgen. VI. *Pentaptera* Eichler (based on the genus *Pentaptera*). Fruits with 4-6 subequal wings; inflorescence paniculate. This is endemic to Asia.
Subgen. VII. *Monoptera* Eichler (including some species of *Pentaptera*). Fruits with 1 dorsal wing; inflorescence paniculate. It is endemic to Asia.

Eichler based his subgenus *Catappa* on *Catappa* J. Gaertner, but also included *T. catappa* as De Candolle had done. In general Eichler's subgenera clearly demonstrate the relationships of the species in the area dealt with, unlike the case with De Candolle's sections.

Engler & Diels (1900) in treating mainly the African members of the genus, introduced an important infrageneric classification in which they divided the genus into twenty sections:

Sect. 1. Myrobalanus (J. Gaertner) DC.

Sect. 2. Eucatappa Engler & Diels

Sect. 3. Circumalatae Engler & Diels

Sect. 4. Stenocarpae Engler & Diels

Sect. 5. Platycarpae Engler & Diels

Sect. 6. Pentaptera (Roxb.) Clarke

Sect. 7. Monoptera (Eichler) Engler & Diels

Sect. 8. Myriocarpae Engler & Diels

Sect. 9. Chuncoa (Pavon ex A. L. Juss.) Clarke

Sect. 10. Vicentia (Allemão) Engler & Diels

Sect. 11. Polyanthae Engler & Diels

Sect. 12. Oblongae Engler & Diels

Sect. 13. Actinophyllae Engler & Diels

Sect. 14. Belericae Engler & Diels

Sect. 15. Complanatae Engler & Diels

Sect. 16. Rhombocarpae Engler & Diels

Sect. 17. Bialatae Engler & Diels

Sect. 18. Dipterae (Eichler) Engler & Diels

Sect. 19. Australes Engler & Diels

Sect. 20. Discocarpae Engler & Diels

In their infrageneric classification, Engler & Diels (1900) considered Eichler's subgenera as sections, but with some changes. For example, subgenus Chuncoa of Eichler was split into 3 sections (Chuncoa, Oblongae and Actinophyllae), and subgenus Catappa was split into 3 sections (Eucatappa, Rhombocarpae and Australes).

Section Eucatappa contained seven species, including the types of both the genus Terminalia and the section Catappa. Sections Myriocarpae, Monoptera and Polyanthae are very closely related and cannot be separated on any single character, as is the case with section Belericae and Myrobalanus.

Exell (1954) in his treatment of the Malaysian species, recognized ten "series" depending on the shape and size of the fruits and leaves. He stated that Engler & Diels's sections were not entirely satisfactory and that the genus should be revised on a worldwide scale before named sections were designated.

Maguire & Exell (1958) published a new section, Pachyphyllum, for a group of five American species (T. virgata, T. opacifolia, T. guiaquinimae, T. quintalata and T. yapacana) which are characterized by having 4-5 merous flowers, 4-5 winged fruits and coriaceous leaves. These taxa, which are somewhat an isolated group, are very closely related to the genus Ramatuella.

Griffiths (1959) divided the African species into two major un-named groups (I and II) depending on the manner of branching and the arrangement of the leaves. Group I contained sections Myrobalanus and Discocarpae, and Group II contained sections Bialatae and Stenocarpae. Section Platycarpae of Engler & Diels fell into both of the major groups.

Capuron (1967, 1973) revised the genus Terminalia in Madagascar. He placed the species into groups according to the growth form, inflorescence structure, leaf margins and the occurrence of domatia. Group A ('Taly') was divided into two un-named subgroups (A1 and A2) depending on the presence or absence of wings on the fruits, while group B ('Fatra') included only species posessing unwinged drupaceous fruits.

Exell (1968), in his studies of the Combretaceae of southern Africa, described three new sections: Abbreviatae Exell (7 species) having leaves in fascicles on spur shoots and spiny branchlets; Psidioides Exell (3 species) characterized by the bark of branchlets peeling off in cylindrical of hemi-cylindric flakes leaving a brown newly exposed surface; and Pteleopsoides Exell (1 species) possessing a fibrous bark, "opposite or subopposite" leaves and a capitulate spike.

All members of sections Abbreviatae and Psidioides were previously placed in section Platycarpae of Engler & Diels. But as mentioned before, members of Platycarpae fall into both Griffiths' major groups. Those falling in group I comprise Exell's section Abbreviatae, and some of those falling in group II comprise his section Psidioides. Exell (1970) recognized another section, Fatrea (Juss.) Exell, based on the genus Fatraea Juss., which was formerly placed in Section Myrobalanus by most authors. Vollesen (1981) proposed the transference of Exell's section Pteleopsoides to the genus Pteleopsis, but the combination has not been made.

Coode (1969a, 1969b, 1973) revised the genus Terminalia in Papua and New Guinea and described several new species but did not recognize sections. Smith (1971) studied the genus in the Pacific islands (Fiji, Samoa and Tonga) and described four new species. He also tried to fit the species rrecognized in his study into Exell's (1954) series. Byrnes (1977) revised the genus in Australia, recognizing 29 species, but no sections were given.

2.3. Previous treatments of Bucida, Ramatuella and Buchenavia

Bucida was named by Linnaeus (1759) and the name has been conserved against Buceras P. Browne (1756). The plant received its name from the shape of the process terminating the spike which resembles a bull's horn. The genus was based on Bucida buceras. De Candolle (1828) described a new species (B. angustifolia) which was later relegated to B. buceras var. angustifolia by Eichler (1867).

Bentham & Hooker (1865) relegated the genus Bucida to Terminalia section Bucida, but Eichler (1867) and later workers have kept it as a separate genus.

Eighteen specific names have appeared under the genus but it has never been revised.

Ramatuella was named by Kunth (1825) after a French horticulturist M. de Ramatuelle. Kunth (1825) originally used the spelling Ramatuela, but the correct spelling has been pointed out by Poiret (1826), De Candolle (1828) and Exell & Stace (1963).

Kunth (1825) based the genus on *Ramatuella argentea*, but he gave no description for the flowers. Eichler (1867) published a new species, *R. virens*. A third species, *R. crispialata* from Brazil, was described by Ducke (1935). Maguire (1953) revised the genus and recognized four species. Exell & Stace (1963) in their revision of the genera *Buchenavia* and *Ramatuella*, recognized six species.

Buchenavia was described by Eichler in 1966. He based the genus on eight Tropical American species which he placed in two un-named groups those with capitate and those with elongate inflorescence. The type species, *B. capitata*, was formerly in the genus *Bucida*.

Ducke (1925, 1935, 1945) presented a great contribution to the systematics of the genus by describing eight new species from Brazil.

By 1963 28 names had appeared under the genus; Exell & Stace (1963) recognized 21 species of these as valid species and described three new ones. (*B. pterocarpa*, *B. acuminata* and *B. pulcherrima*). Three further names have appeared up to 1983.

2.4. Previous studies of taxonomic characters in Terminalia, Ramatuella, Bucida and Buchenavia

The main previous studies on Combretaceae worth mentioning here dealt with leaf, wood and floral anatomy. The greatest contribution to the systematic anatomy of the Combretaceae during the last twenty years was made by Stace (1961, 1963, 1965b, 1969a, 1969b, 1973, 1981), who documented data on the leaf epidermis for 29 species of Terminalia, 15 of Buchenavia, 6 of Ramatuella and 3 of Bucida. But the majority of Stace's research has been concerned with only the leaf epidermis of the genus Combretum. However, he emphasized that further studies of leaf epidermis might elucidate taxonomic difficulties in other parts of the family.

Hooks (1966) studied the wood anatomy of some African species of Terminalia. His results indicated that there is no relationship between the taxonomy and the anatomy of the genus. But it showed that some anatomical features are of taxonomic value between species. Slooten & Gonzalez (1971) described the wood anatomy of Terminalia lucida from America.

Venkateswarlu & Rao (1971) placed Strephonema in a newly constituted monogeneric family, the Strephonemataceae, depending on wood anatomical evidence (differences in characters of vessel elements). But this idea has been rejected by Outer & Fundter (1976), who stated that the wood anatomical differences (particularly number of vessels per square mm) between the genera of Liaguncularieae and the other genera are much greater than those between Strephonema and the other genera of the family.

Rao (1972) studied the anatomy of the woods of 39 species belonging to 15 genera of Combretaceae. Among them were 15 species of Terminalia (of which only T. amazonia was from America), 3 species of Buchenavia (B. capitata, B. oxycarpa and B. fanshawei), Bucida buceras and Ramatuella argentea. He stated that all species examined share common characters such as diffuse-porosity, simple perforation plates, predominantly alternate inter-vascular pitting, semilibriform to libriform fibrous elements, and paratracheal axial parenchyma. However, certain species sometimes show significant differences. He also emphasized that Laguncularieae are the least specialized, Terminalieae the most evolved and Calycopterideae and Combreteae are intermediate.

Lomibao (1973) studied the wood anatomy of 8 species of Terminalia from the Philippines and presented a key to the identification of these taxa, mainly based on the presence or absence of idioblasts and the number of rows of ray cells.

The most important contribution to the wood anatomy of the Combretaceae was made by Van Vliet (1978 & 1979). He described in detail the wood anatomy of all genera (except Meiostemon) of Combretaceae on the basis of 120 samples representing 90 species. Among the taxa studied were 43 species of Terminalia (of which T. acuminata, T. amazonia, T. arbuscula, T. chiriquensis (= T. oblonga), T. dichotoma, T. lucida and T. reitzii are from America), 2 species of Ramatuella (R. argentea and R. virens), 2 of Bucida (B. buceras and B. macrostachya), and 5 of Buchenavia (B. acuminata (= B. sericocarpa), B. fanshawei, B. huberi (= B. grandis), B. kleinii and B. oxycarpa).

He classified the structural variation of vestures in bordered pits, recognizing 2 major types: type A, restricted to Strephonema; and type B, restricted to subfamily Combretoideae.

His results indicated that, although most genera of Combretaceae show a wide overlap in their wood anatomical features, the subfamily Strephonematoideae and subtribe Combretinae are wood anatomically very distinct. His results also showed that the wood anatomy of the subtribe Pteleopsidinae is completely within the range of variation found in the subtribe Terminaliinae. He stated that Laguncularieae cannot be separated wood anatomically from the other genera and suggested a taxonomic status of lower rank.

Phylogenetically Van Vliet (1979) on the basis of wood anatomical evidence considered Strephonema which possesses fibre-tracheids and distinct type of vesturing and parenchyma distribution) as the most primitive, and subtribe Combretinae (which possesses radial vessels and axial vessels of different size classes) as the most derived.

Venkateswarlu & Rao (1970) studied the floral anatomy of 20 species belonging to 9 genera of the subfamily Combretoideae, including 4 species of Terminalia from India and Bucida buceras. Of Engler & Diels' four tribes, they considered the Laguncularieae as the most primitive and the others as more advanced. They based their conclusion on the fact that the Laguncularieae (Lumnitzera racemosa and L. Littorea) possess the highest number (8) of carpellary dorsal bundles in the style and the highest number (3) of sepal traces, while in Terminalieae, Combreteae and Calycopterideae the number of carpel traces is 2 to 5 and the number of sepal traces is one. They also stated that the primitiveness of Laguncularieae is supported by evidence from the wood anatomy.

Venkateswarlu & Rao (1972) published an embryological study of 18 species of Combretaceae, including 6 species of Terminalia from India and Bucida buceras. They mentioned that the taxa studied (except Guiera) showed uniformity in all embryological features. They suggested a separate monogeneric tribe, the Guieraeae (sic), for the genus Guiera. They also stated that the pattern of embryological development in all species studied (except Terminalia chebula) was similar to that in Poivrea as described by Venkateswarlu (1952).

Erdtman (1952) reviewed the palynological literature, mentioning no examples of the subtribe Terminaliinae. There is no published work specifically on Combretaceae pollen (or even on the pollen of a genus of the family), but there are a number of works (regional pollen Floras) that mention the family in passing (Kubitzki 1965, Melhem & Paula 1966, Huang 1967, Maley 1970, Bonnefille 1971, Sowunmi 1973, Guers 1974). All the above works have been based on only light microscopy observations.

Pollen grains of only eight species of Terminalia have been previously studied and only two of them, namely T. fagifolia and T. argentea, were from America. Melhem & Paula (1966) mentioned that the pollen grains of these two species are similar to those in Combretum parviflorum, Eichler (= C. vernicosum), being heterocolporate with psilate ornamentation. Combretum parviflorum and T. fagifolia had been placed in different groups by Mohl (1835) based on the number of colpi, but Mohl's plant was C. parviflorum Reichenb. (= C. micranthum), a totally different species. Kubitzki (1965) described the pollen grains of T. calcicola, Terminaliopsis tetrandra (= Terminalia tetrandra), Poivrea obscura (= Combretum obscurum), Lumnitzera racemosa and Calopyxis subumbellata. Sowunmi (1973), in his studies of Nigerian plants, described the pollen grains of four species of Terminalia (T. avicennioides, T. glaucescens, T. macroptera and T. superba) and one species of Combretum (C. glutinosum), mentioning that the pollen grains are 3-colporate in all species with reticulate ornamentation in the first and third species of Terminalia and in C. glutinosum. But from his Figures it is clear that the pollen grains of all species mentioned are heterocolporate and psilate.

CHAPTER 3

MATERIALS AND METHODS

3.1. Materials

This work was carried out in the herbarium of the University of Leicester (LTR). It was completely based on dried herbarium material. Most of the material used was obtained by loan or gift from American and European herbaria. The herbaria concerned are listed under alphabetical order of the countries concerned:

ARGENTINA - Museo de Botanica y Farmacologia, Buenos Aires (BAF). AUSTRIA - Naturhistorisches Museum, Wien (W). BELGIUM - Jardin Botanique National de Belgique, Meise (BR). BRAZIL - Herbarium Bradeanum, Rio de Janeiro (HB); Centro de Pesquisa Agropecuaria do Tropico Umido, EMBRAPA, Belém (IAN); Herbario da Reserva Ecologia do Instituto Brasileiro de Geografia e Estatistica, Brasilia (IBGE); Instituto Nacional de pesquisas de Amazonia, Manaus (INPA); Museu Botanico Muncipal, Caritiba (MBM); Departamento de Botanica, Museu Nacional, Quinta da Boa Vista, Rio de Janeiro (R); Jardim Botanico do Rio de Janeiro, Rio de Janeiro (RB); Herbario do Estado "Maria Eneyda P. K. Fidalgo", Instituto de Botanica, São Paulo (SP); Departmento de Biologia Vegetal, Funçacão Universidade de Brasilia, Brasilia (UB). COLOMBIA - Herbario Nacional Colombiano, Bogota (COL). CZECHOSLOVAKIA - Universitatis Carolinae Facultatis Scientiae Naturalis Praha (PRC). DENMARK - Botanical Museum and Herbarium, Copenhagen (C). FRANCE - Muséum National d'Histoire Naturelle, Paris (P).

FRENCH GUIANA - Centre O.R.S.T.O.M., Cayenne (CAY). GREAT BRITAIN - British Museum (Natural History), London (BM); Royal Botanic Gardens, Kew (K). GUYANA - Guyana Forestry Commission, Georgetown (FDG). HUNGARY - Botanical Department, Hungarian History Museum, Budapest (BP). MEXICO - Herbario Nacional de Mexico, Mexico (MEXU). NETHERLANDS - Institute of Systematic Botany, Utrecht (U). SWEDEN - Swedish Museum of Natural History (Natuuhistoriska riksmuseet), Stockholm (S). SWITZERLAND - Conservatoire et Jardin botaniques de la Ville de Genève, Genève (G). U.S.A. - Arnold Arboretum and Gray Herbarium of Harvard University, Cambridge (A + GH); John G. Searle Herbarium, Field Museum of Natural History, Chicago (F); Missouri Botanical Garden, Saint Louis (MO); New York Botanical Garden, New York (NY); United States National Herbarium, Washington (US); Department of Botany, University of Wisconsin, Wisconsin (WIS). U.S.S.R. - V. L. Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad (LE). VENEZUELA - Instituto Botanico, Caracas (VEN); Jardim Botanico de Maraciabo, Zulia (VZM). WEST GERMANY - Institut für Algemeine Botanik and Botanischer Garten, Hamburg (HBG); Botanische Staatssammlung, München (M).

The collections in the herbaria of British Museum (Natural History) (BM) and Royal Botanic Gardens, Kew (K) were also studied and several personal visits for this purpose were made. A visit was also made to Italy to study the materials in the herbaria of Universitatis Florentinae, Firenze (FI) and Horti Pisani, Pisa (PI).

The abbreviations of the herbaria mentioned above and indicated parenthetically were used in the citation of specimens throughout this work. Other herbaria cited are: Botanisches Museum, Berlin, W. Germany (B) and Museu Paraense Emilio Goeldi, Belém, Brazil (MG).

More than 4500 specimens of Terminalia, Ramatuella, Bucida and Buchenavia were gross-morphologically studied. Lists of full names of all taxa investigated are given in Appendix 1. Details of all material used in anatomy and pollen morphology in this work are contained in Appendices 2 and 3 respectively. Photographs of the type specimens of the American taxa studied in this investigation are shown in Appendix 4. All American taxa studied in this work are listed in Chapter 9. The lectotypes of species of Terminalia mentioned in Chapter 9 are designated in this work unless otherwise stated, but the lectotypes of Buchenavia and Ramatuella species were previously selected (Exell & Stace 1963, Stace 1971) unless otherwise stated. American specimens of Terminalia, Bucida and Buchenavia seen during this study are listed in Appendix 5.

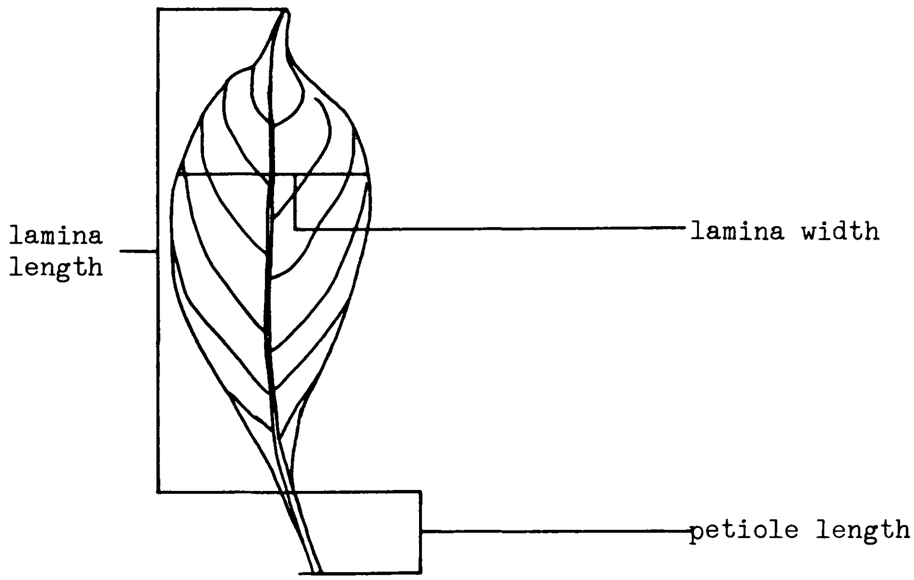
3.2. Methods

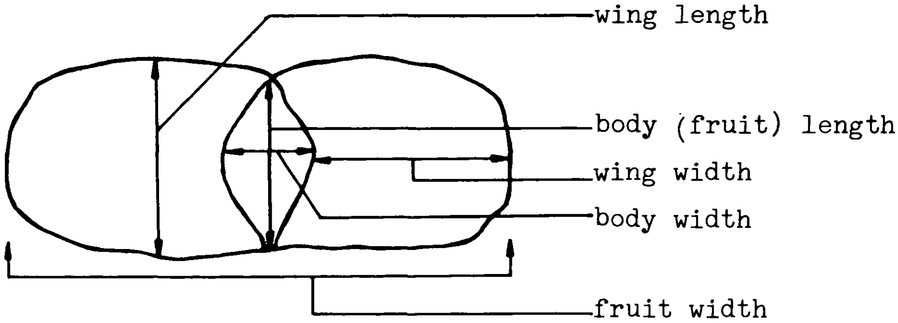
3.2.1. Gross-morphology

Traditional methods were used for gross-morphological information. The measurement involved in the examination of the leaves and fruits are shown in Figure 3/1 A & B. Flowers were softened for microscopical examination by boiling in water for ten minutes and then either directly examined or stored in 70% alcohol for further examination.

3.2.2. Cuticular preparation

Leaves were boiled in water for 30 minutes. A portion from the middle of the leaf was transversely cut to include the primary vein, secondary veins and margin. The portion was then longitudinally cut into 2 parts from the region between the midrib and margin (Fig. 3/1 C). The two parts were soaked in Jeffrey's solution (equal parts of 10% chromium trioxide solution and concentrated nitric acid) overnight at room temperature (the





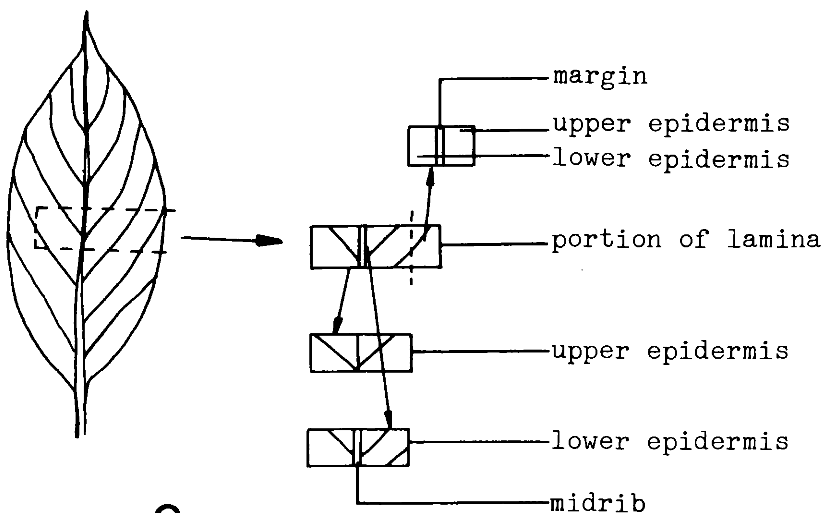


Figure 3/1. Diagrams of leaves and fruits. A and B show measurements involved in the examination of leaves and fruits. C shows portions of leaf macerated.

exact time and dilution depends on the material, but one part Jeffrey's solution and two parts distilled water was suitable for most material). The macerated materials were washed in water 1-3 times (if some cellular tissue remained, the material was remacerated in concentrated solution and rewashed) and then in 70% alcohol. The cuticular membranes were stained with Sudan IV (saturated solution in 70% alcohol) for 20-30 minutes, and then washed twice in water. They were then immersed in 50% glycerol followed by 100% glycerol, and mounted in glycerin-jelly. From each preparation 3 slides were made, one for the upper epidermis, one for lower epidermis and one for the marginal region.

3.2.3. Transverse sections

Leaves were revived by boiling in water for 30-45 minutes, depending on the material. Sections of varying thickness (15-40 µm) were cut with the freezing microtome. Sections were dehydrated in 70% alcohol, stained with Safranin/Fastgreen (Johansen 1940), dehydrated through 95% and 100% alcohol, and mounted in Euparal. Sections were also made of petioles using the same method.

3.2.4. Radiography

Leaves were photographed with x-rays. The apparatus used was a Solus Schall Type F 1947 with a Machlett type AEG 50 x-ray tube. The target was made of copper and the window was 1 mm diameter, made of beryllium.

Leaves were placed on a film (4-12 leaves, depending on the size of the leaves and films) and placed 36 cm from the source of radiation. Very low voltages (10-12 kv) and lengthy exposures of 2.5 minutes at a low current (12 Ma) were used. Films were developed with Kodak Polycon for 4 minutes at 20 C.

3.2.5. Leaf clearings

Whole leaves were cleared by soaking them in 3% sodium hydroxide for 2-3 weeks at room temperature, replacing the solution at intervals. They were then washed several times in water, bleached for 15-30 minutes and washed again. Leaves were stained with 1% aqueous Safranin for 15-20 minutes and washed 2-3 times in water. Cleared leaves were either mounted in glycerin-jelly for later examination or left in water in a petri-dish and photographed immediately by putting the petri-dish containing the leaf (which was held flat by a large microscope slide) directly into the enlarger and projecting on to photographic paper.

3.2.6. S.E.M. preparations

For leaf surface observations, portions of leaves from dried herbarium specimens were mounted on to a stub (10 mm in diameter) using double sided Sellotape. For cuticular observation, cuticular membranes were directly mounted on stubs (after washing in water) and left to dry by evaporation. Stubs were coated with gold for 2 minutes (about 200-300 A^{o} thick). Pollen grains from dried herbarium material or which had previously undergone acetolysis were mounted on stubs using double sided Sellotape and coated with gold. Observations and photographs were made with an ISI-6 Scanning Electron Microscope (Plate 3/1).

3.2.7. Pollen Acetolysis

1. Anthers were removed from flowers of dried herbarium specimens and boiled in 10% potassium hydroxide for 5 minutes.
2. Anthers were macerated by rubbing through a fine screen in a petri dish and flushed with water into a centrifuge tube.
3. Samples were centrifuged and decanted.
4. Samples were washed with glacial acetic acid, centrifuged and decanted.
5. 5 ml of freshly prepared acetolysis mixture (9 parts of acetic anhydride

and 1 part of concentrated sulphuric acid) was added to the residue and stirred with a glass-rod.

6. The centrifuge tubes were transferred to a water bath with boiling water in a fume-cupboard and heated for 3 minutes.
7. Samples were centrifuged and decanted.
8. The debris was washed in distilled water, centrifuged and decanted (repeated 2-3 times).
9. Samples were then either stained with Safranin-glycerine-jelly and mounted on microscope slides for light microscope examination, or dehydrated for SEM examination by passing through 50%, 70%, 90% and 100% ethanol (centrifuging and decanting after each) and then suspended in acetone.
10. Pollen samples were transferred to stubs and coated with gold for SEM observation.

3.2.8. Light microscope observation and illustrations

Light microscope observations were made using a Zeiss microscope equipped with an M35 Zeiss camera. Measurements of the pollen grains were made at x 1000 under oil immersion on unacetolyzed pollen grains. The measurements were based on 20-25 fully developed grains per specimen.

Plate 3/1: ISI-60 Scanning Electron Microscope.

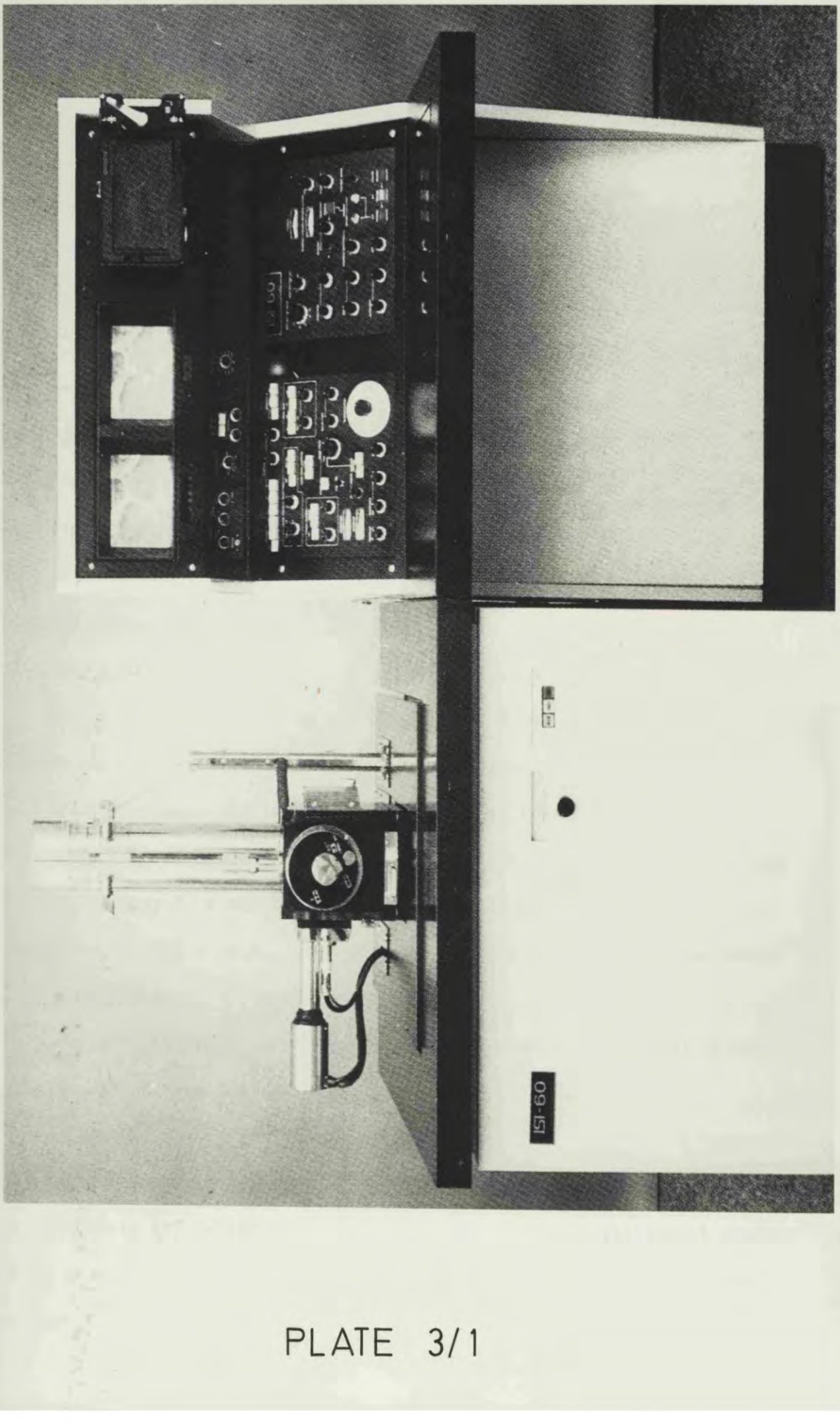


PLATE 3/1

CHAPTER 4

MORPHOLOGICAL DIVERSITY IN *TERMINALIA*, *RAMATUELLA*, *BUCIDA* AND *BUCHENAVIA*

4.1. Vegetative characters

4.1.1. Habit

Most species of American *Terminalia* are small to medium trees, 6-20 m tall, but some are very large (e.g. *T. amazonia* more than 60 m tall) and a few are shrubs, e.g. *T. steyermarkii*, *T. australis* and some plants of *T. triflora*, *T. yapacana* and *T. guaiquinimae*. Most African and Australian species are shrubs or rather small trees, while Asian and New Guinean species are mostly medium to large trees.

All *Ramatuella* species are shrubs or small trees 2-10 (20). *Bucida* are small to medium-sized trees, 5-20 m high. Most species of *Buchenavia* apparently vary from shrubs to small, medium or even large trees ranging from 2 to 20 (45) m high. However, some species are usually large trees, e.g. *B. nitidissima* up to 45 m high.

The growth-form is usually sympodial, but sometimes monopodial as in section *Fatraea* from Madagascar.

Although not absolute, it seems that there is a correlation between the habit and the habitat in most species studied. All species which grow at relatively high altitudes are shrubs or small trees, while most species which grow at low altitudes are tall trees. Also riverine species are shorter than forest species.

4.1.2. Leaves

Leaves of Terminalia provide numerous systematic characters for species recognition. The arrangement, size, shape, texture, base, apex and venation of the leaves show great variation between species and sections and relatively little variation within species. The most important systematic features exhibited by leaves are those associated with leaf architecture and have been dealt with in Chapter 5.

The leaves of Terminalia, Ramatuella, Bucida and Buchenavia are always simple and entire, except in a few species of Terminalia from Madagascar, where they are minutely serrate or shallowly crenate. The largest throughout the genus Terminalia are up to 60 cm long, e.g. T. archipelagi from New Guinea, and the smallest are about 1 cm long, e.g. T. parvula from Africa. Among American species the largest are up to 27 cm long, e.g. T. phaeocarpa, and the smallest are about 3 cm long, e.g. T. triflora. The leaf consistency varies from thinly chartaceous to thickly coriaceous. Section Pachyphullum has the most coriaceous leaves in the genus, e.g. T. guaiquinimae and T. quintalata. The leaves of species which grow at high altitudes are usually small, thickly coriaceous and with revolute margins, e.g. T. guaiquinimae and T. domingensis, while those of species which grow at low altitudes are usually large, chartaceous and with flat margins, e.g. T. dichotoma.

On the sectional level some sections usually possess small-sized leaves, e.g. sections Australes and Actinophyllae from America, Abbreviatae and Fatrea from Africa and Circumalatae from Australia, while other sections usually possess large-sized leaves, e.g. sections Archipelagi, Terminalia and Myrobalanus from Asia and New Guinea.

The majority of the species examined possess narrowly to broadly cuneate leaf bases, but in some species the leaf base is subcordate (e.g. T. catappa), rounded (e.g. T. guaiquinimae), or decurrent (e.g. all members of section Diptera).

Three major types of leaf apex, acute, acuminate and rounded, are found in the species examined. These types are diagnostic characters of many species and sections of Terminalia and Buchenavia. For example, leaf apices of all species of section Pachyphyllum are rounded, whereas they are acute in section Australes and acuminate in section Diptera. The shape of the leaf apex is very constant in most species examined. However, it shows considerable variation in a few species, e.g. T. phaeocarpa has acute, acuminate or rounded leaf apices.

The general shape of the leaves is a variable character in most species, but in some it is very constant. For example, T. australis and T. triflora have elliptic leaves, T. argentea possesses ovate leaves, T. amazonia has obovate leaves, and T. oblonga has oblong leaves. But the majority of species of Terminalia usually possess obovate leaves.

The leaves of herbarium specimens vary in colour from dark green to pale green, but sometimes they are yellowish or brownish. It is not known to what extent the colour of herbarium material is related to that of fresh leaves, but in a number of cases the colour after drying is characteristic of a species or wider taxonomic group. The surface of the leaf is either matt or shiny, but again to what extent this varies in living material is unknown.

The leaves of all species of Ramatuella are remarkbly uniform in most features and show little variation between species. They are very similar to those of section Pachyphyllum of Terminalia in all features.

Throughout the genus Bucida the leaves are also fairly uniform in most characters, but they show significant variation in their size. Although there is a wide range of variation in the size of the leaves of Bucida buceras, the three species of Bucida recognized in this account can be easily identified by their leaf size. The leaves are very small (1 cm long) in B. spinosa, medium (usually less than 10 cm long) in B. buceras and relatively large (12-20 cm long) in B. macrostachya. The leaves of Bucida show similarities with those of section Fatrea of Terminalia from

African and Madagascar.

As in Terminalia characters of the leaves of Buchenavia are invaluable for species recognition, except for the leaf base, which is almost always cuneate and slightly decurrent into the petiole. Most species of Buchenavia have small to medium-sized leaves ranging from 1 to 15 cm long. Some species usually possess large leaves, e.g. B. megalophylla, B. macrophylla, B. pulcherrima, B. nitidissima, B. reticulata and B. guianensis (which possess the largest leaves throughout the genus, up to 40 cm long), and only one species (B. parvifolia) diognostically has small leaves (1-4 cm long). However, B. capitata, B. grandis and B. viridiflora each show considerable variation in most characters of the leaves.

4.1.3. Hairs

Hairs are found in all species examined. They are always simple, nonglandular and compartmented (typical Combretaceious hairs), varying in length from 150 to 1000 µm. Hairs are present on the branchlets, petioles, both surfaces of the lamina, peduncles, rachis, bracts, flowers and fruits. They may be silvery, as in Terminalia argentea and Ramatuella argentea, grey, as in T. guaiquinimae, yellowish-cream as in T. fagifolia and T. eriostachya,reddish, as in section Chuncoa and Vicentia of Terminalia and Buchenavia tomentosa and B. reticulata. The colours of the hairs are of systematic value in many species of Terminalia and Buchenavia, and seem little affected by the process of drying.

The amount of indumentum in most species examined varies with age, but in some species it remains fairly constant. Terminalia argentea, T. steyermarkii, T. eriostachya, T. fagifolia, Ramtuella argentea and Buchenavia tomentosa possess densely sericeous or tomentose leaves. The hairs on the lower surface of the leaves are always more abundant than on the upper surface, except sometimes in T. australis. There is no species with completely glabrous leaves, but there are some with nearly glabrous leaves at maturity, e.g. T. quintalata, T. yapacana, R. virens and Buchenavia nitidissima.

The amount of indumentum on the inflorescences bracts and flowers shows great variation in most species examined, but is of some taxonomic significance in a few species. However, the occurrence of hairs on the style is of considerable systematic value in species of Terminalia. The pubescence of the fruits is of systematic significance in some species of Terminalia and Buchenavia.

4.1.4. Domatia

Two types of domatia, lebetiform and marsupiform were found in Terminalia and Buchenavia, but no domatia were found in Ramatuella and Bucida. The commonest type in Terminalia is the lebetiform while the commonest type in Buchenavia is the marsupiform.

Domatia occur in five species of Terminalia in the new world (T. amazonia, T. acuminata, T. catappa, T. glabrescens and T. latifolia) and in many species of Buchenavia. The presence or absence of domatia on the leaves is of considerable systematic significance in many cases, but in a few species of Buchenavia the presence of domatia on the leaves is not a constant feature.

The domatia usually occur on the primary veins only, as in all species of Buchenavia and most of Terminalia. In T. latifolia and T. catappa domatia are found on the primary, secondary and tertiary veins. In T. pellucida (from the Phillipines) domatia occur at the ends of the secondary veins only.

4.1.5. Petiole

Leaves of Terminalia, Ramatuella, Bucida and Buchenavia are always petiolate (except in a few species of Terminalia from outside America, which are subsessile). The petioles of *Terminalia* vary in length from 0.2 to 10 cm; in American species they do not extend beyond 5 cm and usually they are up to only 3 cm. Most species of *Buchenavia*, *Bucida* and *Ramatuella* similarly have a short or medium petiole up to 3 cm long, but *Buchenavia guianensis* has a very long petiole (up to 7 cm). The petioles vary from cylindrical, e.g. *T. oblonga*, to flattened and slightly winged (e.g. section *Pachyphyllum*).

4.1.6. Glands

One or more glands are usually present on the petioles, but sometimes on the face or margin of the lamina. The position of the glands on the petioles often varies within the same species. It may be near the base or in the middle or at the apex. In American species the glands are always sessile and usually small, except that they are subsessile to shortly stalked in *T. acuminata* (section *Vicentia*). In sections *Myriocarpae* and *Pentaptera* (from Asia) the glands are usually stalked, or otherwise large and very conspicuous, e.g. *T. myriocarpa* and *T. arjuna* respectively.

The glands can also be used as a diagnostic character for *Terminalia pierrei* (from Thailand), which always has two conspicuous glands at the marginal base of the lamina, and for *T. fagifolia* (from America) (Plate 5/1,C Chapter 5), *T. mucronata* (from Thailand) and *T. perrieri* (from Madagascar) (Plate 5/3,D Chapter 5) which have glands along the margins.

In general, however, the taxonomic significance of the glands on the petiole is very limited and should be considered with extreme caution.

4.2. Inflorescence

In all American species of *Terminalia*, *Ramatuella*, *Bucida* and *Buchenavia* the flowers are sessile. In *Terminalia* there are three types of inflorescence: simple elongated spike, branched spike (panicle), and capitate spike. Throughout the genus the majority of the species have long simple spikes. However, some species possess a panicle, e.g. *T. acuminata* (from America) and all species of sections *Myriocarpae* and *Pentaptera* and some of section *Myrobalanus* (from Asia), and some species possess a capitate spike, e.g. *T. eichleriana* and section *Australes* (from America) and *T. capitulata* (from New Guinea). But in America about half of the species possess only slightly elongated (subcapitate spikes).

In *Ramatuella* the inflorescences are subcapitate to slightly elongated, while in *Buchenavia* and *Bucida* they vary from capitate to greatly elongated.

4.3. Bracts

The bracts of *Terminalia*, *Ramatuella*, *Bucida* and *Buchenavia* are very small, varying from 0.5 to 5 mm long. They are linear, lanceolate, narrowly elliptic or oblanceolate in outline with acute, acuminate or obtuse apex. In most species examined the shape and the size of the bracts were found to be of no taxonomic value.

4.4. Flowers (Figure 4/1).

Flowers of Terminalia, Ramatuella, Bucida and Buchenavia provide limited systematic characters at the specific level, although there are a few exceptions. At the generic level, however, Buchenavia (Fig. 4/1 K-M) has flowers characteristically different from those of the other genera.

The flowers of Terminalia and other genera studied are small, usually 3-10 mm long, but in some species of Terminalia from outside America they are up to 15 mm long, e.g. T. archipelagi.

In Terminalia the flowers are usually pentamerous, but sometimes tetramerous as in T. acuminata (section Vicentia) and some specimens of T. guaiquinimae and T. steyermarkii (section Pachyphullum) from America and some species of section Catappa (e.g. T. tetrandra) from Madagascar. In Ramatuella (Fig. 4/1, J) they are usually tetramerous but sometimes pentamerous, and in Buchenavia and Bucida they are always pentamerous. In Terminalia and Ramatuella the flowers are usually hermaphrodite and male on the same plant, but sometimes they are all hermaphrodite as in section Australes. When the plants are andromonoeceous the hermaphrodite and male flowers are usually on the same inflorescence, but occasionally on different inflorescences, and the hermaphrodite flowers usually occur towards the base of the inflorescence. In Ramatuella and some species of Terminalia the hermaphrodite flowers are at the apex of the inflorescence. In Buchenavia and Bucida the flowers are usually hermaphrodite.

As in all genera of Combretaceae (except Strephonema) the ovary is completely inferior and the receptacle is composed of two distinct parts: a lower part which surrounds and is fused with the ovary (and often extends below or above it as in Terminalia from Africa and Buchenavia) and is called the lower receptacle; and an upper part which expands into a bell or cup-shaped upper receptacle terminating in the calyx lobes or teeth.

In Terminalia the general shape and the size of the lower receptacle are of some taxonomic value at species or sometimes sectional levels, e.g. T. quintalata has a long, more or less tubuliform lower receptacle, while T. amazonia (Fig. 4/1 F-H) has a short, ovoid lower receptacle. In Africa most species have the lower receptacle conspicuously extending below the ovary, forming a pedicel-like stalk (Fig. 4/1 A). The lower receptacles of Ramatuella and Bucida are similar to that in Terminalia. But the lower receptacle of Buchenavia is different from the other genera in having a narrow conspicuous pedicel-like apex (Fig. 4/1 K-L).

The upper receptacles of Terminalia, Ramatuella and Bucida are usually campanulate, sometimes infundibuliform, or occasionally cupuliform (e.g. T. acuminata and T. actinophylla), and with deltoid or triangular, erect or reflected calyx lobes. But in Buchenavia they are always cupuliform and broader than long, with scarcely developed calyx lobes. The calyx lobes of Bucida (Fig. 4/1 N) are shorter and less developed than those of Terminalia, but more conspicuous than those of Buchenavia.

Nectariferous disks are well developed in most species, they are circular or lobed, prominent or flattened, and usually 1-3 mm diameter. They are of little taxonomic value.

Petals are absent in the genera Terminalia, Ramatuella, Bucida and Buchenavia.

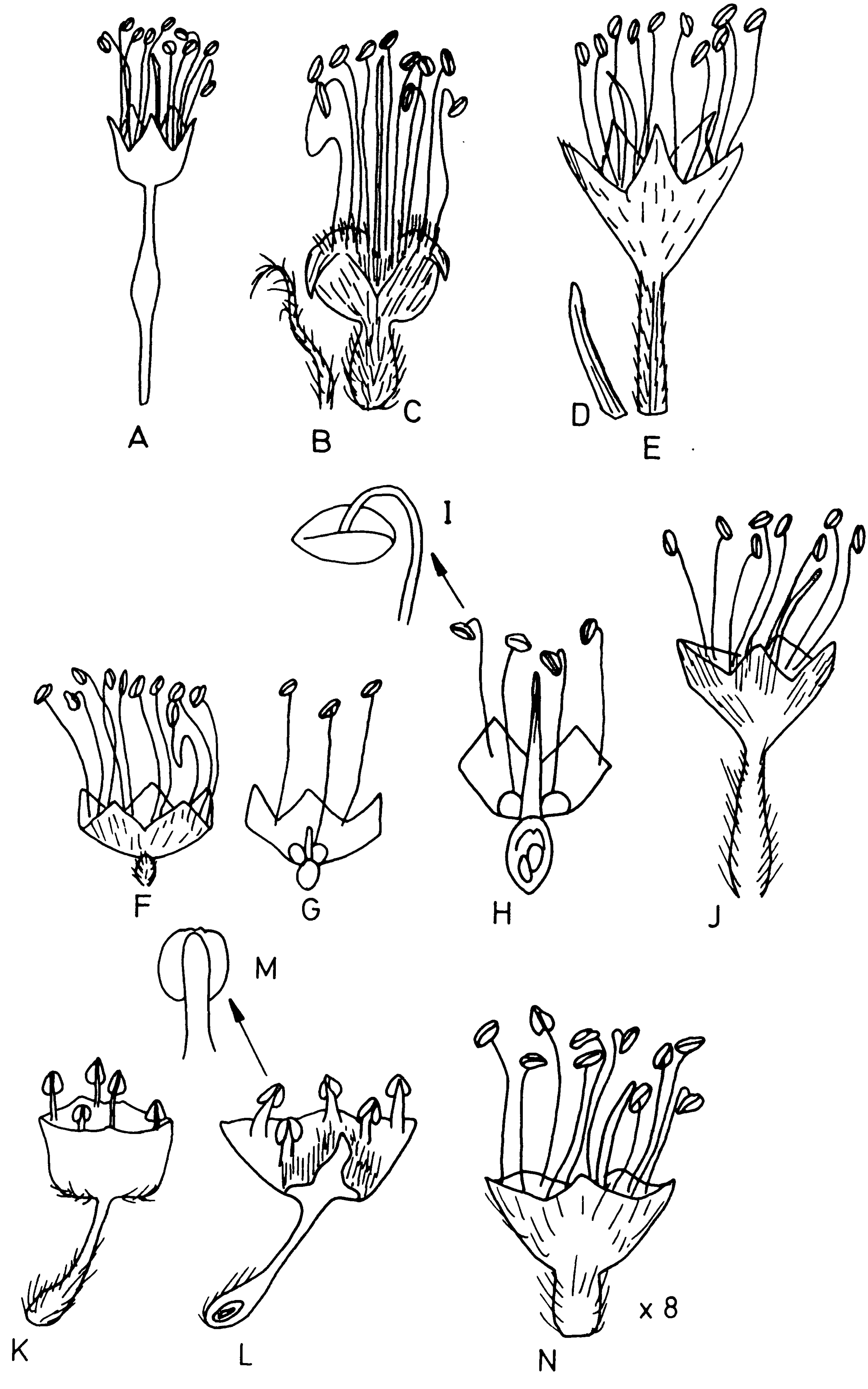
The stamens of Terminalia, Ramatuella, and Bucida are similar. They are glabrous, exserted and usually 3-7 mm long, but in some species of Terminalia (not from America) (e.g. T. grandiflora and T. archipelagi) they are up to 16 mm long. They are always with versatile anthers. In most species of Terminalia the stamens are ten and in two whorls, but in some species they are eight and in two whorls, e.g. T. acuminata. In other species they are sometimes ten and sometimes eight as in T. guaiquinimae and T. steyermarkii (section Pachyphyllum) and several species from Madagascar. In one species T. tetandra (from Madagascar), they are four or occasionally five in one whorl.

In Ramatuella the stamens are usually eight or sometimes ten, while in Bucida and Buchenavia they are always ten. But in Buchenavia the

Figure 4/1: Flowers of Terminalia, Ramatuella, Buchenavia and Bucida.

A. T. macroptera (from Africa) hermaphrodite fl. showing long fusiform lower receptacle (x 4). B and C. T. argentea, B. bract, C. hermaphrodite fl. showing short ovate lower receptacle and reflected calyx lobes (x 7). D.and E. T. yapacana, D. bract, E. hermaphrodite fl. showing tubuliform lower receptacle and erect calyx lobes (x 8). F-I. T. amazonia, F. hermaphrodite fl., G. Section of male fl. showing rudimentary style, H. section of hermaphrodite fl. showing one locule and two ovules (x 8), I. versatile anther (x 40). J. R. argentea showing tetramerous flower (x 8). K-M. Buchenavia capitata, K. fl. showing lower receptacle gradually tapering in a pedicel-like apex, and scarcely developed calyx lobes (x 8), L. section showing short style, and stamens (x 8), M. adnate anther (x 30). N. Bucida buceras showing short calyx lobes (x 8).

Figure 4/1



filaments are always clearly shorter (up to 3 mm long) and thicker than those in the other genera and always with filaments adnate to the anthers.

The styles of Terminalia, Ramatuella and Bucida are usually exserted, but measuring less than 10 mm long. However, in some species of Terminalia from outside America, e.g. T. archipelagi and T. kaernbachii, they are up to 30 mm long. The styles in all species of Buchenavia are characteristically short, usually less than 2 mm long, and included.

4.5. Fruits (Plate 4/1 and Figure 4/2).

The fruits of Terminalia provide excellent systematic characters by which most sections and species can be easily recognized. These characters are:

1 - Shape.

2 - Size.

3 - Number, size, shape and consistency of the wings.

4 - Size, shape, thickness and structure of the body.

5 - Pubescence.

4.5.1. Shape

The fruits of all American species of Terminalia except T. catappa (introduced), T. latifolia and perhaps T. arbuscula (fr. unknown) (the latter two from Jamaica) are distinctly winged. The winged fruits are usually wider than long, being transversely-oblong or -elliptic, rhomboid, triangular or suborbicular, but in T. australis (Plate 4/1 Fig. 22) and other narrowly winged species the fruits are longer than broad. The fruits of T. latifolia (Plate 4/1 Fig. 2) and T. catappa (native of Asia

(Plate 4/1 Fig. 1) are drupaceous and longer than broad.

The fruits of all African (excluding Madagascar) species of Terminalia except T. boivinii are always distinctly winged, but they are usually longer than broad and always with a pedicel-like stalk up to 12 mm long.

In Madagascar, South-East Asia, Melanesia and Australia most of the species possess unwinged drupaceous fruits, while in Tropical Asia about half of the species possess winged fruits and half possess unwinged drupaceous fruits. The drupaceous fruits may be fleshy, leathery, woody or corky, and with a globose, ovoid, ellipsoid, cylindrical or variously compressed shape.

In Ramatuella the fruits are similar to those in section Pachyphyllum of Terminalia. They are almost uniform in shape, with 4-5 radially symmetrical wings (Plate 4/1 Figs. 15-17, Figure 4/2 S).

In Bucida the fruits are uniform in all features. They are always small (up to 10 mm long), unwinged and drupaceous, with no systematic significance at the specific level. But they are characteristic of Bucida, differing from Terminalia, Ramatuella and Buchenavia in having the upper receptacle persistent until the maturity of the fruits (Fig. 4/2 T). However, this character may be found in some species of section Catappa from Madagascar, e.g. T. tetrandra.

The fruits of Buchenavia are always unwinged and drupaceous. However, they show great variation between species. They are similar to those in sections Terminalia, Myrobalanus, Catappa and Fatrea, varying between spherical ovoid, ellipsoid, oblong and cylindrical. The surface of the fruits may be smooth, as in most species, or warted to irregularly ridged, e.g. B. ochroprumna. In some species the fruits are distinctly and regularly angled, e.g. B. oxycarpa. In most species the fruits are without a beak but in some they are with a long straight or curved beak, e.g. B. megalophylla (which has a beak up to 20 mm long), B. oxycarpa (Fig. 4/2 W) B. suaveolens and B. ochroprumna. The fruits are either completely sessile or shortly stipitate. The apices may be rounded, obtuse, acute, apiculate or acuminate.

4.5.2. Size

The fruits of American species of Terminalia vary in their longest axis from less than 1 cm long, e.g. T. yapacana (Plate 4/1 Fig. 13) (the smalles fruits in the genus), to about 11 cm broad, e.g. T. januariensis (Plate 4/1 Fig. 28). At the sectional level, most American sections have medium-sized fruits but some, e.g. section Pachyphyllum, have very small fruits (up to 13 mm long) and others, e.g. section Diptera, have large fruits (up to 11 cm broad) (Plate 4/1 Figs. 28-33). Among the non-American drupaceous taxa section Fatrea (from Madagascar) has the smallest fruits (up to 2 cm long) and section Terminalia has the largest (e.g. T. kaernbachii has the largest fruits in the genus, up to 17 cm long). The fruit dimensions of the non-American winged taxa fall within the range of the American taxa.

In Ramatuella and Bucida the fruits are very small or small, and almost of no taxonomic value at specific level. The fruits of Bucida are up to 1 cm long, while those of Ramatuella are up to 2 cm long. In Buchenavia they are small or medium and of considerable systematic significance at specific level. The smallest are 1-2 cm long (B. parvifolia) and the largest up to 6 cm long (B. guianensis).

4.5.3. Wings (Figures 4/2 H-S)

Most species of Terminalia throughout the world (55%) have unwinged drupaceous fruits (Fig. 4/2 A-G). In the species which have distinctly winged fruits, the wings are usually 2 (Fig. 4/2 H-K) but they may be 3, as in T. acuminata (Plate 4/1 Fig. 9 and Fig. 4/2 L-M), T. eichleriana (Plate 4/1 Fig. 10), T. triptera; 3 but 2 of them rudimentary, as in T. paniculata; 4, as in T. guaiquinimae and T. polyantha (Fig. 4/2 N-O); 5, as in T. quintalata (Plate 4/1 Fig. 14), T. yapacana and all species of section Pentaptera (Fig. 4/2 R); or 5 but 3 of them rudimentary, as in section Chuncoa (Plate 4/1 Figs. 7 & 8 and Fig. 4/2 P-Q).

In length the wings of American species vary from 6 mm, e.g. *T. yapacana* and *T. eichleriana*, to 40 mm, e.g. *T. valverdeae* (Plate 4/1 Fig. 30), but in African species the wings are often much longer, e.g. *T. macroptera* up to 10 cm long. Also the width of the wings may vary from 3 mm, as in *T. australis* (from America) (Plate 4/1 Fig. 22), to 50 or 60 mm, as in *T. januariensis* (from America) and *T. platyptera* (from Australia).

All species of *Ramatuella* possess distinctly winged fruits. The number of wings varies from 4 to 5 (but usually 5) within the same species. In shape and size the wings show considerable taxonomic significance, the shortest being 1-5 mm long (*R. argentea*) and the longest up to 20 mm long (*R. crispialata*). They are either pointed (triangular) or rounded, and with an entire or crispéd margin.

In *Bucida* and *Buchenavia* wings are absent (Fig. 4/2 U-Z).

4.5.4. Body

Characters of the body are of taxonomic value at specific level. The body of fruits of American species of *Terminalia* is usually narrower than the wings but in few species the body wider, e.g. *T. australis* (Plate 4/1 Fig. 22), *T. dichotoma* and some specimens of *T. lucida*. The body varies in shape from rounded, e.g. *T. argentea*, to elliptic, e.g. *T. januariensis*, or fusiform, e.g. *T. guyanensis* (Plate 4/1 Fig. 29). In most species the body bulges on either one or both surfaces or is flat on both surfaces. In a few species the body is characteristically keeled, e.g. *T. valverdeae*. In some species the body is very small or inconspicuous, e.g. *T. eichleriana*, *T. actinophylla* and all species of section *Pachyphyllum*. The body may be highly sclerenchymatous and very hard to cut in section as in most species of section *Diptera* or slightly sclerenchymatous and very easy to cut in section as in sections Chuncoa, Pachyphyllum and Chicharronia (Plate 4/1 Figs. 23-27).

In Ramatuella the body is very small or inconspicuous, slightly sclerenchymatous and easy to cut through. It is uniform throughout the genus. As mentioned before, the fruits of Bucida are of no taxonomic value at specific level.

In Buchenavia the body of the fruits of most species is highly sclerenchymatous and hard to cut through but in some species it is slightly sclerenchymatous, e.g. B. ochroprumna and some specimens of B. suaveolens. The endocarp may be variously furrowed, as in most species, or ridged or angled or occasionally narrowly winged. In B. guianensis the body possesses 6 distinct longitudinal angles but 3 of them are stronger than the other 3. However, in some species, e.g. B. reticulata and B. suaveolens, the endocarp is very variable in shape.

4.5.5. Pubescence

In most species of Terminalia the fruits when young are pubescent but become glabrous after full maturity or when they become very old. However in some species, e.g. T. guyanensis, T. januariensis and T. dichotoma the fruits are essentially glabrous and in others the fruits always remain pubescent, e.g. T. fagifolia and T. argentea.

In Ramatuella and Bucida the pubescence of the fruits is of no systematic value, but in Buchenavia it is of considerable systematic significance. For example, B. capitata always has glabrous fruits, while the closely related B. kleinii always has puberulous fruits. However, in a few cases, e.g. B. grandis, the fruits may vary from densely pubescent to glabrous within the same species.

Figure 4/2: Fruits of Terminalia, Ramatuella, Bucida and Buchenavia. All natural size except P and Q (x 2), S (x 4) and T(x 6).

A-C. T. catappa, A. fruit showing 2 angles, B. section, C. seed. D-E. T. sulcata, D wingless fruit, E section, F-G T. fatraea F. fruit, G Section showing five angles. H-I T. sericea showing two long wings. J-K. T. argentea showing two broad wings. L-M. T. acuminata showing 3 wings. N-O T. polyantha showing 4 wings. P-Q T. amazonia showing five unequal wings. R. T. arjuna showing 5 equal wings. S. R. argentea showing 5 wings. T. Bucida buceras showing unwinged drupaceous fruit with persistent calyx. U-Z. Buchenavia, U-V. B. nitidissima showing rounded apex. W-X. B. oxycarpa showing beak, Y-Z. B. ochroprumna showing irregular ridges.

Figure 4/2

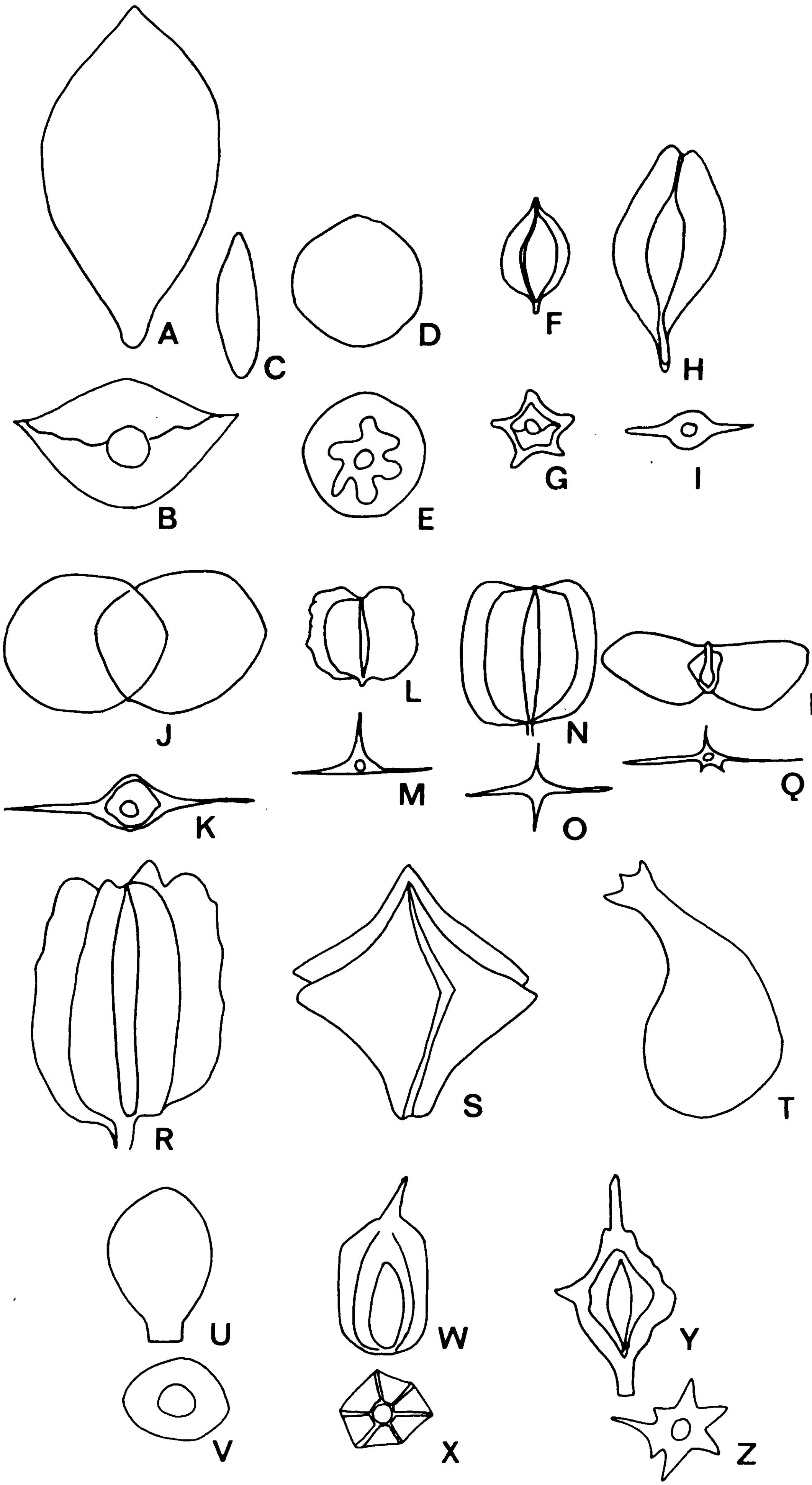


Plate 4/1: Fruits of Terminalia and Ramatuella.

1. *T. catappa* 2. *T. latifolia* 3. *T. dichotoma* 4. *T. lucida*
5. *T. oblonga* 6. *T. bucidoides* = *T. oblonga* 7. *T. amazonia*
8. *T. glabrescens* 9. *T. acuminata* 10. *T. eichleriana*
11. *T. fagifolia* 12. *T. actinophylla* 13. *T. yapacana*
14. *T. quintalata* 15. *R. crispialata* 16. *R. virens* 17. *R. argentea*.
18. *T. uleana* 19. *T. reitzii* 20 & 21 *T. triflora* 22. *T. australis*
23 *T. chicharronia* subsp *chicharronia* 24. *T. chicharronia* subsp *orentensis* 25. *T. chicharronia* subsp. *domingensis* 26. *T. chicharronia* subsp. *neglecta* 27. *T. eriostachya* 28. *T. januariensis*
29. *T. guyanensis* 30 *T. valverdeae* 31. *T. phaeocarpa* 32 *T. kuhlmanii*
33 *T. argentea*.

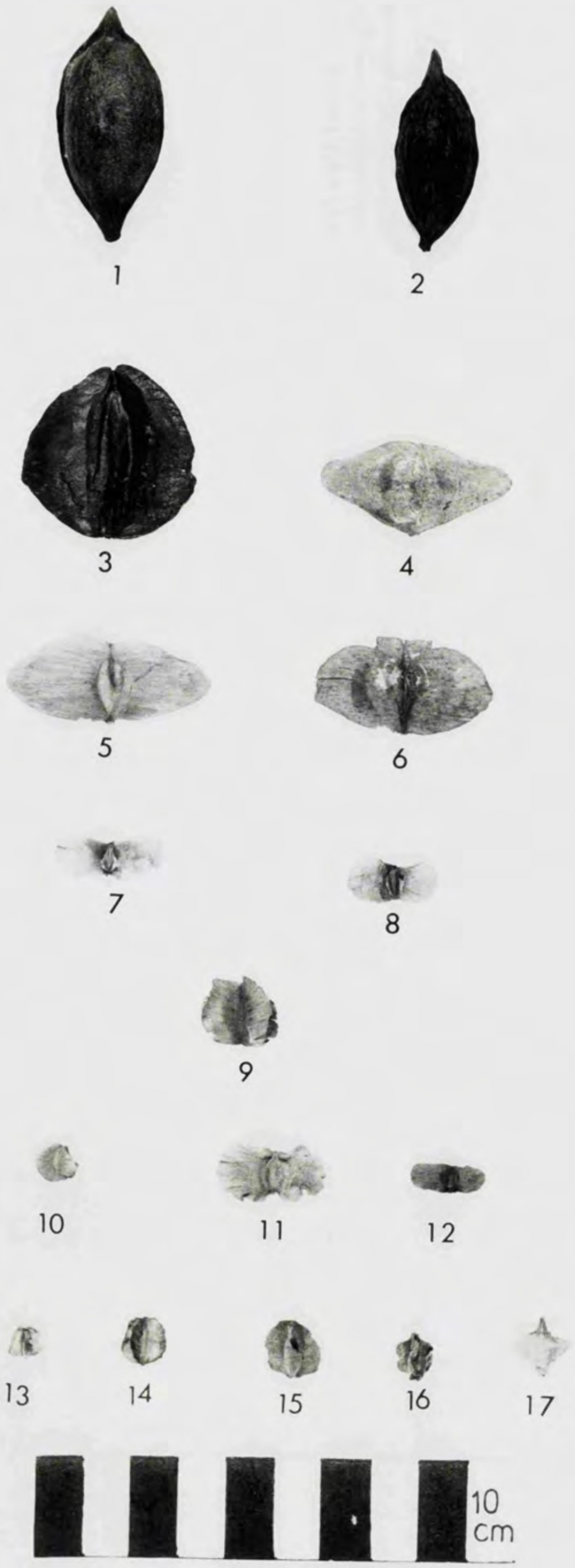


PLATE 4/1

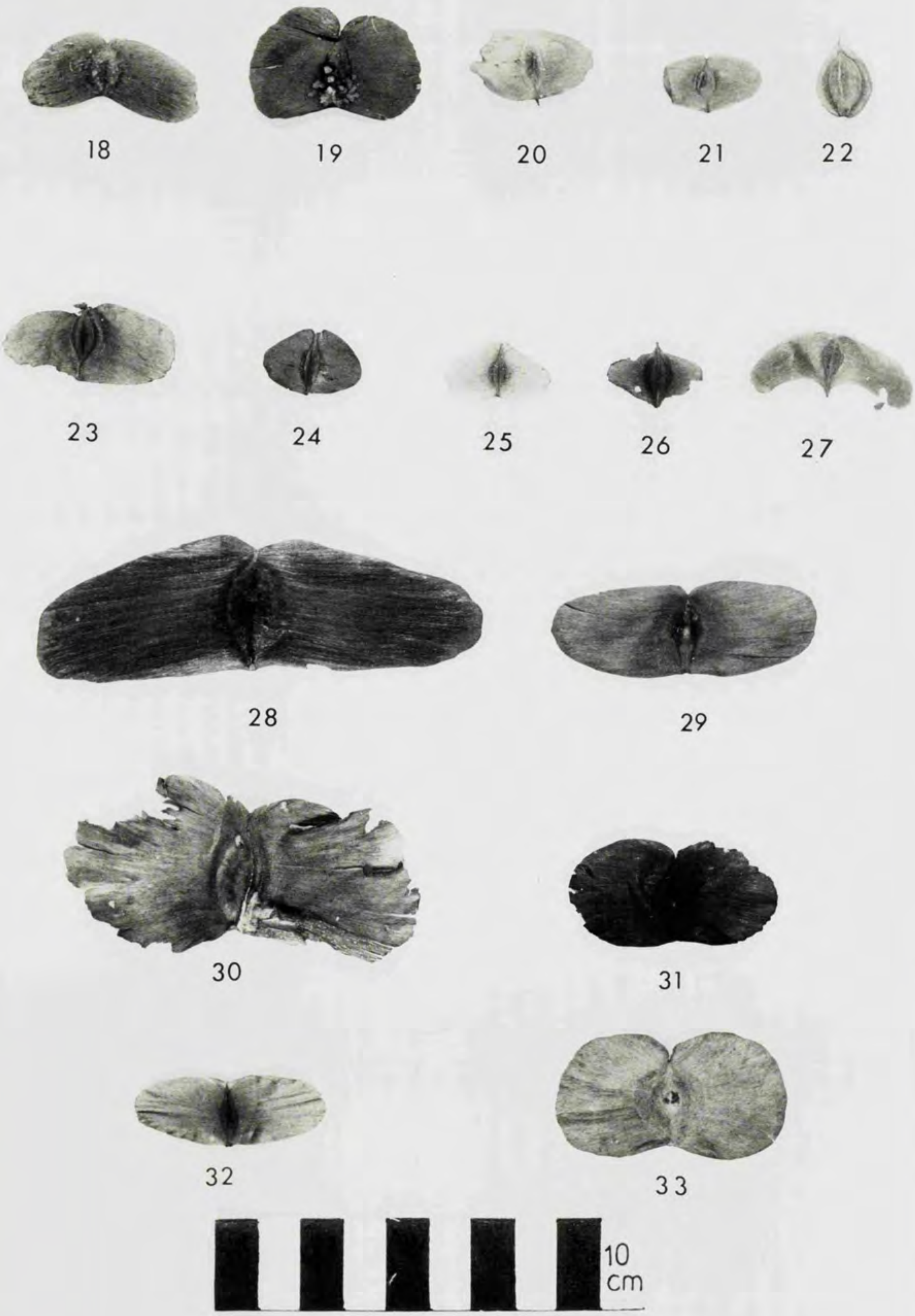


PLATE 4/1

CHAPTER 5

LEAF ARCHITECTURE

5.1. Introduction

Leaf architectural characters provide valuable taxonomic data which can help in understanding and classifying the variation in various groups of plants. Venation patterns, which are the most conspicuous features of the leaves, have long been neglected in taxonomic and descriptive studies. Several authors have recently attempted to employ leaf architectural data for studying evolutionary trends and relationships (Hickey & Wolf 1975; Doyle & Hickey 1976; Hughes 1976; Rury & Dickison 1977).

This study was undertaken to present a description of venation patterns in the Combretaceae with especial reference to *Terminalia*, *Ramatuella*, *Buchenavia* and *Bucida*, and to attempt to determine their taxonomic and phylogenetic value. Opportunity was also taken to test the value of X-ray radiography in studying leaf venation patterns.

5.2. Recent leaf architectural studies in plant taxonomy

Early studies concerning venation were generally restricted to the study of vein histology in a single genus or species (Foster 1950 ; Pray 1954, 1955a, 1955b, 1955c). A literature review concerning the ontogenetic aspects of venation has been given by Foster (1952). He discussed the importance of the study of foliar venation of angiosperms and emphasized the need for investigating more species before relating the venation pattern to phylogeny.

Melville (1969) presented a hypothesis that the leaf venation patterns of flowering plants provide evidence suggesting the origin of angiosperms from Glossopteris and its allies. Alvin (1970) suggested parallel evolution in leaf venation patterns in Glossopteris and angiosperms as an alternative view of angiosperm origins.

Four ranks of leaf organization were suggested by Hickey (1971) from a study of the comparative morphology of recent dicotyledonous leaves, and developed by Hickey & Doyle (1972). These ranks can be outlined as follows:

First rank - leaves whose intercostal areas are not uniform, and whose secondaries and higher order veins follow an irregular course.

Second rank - leaves with regular secondaries and uniform intercostal areas but with random tertieries.

Third rank - leaves with percurrent venation but with irregular areolation.

Fourth rank - leaves whose areolation is regularly organized.

These ranks were applied to the elucidation of phylogenetic relationships by Doyle & Hickey (1976) and Hickey (1977) (Fig. 5/1).

Until Hickey's (1973) classification there was no standarized system of leaf architecture classification. Hickey (1973) defined the main types of venation pattern in dicotyledonous leaves, later (Hickey 1979) developed his system to include a classification of compound leaf configuration and details of tooth architecture. The importance of Hickey's classification scheme in evolutionary studies has been stressed by Dilcher (1974). But Melville (1976) did not accept Hickey's terminology for venation types and presented an alternative system for all flowering plants and gymnosperms. Despite this objection to Hickey's classification the latter has now become widely accepted (Jones 1980).

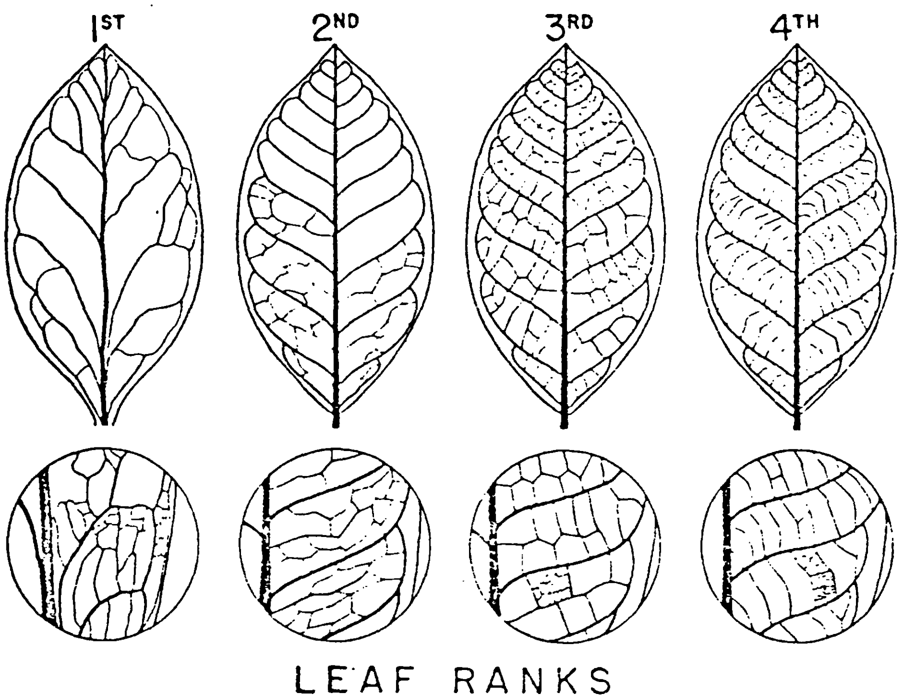


Fig. 5/1: Levels of increasing regularity of venation, or leaf ranks of dicot. leaves (Hickey 1977).

Several attempts have been made to investigate the evolutionary significance of the leaf architectural features in the woody dicotyledons (Hickey 1971, 1977; Hickey & Doyle 1972; Hickey & Wolfe 1975; Doyle & Hickey 1972, 1976; Wolfe, Doyle & Page 1975; Hughes 1976). Rury & Dickison (1977) studied venation patterns of the genus Hibbertia (Dilleniaceae) and discussed their taxonomic and phylogenetic value. They also attempted to present an evolutionary hypothesis for the genus based on leaf architectural characters.

Most taxonomists, morphologists, anatomists and paleobotanists use cleared leaves to study the finest details of leaf venation. X-ray radiography has rarely been used for this purpose (Simola 1968; Jones 1980). The advantages of this technique over clearing technique have been discussed by Jones (1980). She also discussed the significance of leaf architectural characters in the taxonomy of Garcinia (Clusiaceae) and its related genera and suggested several evolutionary trends concerning leaf architecture in the genera of that family.

5.3. Terminology

I have followed the terminology of Hickey (1973). The terms used in the description of venation types are illustrated in Figure 5/2.

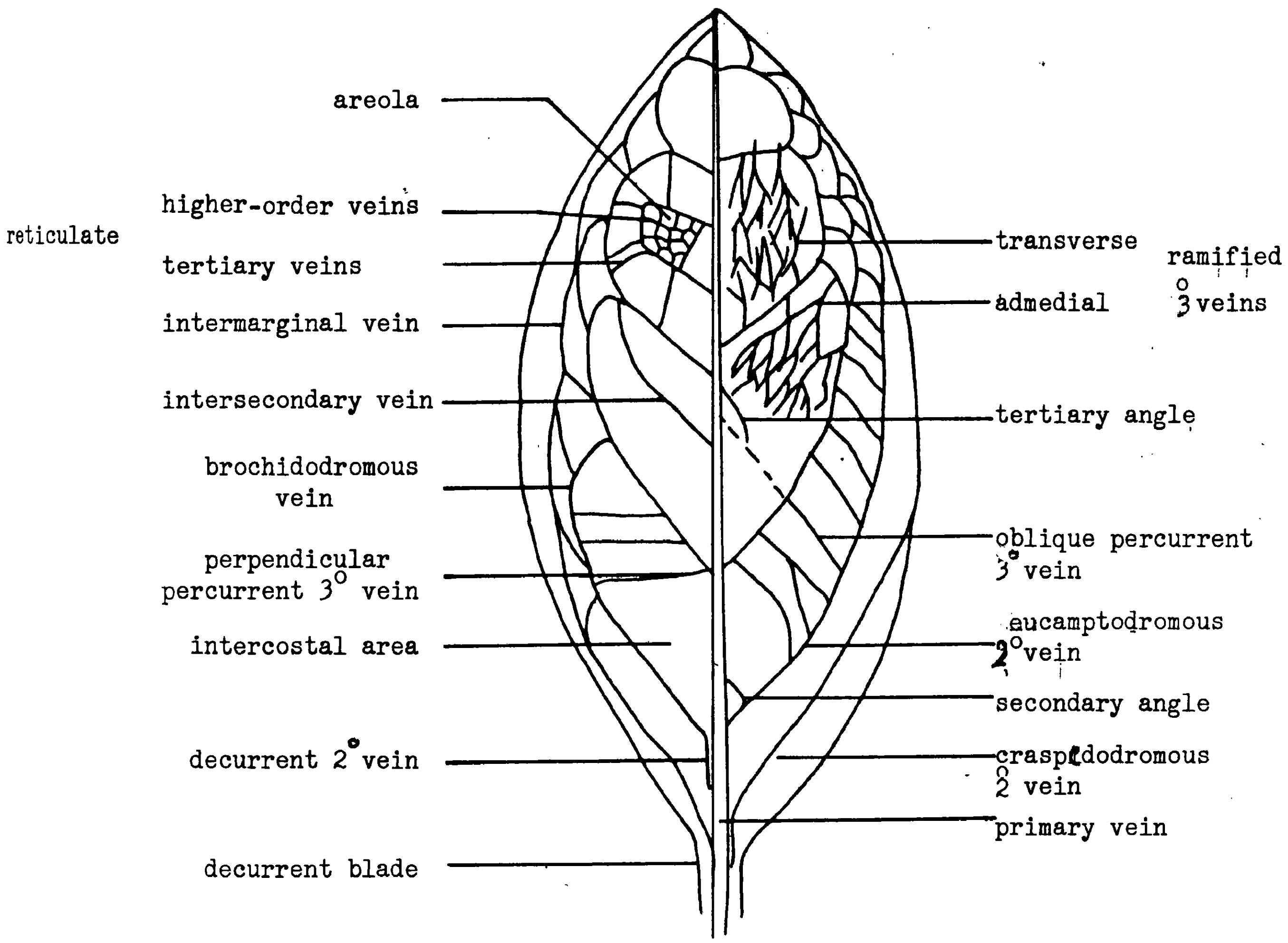


Fig. 5/2: Explanation of terms used in the description of venation patterns of Combretaceous leaves.

5.4. Results

The great diversity of the leaf venation patterns present in the genus Terminalia and in the other genera of Combretaceae can be conveniently grouped into six basic types. This is mainly based on: (1) thickness, course and behaviour of the secondary veins; (2) differentiation and regularity of the tertiary venation; and (3) development and organization of higher-order venation. These types are:

Type I. Irregularly brochidodromous (Fig. 5/3 A and B).

Primary veins flattened and often composed of more than one strand near its base. Secondary veins relatively fine to hair-like, usually irregularly brochidodromous or sometimes cladodromous mixed with brochidodromous, partly obscured by their immersion in the leaf tissue, (hyphodromous sensu Hickey 1973), decurrent upon the primary vein and divergent at variable acute angles. Intercostal areas irregular in shape and size and not supported by obvious intersecondary and tertiary veins. Tertiary veins if present very poorly developed and not distinct from the secondary veins. Higher-order venation and areolation lacking.

This type has been found in Terminalia, Lumnitzera and Macropteranthes.

Type II. Weakly brochidodromous (Fig. 5/3 C, D and E; 5/4A; 5/5 E and G and plates 5/1 A and D; 5/3 C).

Primary veins slightly raised, composed of one compact strand. Secondary veins fine to hair-like or moderate, weakly (not prominently) brochidodromous, slightly irregular in course and usually decurrent upon the primary veins, sometimes irregularly branched and usually repeatedly looped "festooned brochidodromous" by Hickey & Wolfe (1975). Intercostal areas of slightly irregular shape and size and supported by several intersecondary and tertiary veins. Tertiary veins admedially and/or transversely ramified or randomly reticulate, sometimes not well differentiated. Higher-order venation usually indistinct, and areolation incomplete and/or imperfect with freely terminating veinlets, or areolation sometimes lacking.

This pattern of venation has been encountered only in Terminalia, Ramatuella, Bucida and some Laguncularia.

Type III. Brochidodromous (Fig. 5/4 B; 5/5 A, C and K and Plates 5/2 B; 5/3A; 5/4 B; 5/5C; 5/6C; 5/7 H and I).

Primary veins usually prominently raised, composed of one solid strand. Secondary veins moderate or thick, with straight or sometimes sinuous course, regularly and often prominently brochidodromous; intersecondary veins occasionally present. Intercostal areas of regular shape and size. Tertiary veins well differentiated and strongly developed, orthogonally or randomly reticulate, or sometimes weakly percurrent or occasionally ramified. Higher-order venation usually distinct, but if indistinct then orthogonally arranged; highest order venation sixth to seventh; areolation usually well developed and orientated but sometimes incomplete/ and/or imperfect and radomly arranged; freely ending veinlets present or not.

This type of venation has been seen in many species of Terminalia, Buchenavia, Combretum, Calopyxis and Pteleopsis, and some species of other genera.

Type IV. Eucamptodromous-Brochidodromous (Fig. 5/4 E and Plate 5/7A and E).

Primary veins moderate to stout, composed of one solid and prominent strand. Upper secondary veins usually brochidodromous and lower secondary veins eucamptodromous intersecondary veins present. Intercostal areas of regular shape and size. Tertiary veins consistent in course, weakly percurrent or the lower ones percurrent and the upper ones reticulate. Higher-order venation distinct or sometimes indistinct with 4°, 5° or 6° veins, usually randomly arranged; areolation imperfect and/or incomplete, randomly orientated; freely ending veinlets common.

Most species of *Terminalia*, *Buchenavia*, *Combretum*, *Thiloa* and *Quisqualis* possess this type of venation.

Type V. Eucamptodromous (Fig. 5/4 C, F and ; 5/5 B, H and J and plates 5/1 B; 5/2 A; 5/3 B; 5/5 D and E; 5/6A; 5/7 D, F And G).

Primary veins moderate to stout, composed of one prominent strand. Secondary veins moderate or thick, eucamptodromous often following a uniform curved course, but sometimes abruptly curved or straight, gradually curving apically towards the margin, occasionally branching above midway, or ascending along the margin, mostly connected to the superadjacent secondary by a series of percurrent tertiary veins; intersecondary veins rarely present. Intercostal areas of regular shape and size. Tertiary veins always percurrent, regular, oblique or perpendicular to the primary vein. Higher-order venation distinct, with 4^{o}, 5^{o} or 6^{o} veins, usually orthogonally reticulate; areolation well developed or imperfect, orientated, with or without freely terminating veinlets.

This type is common in *Terminalia*, *Buchenavia*, *Combretum*, *Calycopteris*, *Anogeissus*, *Finetia* and *Strephonema*.

Type VI. Craspidodromous

Primary veins moderate, slightly to prominently raised, composed of one solid strand. Secondary veins, their branches, or a few strongly developed tertiary veins running directly to the margin; secondaries of moderate thickness, and straight or curved in course; intersecondary veins usually lacking. Intercostal areas regular in shape and size. Tertiary veins percurrent or randomly reticulate. Higher-order venation distinct; 4^{o} veins orthogonally or randomly arranged; areolation well developed or imperfect, random or orientated.

This type of leaf venation occurs only in two sections of the genus *Terminalia* (*Catappa* and *Actinophyllae*).

This pattern of leaf venation can be divided into two subtypes.

Subtype A. Semicraspidodromous (Plates 5/4 A; 5/5 A).

This pattern of venation is associated with a serrate, subserrate or crenate leaf margin and with the brochidodromous venation type. Secondary veins of moderate or fine thickness, usually curved, branching just within the margin, one branch going to the margin and the other joining the superadjacent secondary; intersecondary veins occasionally present. Tertiary veins randomly reticulate or weakly percurrent. Higher-order venation distinct or not, usually randomly organized.

This subtype is found only in few species of *Terminalia* section *Catappa*

Subtype B. Mixed craspidodromous (Fig. 5/4 D and Plate 5/1 C).

This venation pattern is associated with an entire leaf margin and eucamptodromous venation. Secondary veins of moderate thickness, often straight in course, some, (particularly the lowers) and some of the strongly developed tertiary veins running to the margin, the rest of the secondaries eucamptodromous; intersecondary veins lacking. Tertiary veins always regularly percurrent. Higher-order venation distinct; 4^{o} veins usually orthogonally organized.

This subtype of venation is found only in section *Actinophyllae* of *Terminalia*.

5.5. Discussion

Vein architecture in *Terminalia*, *Ramatuella*, *Buchenavia* and *Bucida*

All the six types of leaf venation recognized here are found in the genus *Terminalia* (Table 5/1). Type I, which may be the least specialized type in the genus and in the whole family, occurs in few species of

Table 5/1: Distribution of venation types among genera of the Combretaceae.

± = occasionally

GENUS	VENATION TYPES I	II	III	IV	V	VI
Strephonema					+	
Combretum			+	+	+	
Quisqualis			±	+		
Calopyxis			+			
Meiostemon			+	±		
Thiloa			+	+	+	
Guiera				+	+	
Calycopteris					+	
Pteleopsis			+	+	+	
Terminalia	+	+	+	+	+	+
Ramatuella		+				
Bucida		+				
Buchenavia			+	+	+	
Anogeissus					+	
Finetia					+	
Conocarpus			+			
Laguncularia		±	+			
Lumnitzera	+					
Macropteranthes	+					
Dansiea		±	+			

Terminalia section Catappa (e.g. T. Monoceros (Figure 5/3 A) and T. divaricata but it is more characteristic of Lumnitzera and Macropteranthes.

The weakly brochidodromous venation pattern designated as Type II occurs in five sections of Terminalia (Table 5/2) and it is characteristic of Ramatuella (Figure 5/3 D), Bucida (Figure 5/3 E) and Terminalia sections Pachyphullum (Figure 5/4 A) and Fatrea. This type of venation which is slightly more specialized than the type I venation, has some advanced characters, for example the development of marginal ultimate venation as in T. quintalata, T. guaiquinimae (Plate 5/1 D) and Bucida buceras, the presence of one or more incomplete intermarginal veins as in T. yapacana (Plate 5/1 A) and the tendency for the secondary veins to diverge at wide acute angles as in Ramatuella virens. The venation patterns in Ramatuella are very similar or identical to that in Terminalia section Pachyphyllum whereas the venation patterns in Bucida are similar to that in Terminalia section Fatrea, or to that in some species of section Catappa (for example T. arosterata Figure 5/3 C) with respect to their tertiary venation.

Type III venation is the commonest pattern in the family (Figure 5/6); it occurs in ten out of the twenty genera examined (Table 5/1 and Figure 5/6). It is also very common among species of Terminalia (Table 5/3 and Figures 5/7, 5/8) and Buchenavia (Table 5/4), for example Terminalia chicharronia (Figure 5/4 B) and Buchenavia capitata (Plate 5/7 H and I). Good examples can also be found in species of Combretum and Calopyxis (Plates 5/3 A, 5/6 C).

Type IV venation is the commonest type in the genera Terminalia (Table 5/3 and Figure 5/8) and Buchenavia (Table 5/4). Good examples can be found in T. argentea (Figure 5/4 E) and B. fanshawei. This type is also common in other genera of Combretaceae such as Combretum, Quisqualis, Thiloa and Pteleopsis. Venation patterns of Types IV and III can be seen in the same species, for example Terminalia oblonga, T. januariensis and Buchenavia grandis. Also Types IV and V venation can be seen together in species such as Terminalia latifolia, T. phaeocarpa and Buchenavia reticulata.

Most of the Asiatic genera and species of Combretaceae have eucamptodromous (Type V) venation. In addition the eucamptodromous venation type is widely distributed among America, Africa and Australian genera of Combretaceae (Table 5/1). It is characteristic of Strephonema. Good examples are found in Terminalia amazonia (Plate 5/1 B) and T. acuminata (Plate 5/2 A) and Buchenavia congesta and B. pallidovirens (Plate 5/5 D) from America; Terminalia arjuna (Plate 5/7 D) and T. myriocarpa (Figure 5/4 C) from Asia; and T. sericocarpa (Plate 5/3 B).

Type VI (craspidodromous) venation is restricted to the genus Terminalia. Mixed craspidodromous venation (subtype VI B) is the most specialized pattern of venation in the entire family. It occurs in Terminalia fagifolia (Figure 5/4 D and Plate 5/1 C), and some of T. eichleriana and T. mucronata. The semicraspidodromous venation (subtype II a) occurs in some species of section Catappa for example T. subserrata (Plates 5/4 A and 5/5 A) and T. bentzoe. This type of venation is considered less specialized than the subtype VI B with respect to the tertiary and higher-order veins.

Vein architecture and taxonomy

Despite the wide variation in the degree of regularity of leaf venation among taxa of Terminalia and other genera of Combretaceae, vein architecture is more or less a constant character at the specific level and to some extent at the sectional and generic levels. However, two different species may have the same venation pattern, even if they are very remote from each other in both taxonomic and geographical senses. For example the American Buchenavia congesta has the same vein architecture as the Australian Terminalia sericocarpa, and sometimes in the same species, for example T. dichotoma, T. calamansani and Buchenavia grandis, more than one pattern of venation can be found.

Most species of Terminalia and Buchenavia can be easily identified by their characteristic basic venation types. In Terminalia amazonia,

T. fagifolia, T. eriostachya, T. chicharronia, T. subserrata, Buchenavia suaveolens and B. pallidovirens it is a major taxonomic character. Finer details of the venation pattern also provide useful taxonomic characters for the identification of species or subspecies. For example the two closely related species Terminalia amazonia and T. oblonga, which are distributed in the same geographical area, can be separated by their tertiary veins which are perpendicularly percurrent in T. amazonia and randomly reticulate or weakly percurrent in T. oblonga.

The four subspecies of Terminalia chicharronia can be separated by the following key:

1. Tertiary veins randomly reticulate
    2. Higher-order veins distinct from each other; areolation well developed and orientated ....subsp. chicharronia
    2. Higher-order veins indistinct from each other; areolation imperfect and random ....subsp. orientensis
1. Tertiary veins weakly percurrent or orthogonally reticulate
    3. Tertiaries weakly percurrent.....................subsp. domingensis
    3. Tertiaries orthogonally reticulate...............subsp. neglecta

However, the degree of organization of higher-order venation, the occurance of veinlets, and the number and shape of veinlets in the areoles may vary within the same species. For instance all the three types of areolation (incomplete, imperfect and well developed) can be seen in Terminalia argentea, and from 0-3 veinlets (simple, or branched once, twice or 3 times) can be seen in many species of Terminalia and other genera. This considerable architectural variation, which might be the result of environmental factors, makes the higher-order venation and the veinlets of little taxonomic value.

The taxonomic importance of leaf architecture at the sectional level is clear in Terminalia (Table 2). From 26 sections studied fourteen have

Table 5/2: Distribution of venation types among sections of the genus *Terminalia*   ± = occasionally

SECTION	VENATION TYPES I	II	III	IV	V	VI
Abbreviatae		±	+			
Actinophyllae				+	+	+
Australes			+	+		
Belericae					+	
Bialatae			+	+	+	
Catappa	+	+	+	+	+	+
Chicharronia			+			
Chuncoa					+	
Circumalatae		+				
Complanatae				±	+	
Discocarpae			+			
Dipterae			+	+	+	
Fatraea		+				
Monoptera					+	
Myriocarpae					+	
Myrobalanus				+	+	
Oblongae			+	+		
Pachyphyllum		+				
Pentaptera					+	
Platycarpae			±	+	+	
Polyanthae					+	
Psidioides			+			
Rhombocarpae			+	+		
Stenocarpae				+	+	
Terminalia				+		
Vicentia					+	

only one basic venation type each, seven have two basic venation types (usually Types III and IV, or Types IV and V), four have three basic venation types (usually Types III, IV and V or IV, V and VI), and one (section Catappa) has all six basic types. This constancy can often be used alone (for example section Vicentia, Chicharronia, Pachyphyllum and Chuncoa) or together with other characters for sectional recognition.

Evolutionary trends

The four different levels of leaf venation specialization (leaf ranks) suggested by Hickey (1971) were defined earlier in this chapter.

Leaf venation patterns in Terminalia and the rest of the family are basically camptodromous or sometimes (in Terminalia) craspidodromous. In comparison to woody dicotyledons as a whole this may be considered relatively primitive. The simple entire leaf with pinnate venation is considered by many authors as the msot primitive among the modern flowering plants (Takhtajan 1969, Hickey 1971, Hickey & Wolf 1975, and Doyle & Hickey 1972).

All the species of Combretaceae which have a venation pattern of Type I are referable to the first rank leaf venation of Hickey (1971), and all those which possess Type II venation to the second rank leaf venation, although some of these species sometimes have very irregular intercostal areas and secondary veins. Most species of Terminalia, Buchenavia, Pteleopsis, Combretum and other genera of Combretaceae have third rank leaf venation, particularly those species which possess Type III and Type IV. Fourth rank leaf venation is not common in Combretaceae. It is seen in a few of the species of Terminalia and Buchenavia which have venation of Type V, for example T. pierrei and T. mucronata (Figure 5/5 B and Plates 5/6 A, 5/8 A) from Siam and Buchenavia pallidovirens (Fig. 5/5 H and Plate 5/5 D) from South America, and also in T. fagifolia which has mixed craspidodromous (Type VI) venation.

It is interesting to mention here that several species of Terminalia and Pteleopsis have random reticulate tertiary venation, a second rank condition as described by Hickey (1971), and well developed andorientated areolation, a fourth rank condition according to Hickey e.g. Terminalia chicharronia (Plate 5/4 B) and Pteleopsis suberosa. Decurrency of the secondary veins, a first rank condition, has been seen in species predominently exhibiting characters of second, third and fourth rank leaf venation, e.g. Terminalia mauritiana (Plate 5/2 C), and T. mucronata (Plate 5/6 A).

Hickey (1977) mentioned that some of the more stable characters of leaf architecture are basic venation type, configuration of tertiary venation, shape of areolation and features of marginal venation. However, in Terminalia and Buchenavia there is a broad overlap between the pattern of leaf architecture which characterizes Hickey's second to fourth leaf ranks.

Randomly reticulate, weakly percurrent and regular percurrent tertiary venation have been seen in the same species and even in the same plants (for example Terminalia oblonga, T. catappa and Buchenavia grandis). Therefore intermediate situations between two ranks of leaf venation are quite frequent.

Aspects of the secondary veins are the most important characters of the vein architecture of most taxa studied here. In types I and II (comparable to first and second rank venation of Hickey and not common in Combretaceae) secondaries are irregular in their course, manner of branching and angle of divergence. But in Types III, IV, V and VI (comparable to third and fourth rank venation of Hickey and very common in most genera of the family) secondaries are regular in their course, manner of branching and anastomosing, and angle of divergence. They usually originate from the primary veins at moderate to wide acute angles and follow curved or straight courses. The tendency in Terminalia and Buchenavia seems to be the development of more secondary veins which follow more regular and straighter courses and to have wider secondary angles.

Eucamptodromous venation is the most specialized type of venation in Terminalia, Buchenavia and most of the other genera. The tendency for the secondary veins to become eucamptodromous is clear in all species of Type IV venation and in some of Type III venation, and for the eucamptodromous to become craspidodromous is clear in Terminalia fagifolia and T. pierrei.

The supposed development of the tertiary veins and the higher-order venation is also obvious in many species of Terminalia. The least differentiation of tertiary veins from higher-order veins is shown in section Pachyphyllum of Terminalia and also in Ramatuella and Bucida. The tertiary veins are more regular and percurrent in most species of Buchenavia and Terminalia. But the higher-order venation and the areolation are randomly arranged in most species. The trends in most species examined are from irregularly ramified to randomly reticulate to weakly percurrent to regularly percurrent tertiary veins, and from irregular areolation to orthogonally arranged areolation.

This is in general agreement with the evolutionary lines suggested by Hickey, but it must be pointed out that many examples from the Combretaceae can be quoted that do not demonstrate such an agreement. Most notably, the supposedly most primitive genus of the family, Strephonema, has Type V (third rank) venation, a relatively advanced characteristic.

The main trends in leaf architecture in the Combretaceae discussed above are summarized diagrammatically in Figure 5/9.

Radiography and Clearing Techniques

Ninety four species of Terminalia, Ramatuella, Buchenavia and Bucida were studied by X-ray radiography using low voltage and lengthy exposures at a low current. Fifty species of different genera of Combretaceae were also studied by clearing. In order to get better comparison between the results obtained by radiography and that obtained by clearing technique the same leaves of different species were first radiographed and then cleared.

Radiography has several advantages over clearing, such as speed and accuracy, greater penetration of thick leaves, and its non-destructiveness (Jones 1980). But this does not mean that radiography is an alternative to the clearing methods or that radiography always works very well on every single species. The results show that both radiography and clearing techniques have some advantages and disadvantages and neither of them alone is adequate in the investigation of leaf architecture. In the Combreteaceae the radiography technique has been found to work very well on species which have coriaceous leaves such as Terminalia yapacana and T. guinquininimae (Plate 5/1 A and B),but the results usually vary from species to species dependent on the prominence of the veins. The more prominent is the venation, the better is the resolution in radiographs (for example Buchenavia reticulata and Terminalia arjuna (Plate 5/7 C and D); in several species which possess thinly chartaceous leaves details of higher-order venation and veinlets can hardly be observed.

Clearing techniques on the other hand have been found to work very well on species which have thinly chartaceous to thinly coriaceous leaves, for example Buchenavia capitata (Plate 5/7 H and I) and Terminalia eichleriana (Plate 5/7 F and G).

These techniques have been found unsuitable for most species with thickly coriaceous leaves, as in Terminalia quintalata, Ramatuella crispiallata, and all species of Lumnitzera, Macropteranthes, Laguncularia and Conocarpus.

The distribution of glands in Terminalia fagifolia can usually be easily observed by radiography (Plate 5/1 C) whereas it can be hardly seen by clearing techniques. However, crystals (druses) can be easily examined under the binocular microscope in cleared leaves (Plate 5/8 C).

5.6. Conclusions

The six basic venation types recognized in Terminalia studied here represent the whole diversity in the leaf venation patterns in the entire family of Combretaceae. Leaf venation pattern in the Combretaceae is basically camptodromous or sometimes craspidodromous, but it displays considerable variation. The greatest diversity is in American and Madagascan species of Terminalia. The asiatic species of Terminalia and other genera of the family exhibit almost always one basic venation type (eucamptodromous).

Leaf venation pattern in Terminalia and Buchenavia is of considerable taxonomic value, but in some other genera of the family it is uniform and of relatively little taxonomic value. The relationship between vein architecture and taxonomy in Terminalia is sometimes easy to see, for example in the characteristic venation pattern which relates Ramatuella to Terminalia through section Pachyphylla and Bucida to Terminalia through section Fatrea and T. arostrata. On the relation of Buchenavia with other genera, the evidence of leaf architecture supports its affinity with Terminalia.

Most species of Terminalia, Buchenavia and other genera of Combretaceae possess the third rank leaf venation of Hickey (1971), although all of the four rank levels of vein organization occur. Vein architectural trends seen within Terminalia are generally agreed with that seen elswhere in the angiosperms, but there are exceptions.

Some evolutionary trends in leaf venation observed within Terminalia and other genera of Combretaceae studied here are as follows;

1 - The vein order becoming more regular.

2 - Brochidodromous venation becoming eucamptodromous and craspidodromous.

3 - Secondaries originating at wider angles.

4 - Number of secondaries increasing.

5 - Secondaries becoming straight and parallel to each other.

6 - Ramified tertiary venation becoming reticulate to percurrent.

7 - Differentiation of higher-order venation increasing.

8 - Randomly arranged higher-order venation becoming orthogonally arranged.

9 - Areoles becoming orientated and well developed.

10- Number of intersecondary veins decreasing.

Table 5/3: Distribution of venation types among species of Terminalia in the New World. ± ≐ occasionally.

Species	Venation types I	II	III	IV	V	VI
1. T. actinophylla			+	+		
2. T. acuminata					+	
3. T. amazonia				±	+	
4. T. arbuscula			±	+		
5. T. argentea				+		
6. T. australis			+	+		
7. T. bipleura = 17			+			
8. T. biscutella = 5				+		
9. T. brasiliensis = 14					+	
10. T. bucidoides = 33			+	+		
11. T. camuxa = 24			+	+		
12. T. catappa			±	+	±	
13. T. chicharronia			+			
14. T. dichotoma				+		
15. T. domingensis = 13			+		+	
16. T. eichleriana						
17. T. eriostachya			+			
18. T. fagifolia					+	+
19. T. glabrescens					+	
20. T. grandialata = 24			+	+		
21. T. guaiquinimae		+				
22. T. guyanensis			+	±		
23. T. hylobates = 37					+	
24. T. januariensis			+	±		
25. T. kuhlmannii			+	+		

	I	II	III	IV	V	VI
26. T. latifolia				+	+	
27. T. lucida			+	+		
28. T. mameluco			+			
29. T. neglecta = 13			+			
30. T. nipensis = 13			+			
31. T. nyssaefolia = 27			+	+		
32. T. obidensis = 33				+		
33. T. oblonga			+	+		
34. T. opacifolia = 21		+				
35. T. orientensis = 13			+			
36. T. pachystyla = 13			+			
37. T. phaeocarpa				+	+	
38. T. quintalata		+				
39. T. reitzii				+		
40. T. riedelii			+			
41. T. steyermarkii		+				
42. T. subsericea = 5				+		
43. T. tarapotensis = 33				+		
44. T. triflora			+			
45. T. uleana				+		
46. T. valverdeae				+		
47. T. virgata = 21		+				
48. T. yapacana		+				

Table 5/4: Distribution of venation types among species of the genus *Buchenavia* ± = occasionally

SPECIES	VENATION TYPES				
	II	III	IV	V	VI
B. acuminata		+	+		
B. amazonia		+	+		
B. callistachya			+	+	
B. capitata		+			
B. congesta				+	
B. fanshawei			+		
B. grandis		+	+		
B. guianensis				+	
B. hoehneana		+			
B. huberi		+	+		
B. igaratensis			+		
B. kleinii		+	+		
B. longibracteata				+	
B. macrophylla			±	+	
B. megalophylla				+	
B. nitidissima				+	
B. ochroprumna		+			
B. oxycarpa		+	±		
B. pallidovirens				+	
B. parvifolia		+			
B. pterocarpa		+			
B. punctata			+		
B. rabelloana		+			
B. reticulata			+		
B. seriococarpa		+	±		
B. suaveolens	±	+			
B. tomentosa			±		
B. viridiflora		+	+		
B. pulcherrima				+	

Fig. 5/3: Diagramatic sketches showing leaf venation of Combretaceae. A. Terminalia monoceros, Type I(x3). B. Lumnitzera raceomosa, Type I (x 3.5). C-E. Type II (all natural size): C. Terminalia arostrata; D. Ramatuella virens; E. Bucida buceras

Fig. 5/4: Diagramatic sketches based on radiographs showing the basic venation patterns in Terminalia and Buchenavia (all natural size). A. T. guaiquinimae, Type II. B. T. chicharronia, Type III. C. T. amazonia, Type V. D. T. fagifolia, Type VI. E. T. argentea, Type IV. F. Buchenavia magalophylla, Type V, showing opposite secondary veins. G. T. myriocarpa, Type V, showing opposite and alternate secondary veins.

Fig. 5/5: Diagramatic sketches showing Tertiary and Higher-order venation of Combretaceae. A. Terminalia lucida, showing quaternary and quinternary veins. (X7). B. T. mucronata, showing percurrent tertiaries and indistinct higher-order venation (X6). C. T. chicharronia subsp. neglecta, showing reticulate tertiaries and higher-order venations (x 6.5). D. T. perrieri, showing admedially ramified tertiary veins (note the tips of veinlets) (X 7). E. T. yapacana, showing tertiaries and higher-order venations randomly arranged (X 8). F. T. argentea (note the areoles) (X 7). G. Ramatuella virens (compare with E) (X 8). H. Buchenavia pallidovirens (X 7). I. Bucida buceras (X 9). J. Strephonema pseudocola (X 6.5). K. Combretum pyramidatum (X 6). L. Conocarpus erecta (X 6).

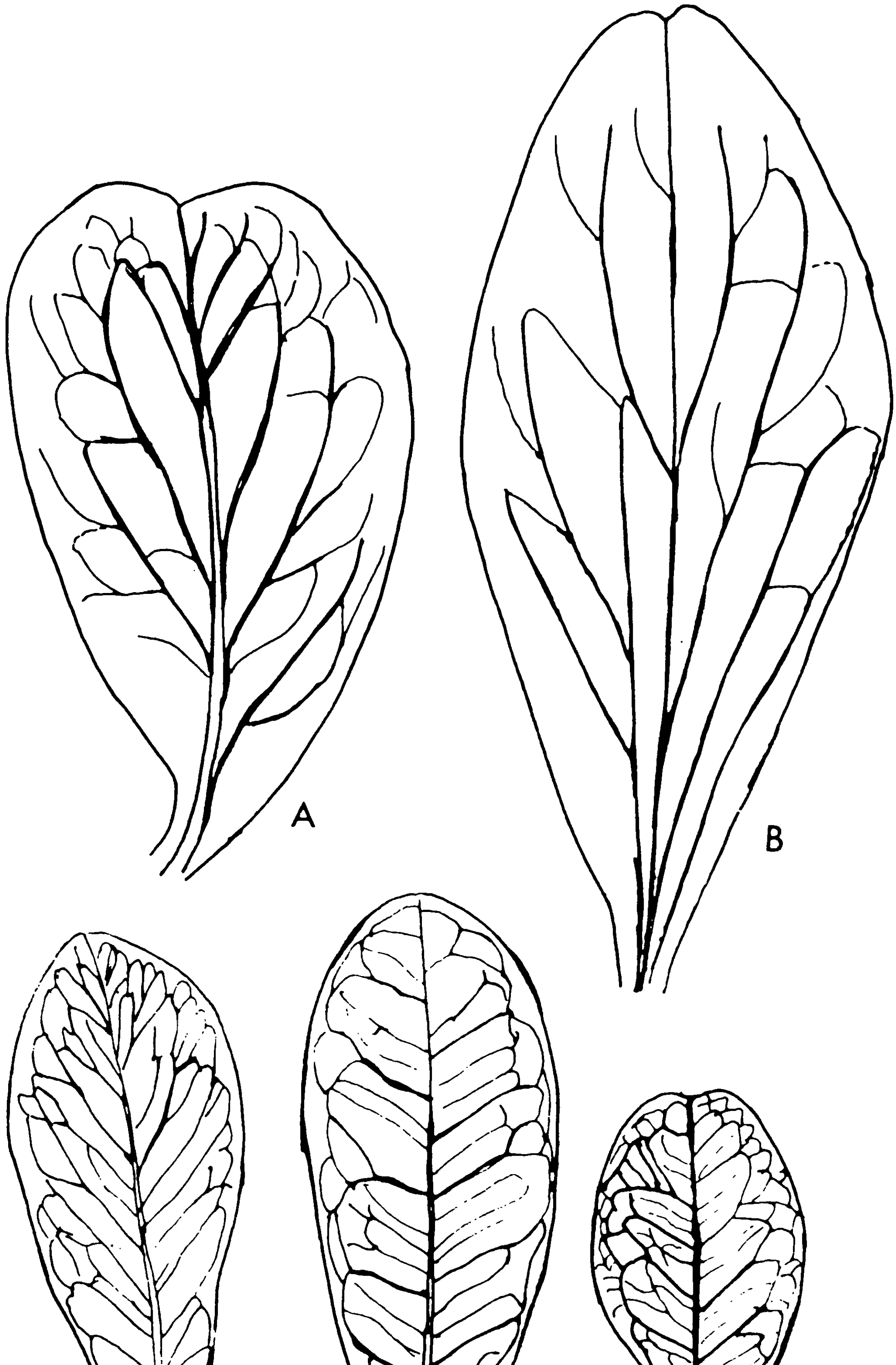


Figure 5/3

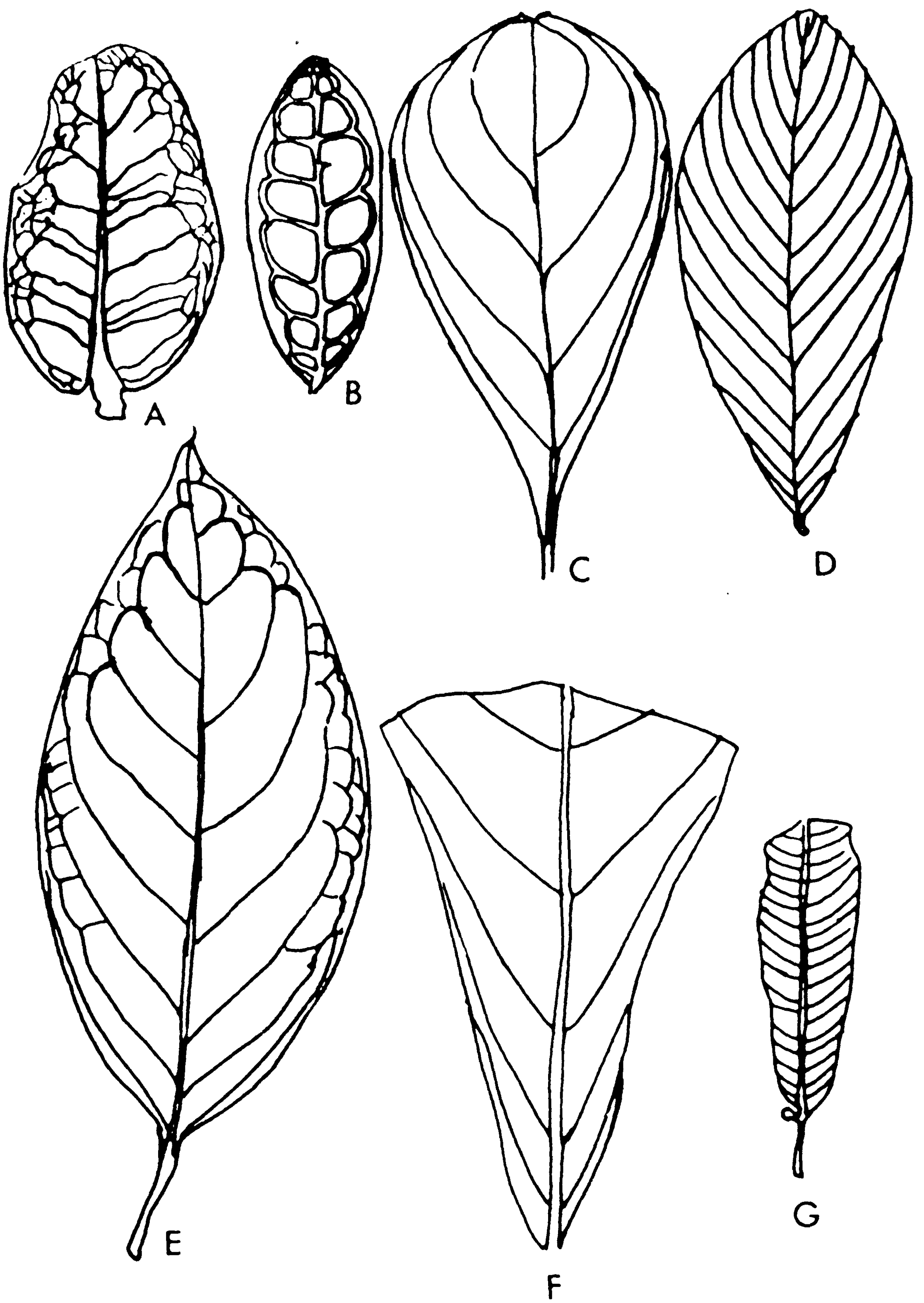


Figure 5/4

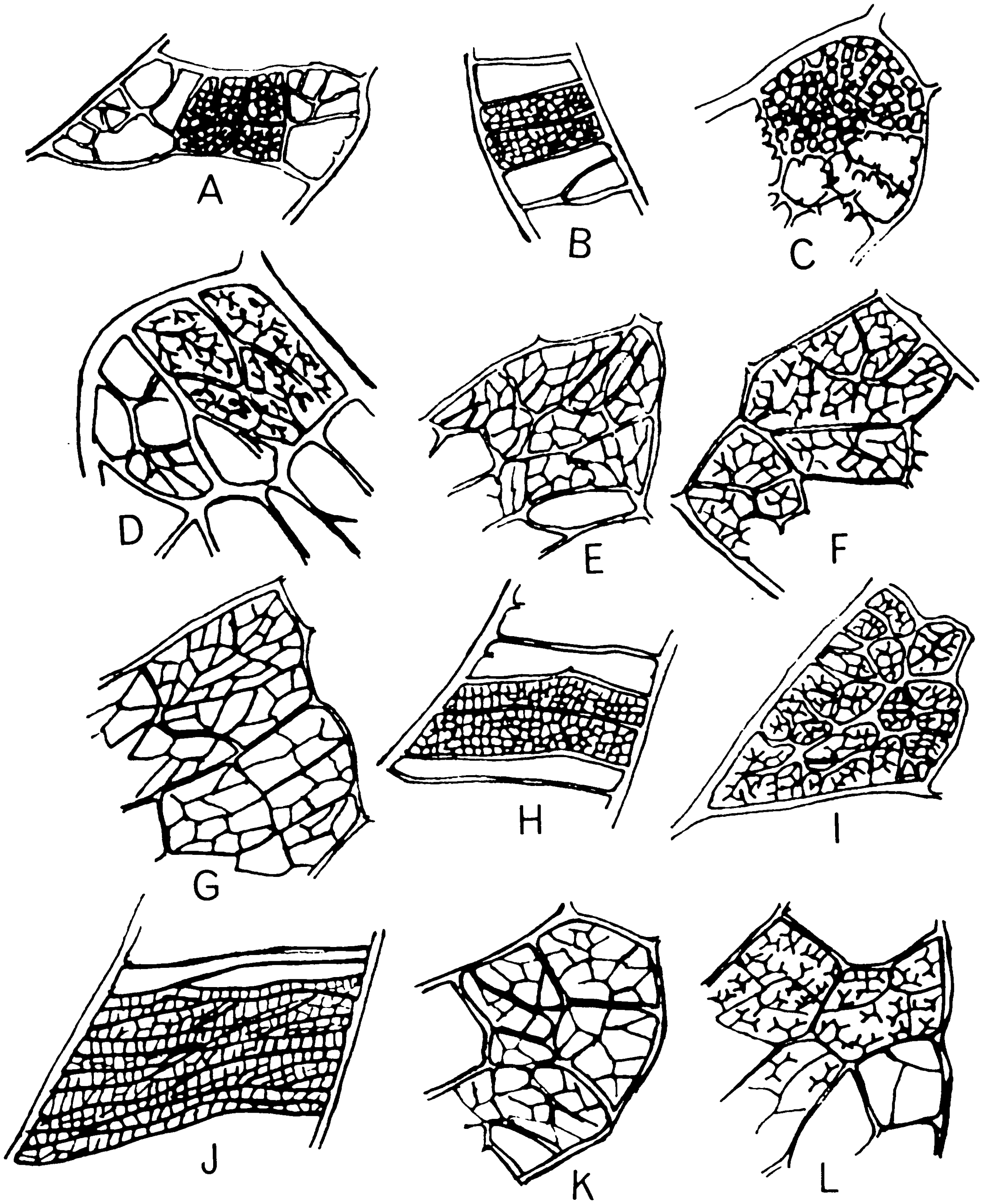


Figure 5/5

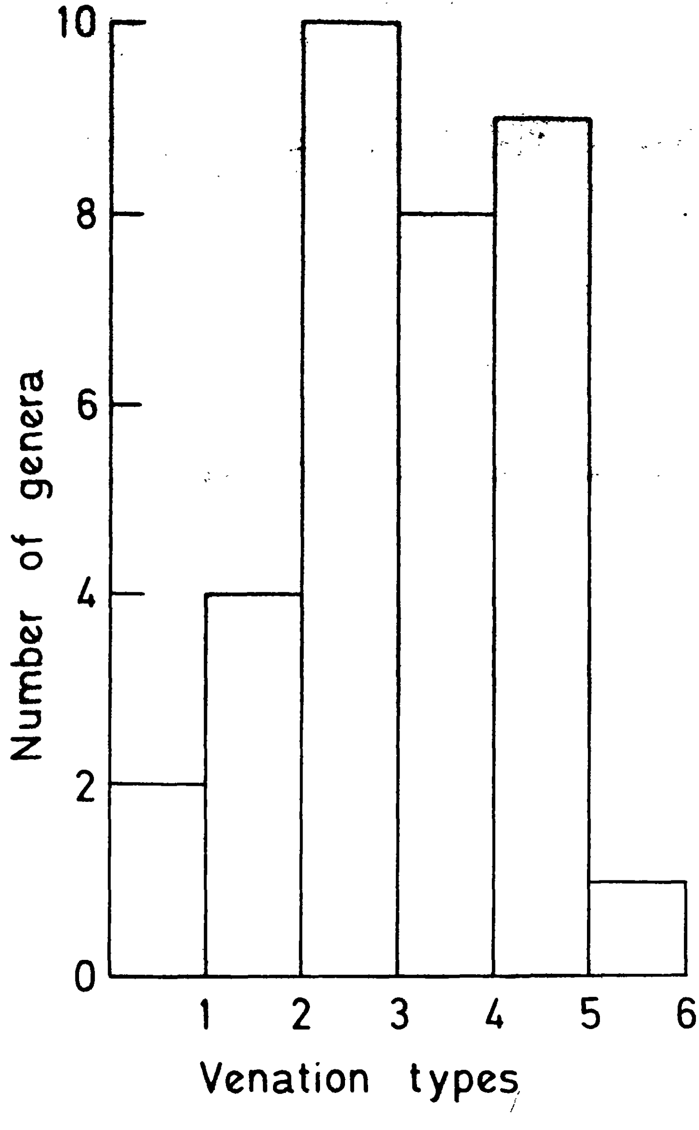


Fig. 5/6: Histogram of venation types distribution among genera of Combretaceae

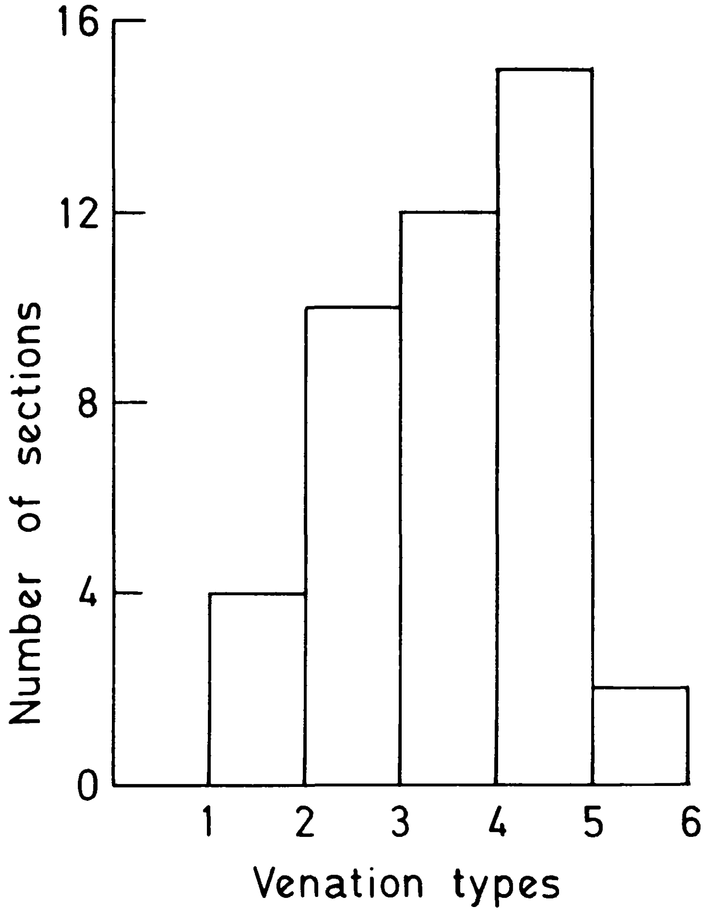


Fig. 5/7: Histogram of venation types distribution among sections of <u>Terminalia</u>

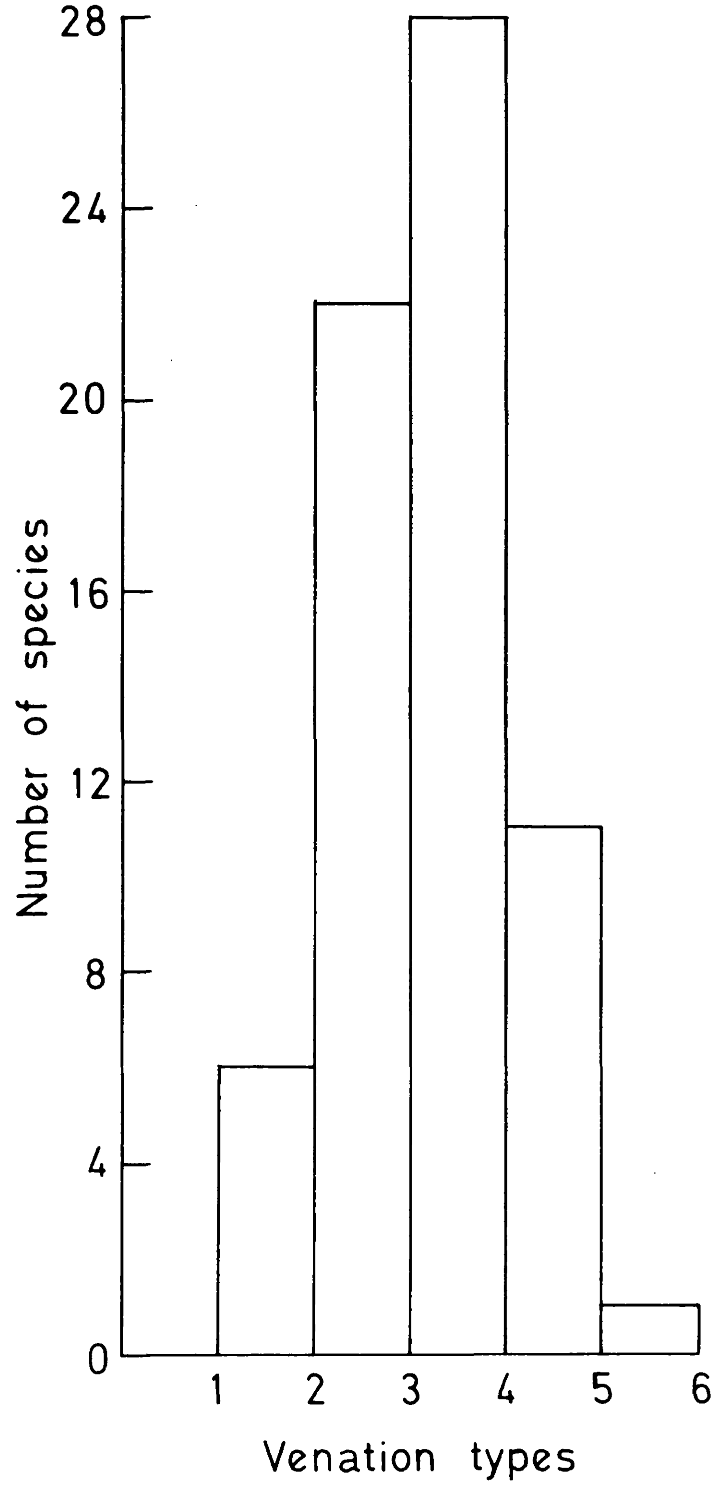


Fig. 5/8: Histogram of venation types distribution among species of Terminalia in America

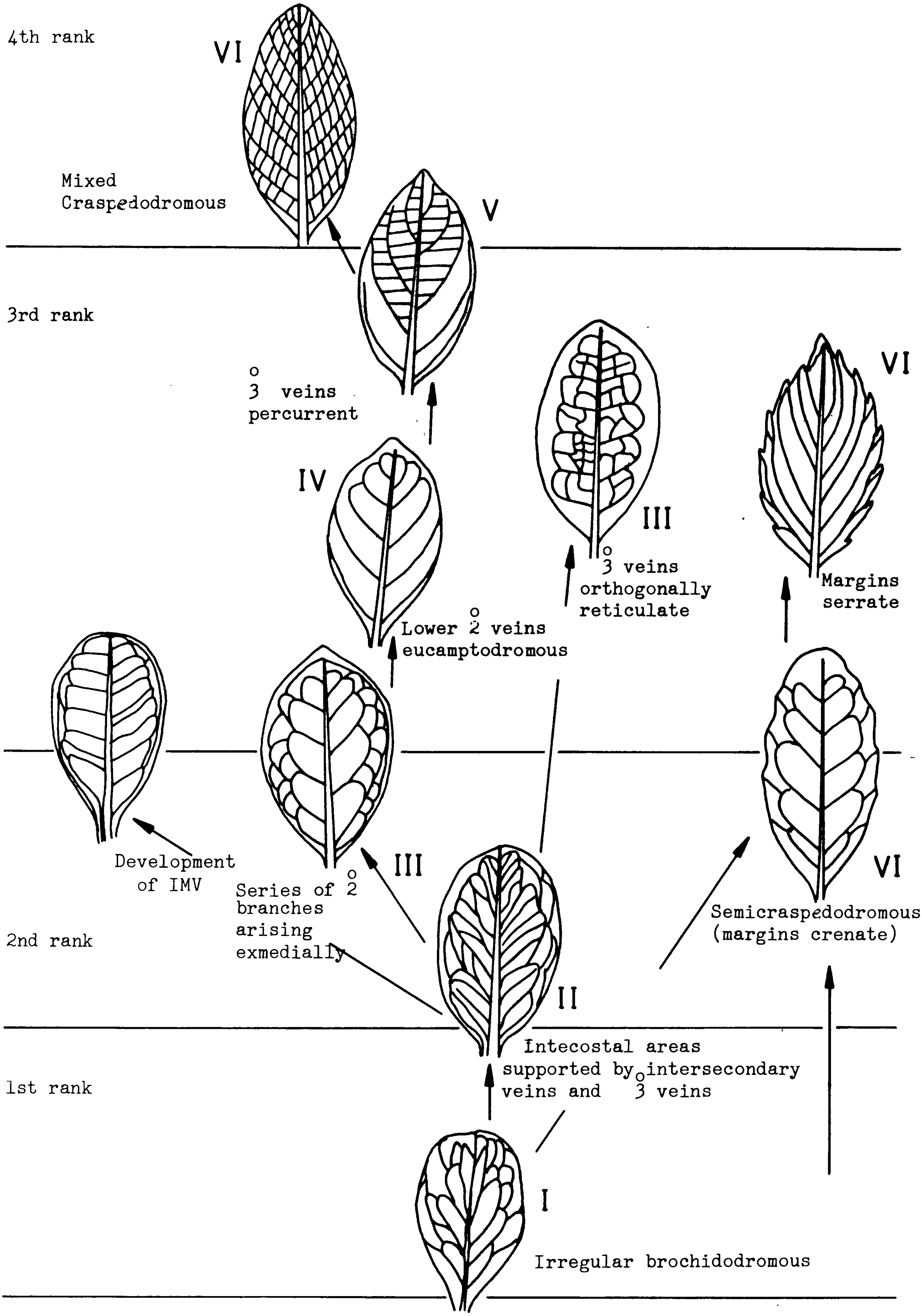


Fig. 5/9: Trends in the leaf venation of <u>Terminalia</u>

Plate 5/1: Radiographs showing venation patterns in Terminalia.
A. T. yapacana. B. T. amazonia. C. T. fagifolia (note the lower secondary veins reaching the margin of the position of a gland).
D. T. guaiquinimae (all x 2).

Plate 5/2: Cleared leaves of Terminalia, showing behaviour and manner of branching of the secondary veins. A. T. acuminata. B. T. lucida.
C. T. mauritiana (note the decurrency of the secondaries upon the midrib). (all x 3).

Plate 5/3: Parts of cleared leaves showing tertiary venation.
A. Combretum pyramidatum, weakly percurrent-random reticulate (x 6).
B. Terminalia sericocarpa, percurrent (x 9). C. Ramatuella virens, randomly ramified (note marginal alternate venation) (x 8).
D. Terminalia perrieri, showing admedially ramified tertiary venation (note the vein endings) (x 13).

Plate 5/4: Parts of cleared leaves of Terminalia, showing development of higher-order venation and aerolation. A. T. subserrata (x 7).
B. T. chicharronia, showing well developed areolation without veinlets (x 6.5). C. T. arbuscula, with imperfect areolation (x 6).
D. T. grandiflora, with poorly developed areolation (x 10).
E. T. argentea, with incomplete areolation (note the vein endings) (x 7).

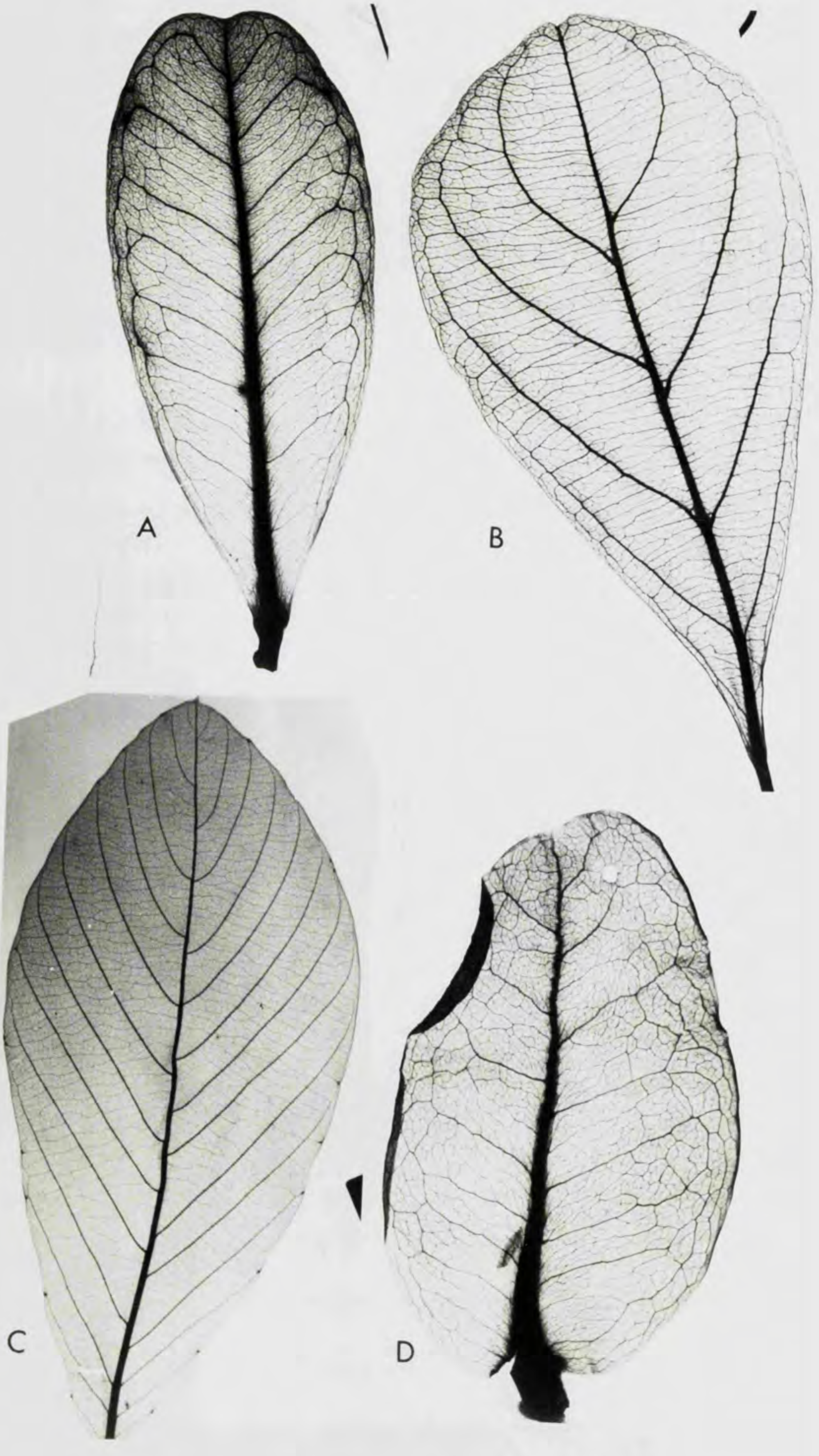


PLATE 5/1

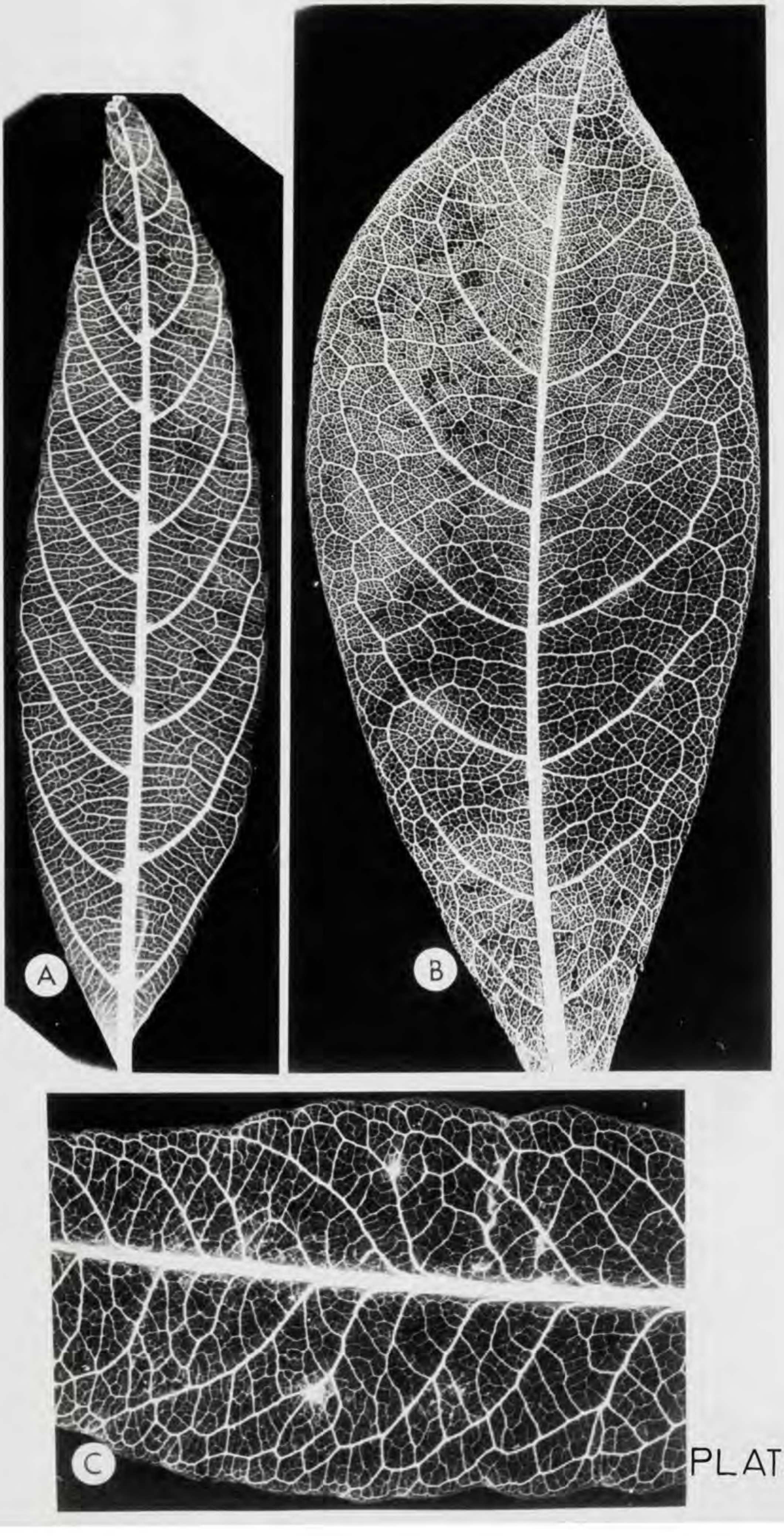


PLATE 5/2

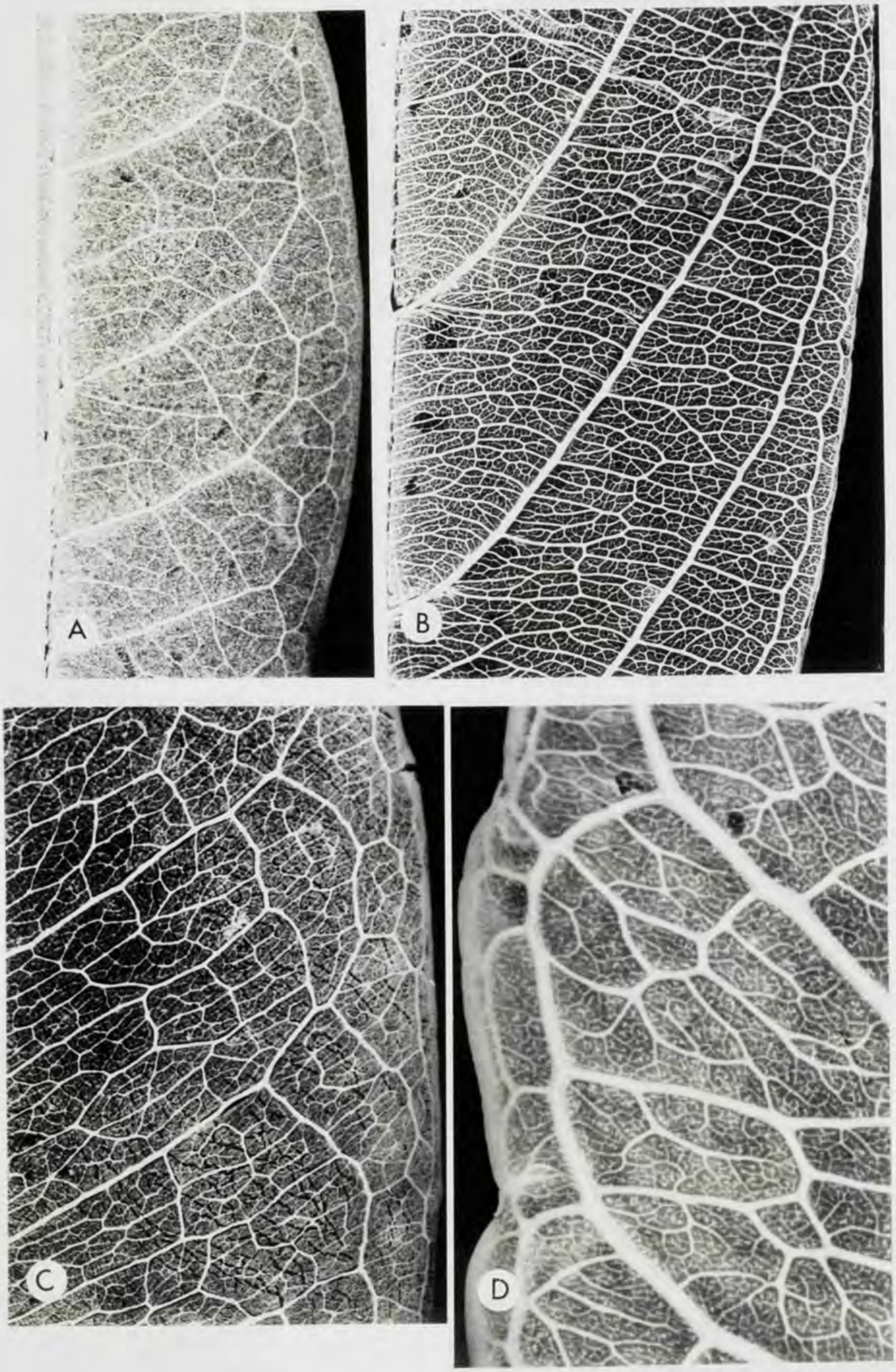


PLATE 5/3

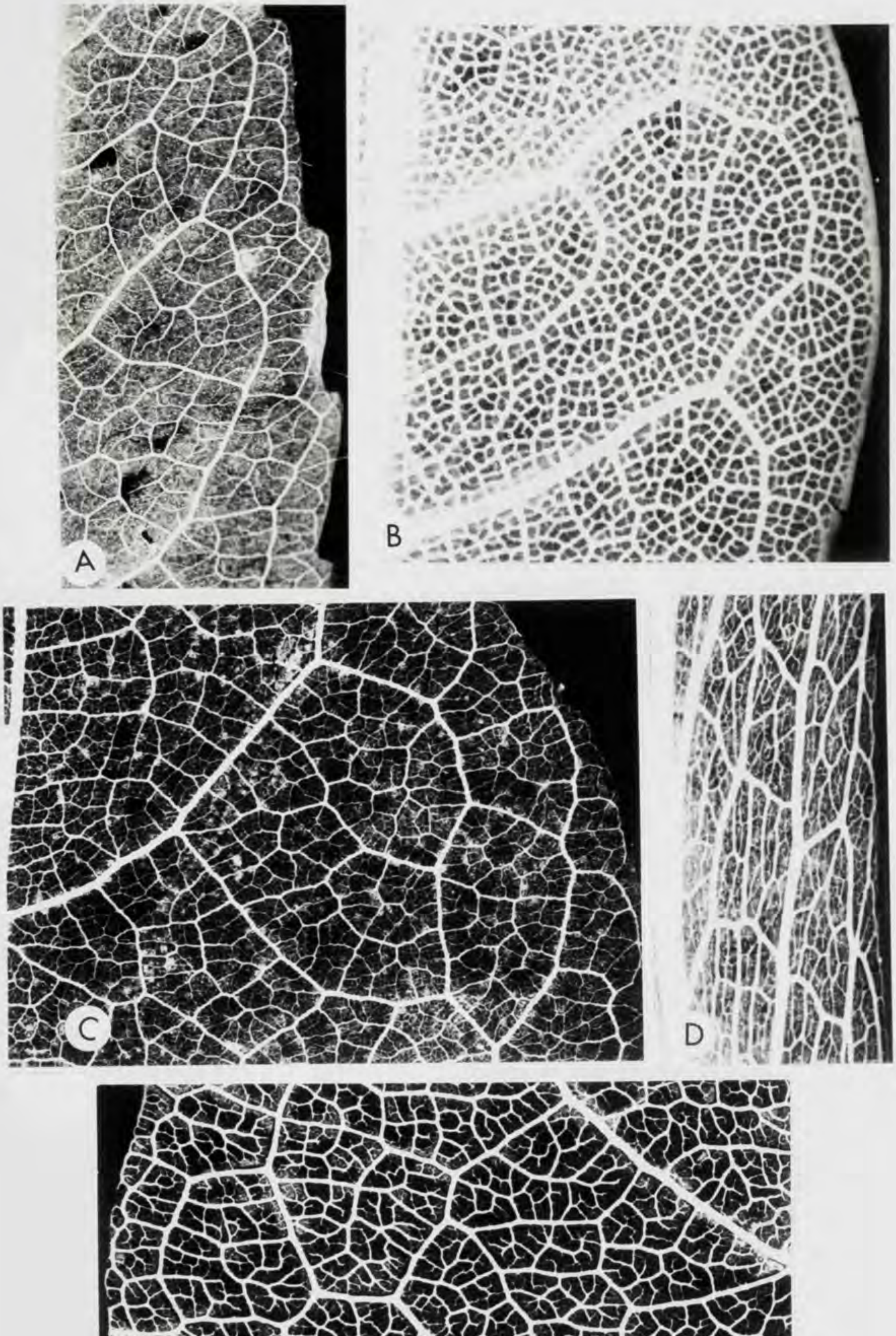


PLATE 5/4

Plate 5/5: Cleared leaves. A. Cleared leaf of Terminalia subserrata showing semicraspidodromous venation (x 2.5). B-E. Parts of cleared leaves of different genera of Combretaceae showing higher-order venation and areolation. B. Thiloa paraguariensis, with veinlets branched twice or three times. C. Combretum pisonioides, with imperfect areoles with few simple veinlets. D. Buchenavia pallidovirens, with well developed areolation. E. Anogeissus pendula (all x 8).

Plate 5/6: Cleared leaves showing venation patterns. A. Terminalia mucronata (x 3). B. Terminalia pterocarya (x 5). C. Calopyxis eriantha (x 3.5). D. Pteleopsis anisoptera (x 5).

Plate 5/7: A-F and H. Radiographs. G. and I. Cleared leaves. A. Terminalia uleana (x 1). B. Same leaf, showing crystals in the areoles (x 3.5). C. Buchenavia reticulata (x 1). D. Terminalia arjuna (note glands at the leaf base). (x 1). E. Buchenavia tomentosa, with lower secondaries, eucamptodromous and upper ones brochidodromous (x 1). F. Terminalia eichleriana (x 1.2). G. Same leaf, cleared (x 1). H. Buchenavia capitata(x 1). I. Same leaf, cleared (x 1.2).

Plate 5/8: Cleared leaves showing areoles and veinlets. A. Terminalia mucronata. B. T. eichleriana. C. T. subserrata, showing various sizes of crystals. D. Bucida buceras. E. Buchenavia pallidovirens (note the dilated tracheidal elements at the vein endings) (all x 50).

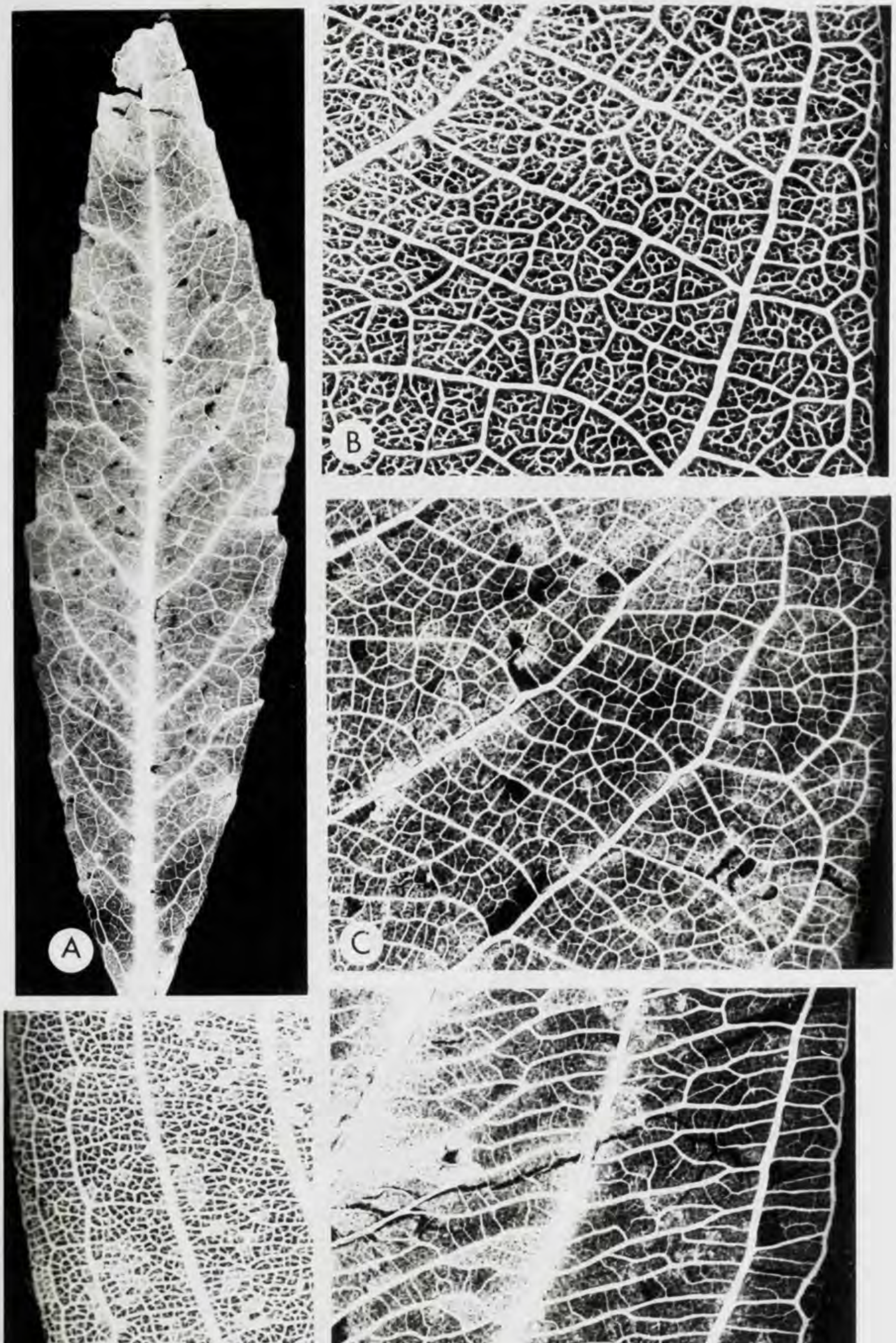


PLATE 5/5

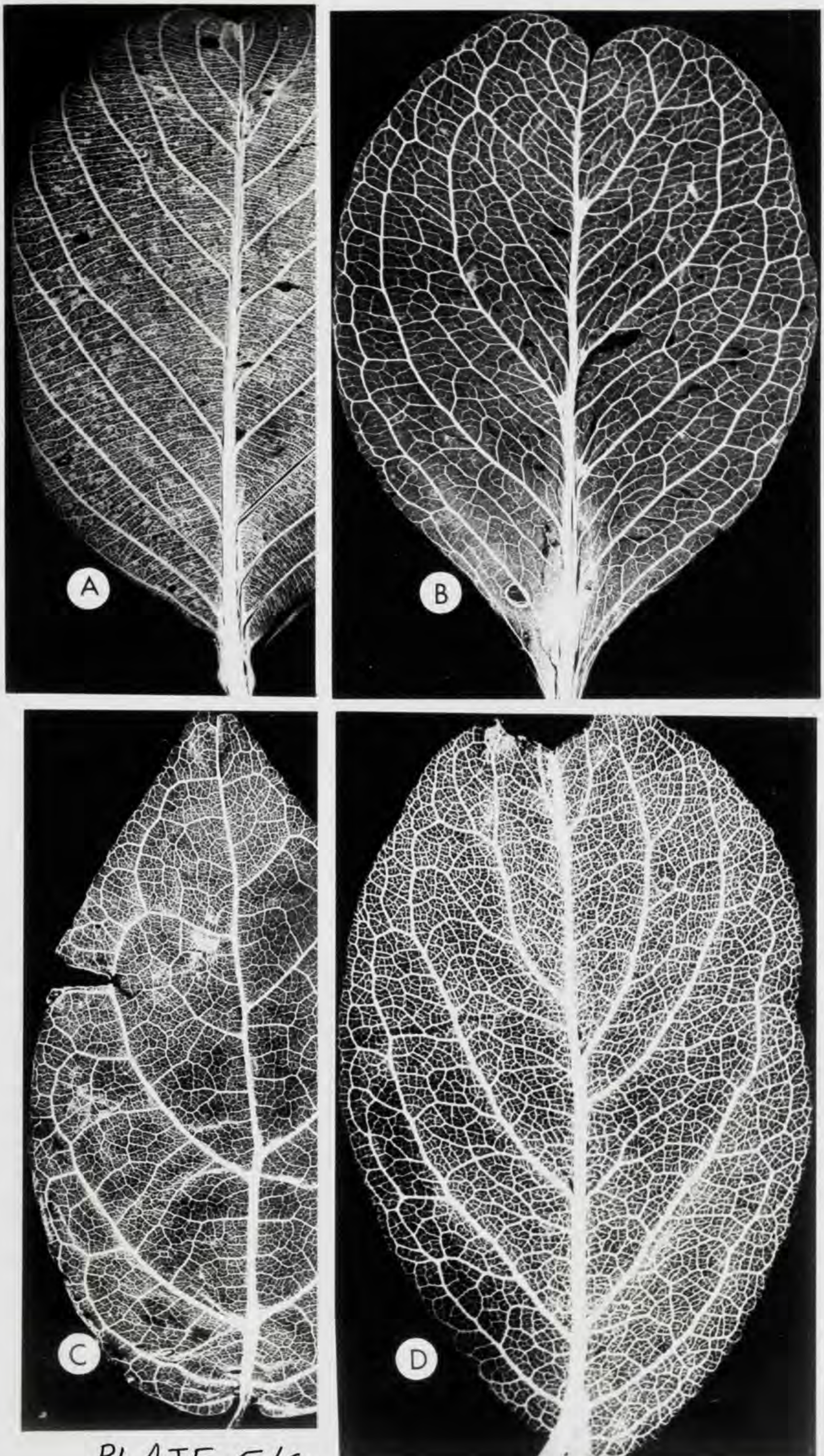


PLATE 5/6

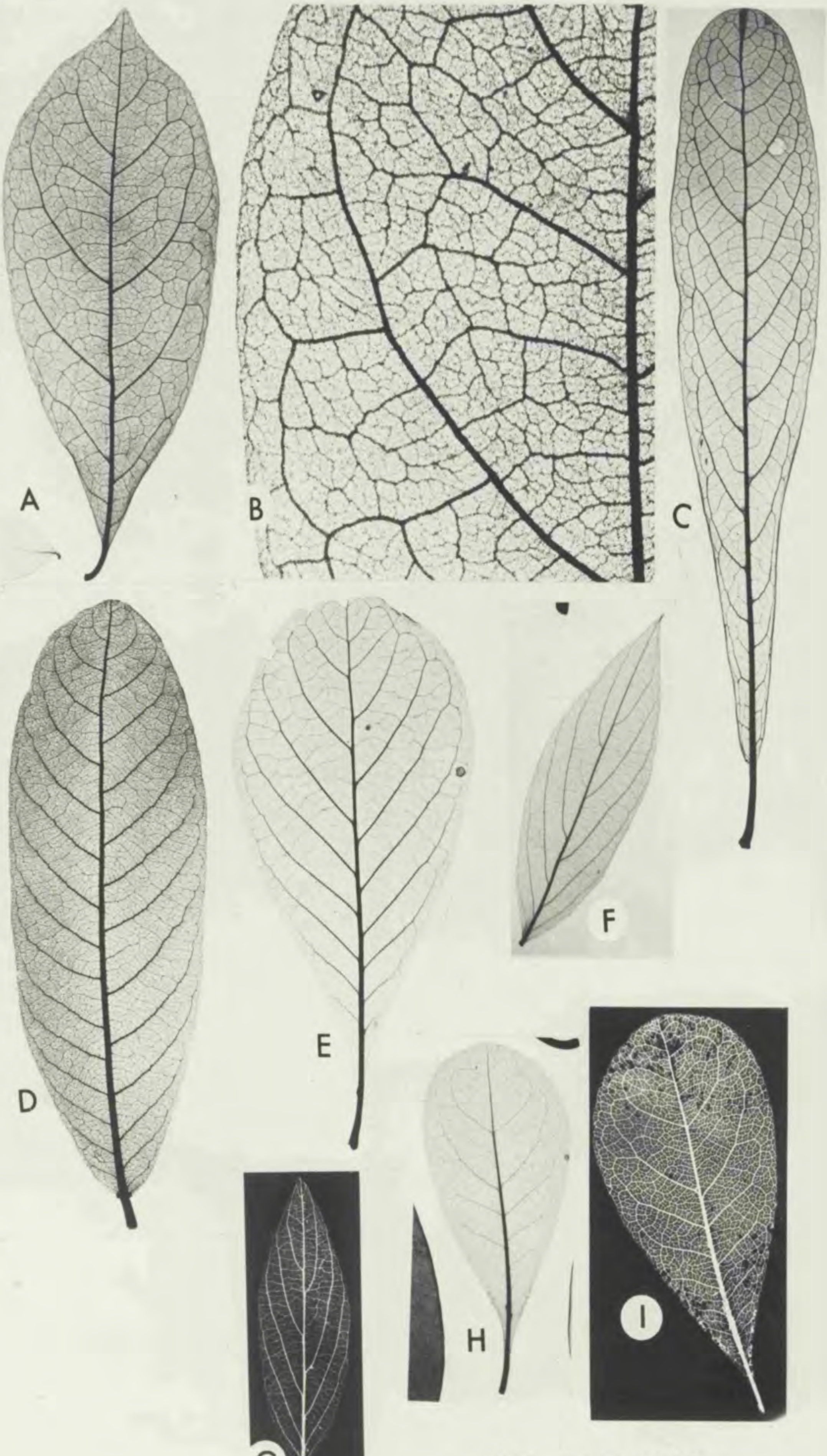


PLATE 5/7

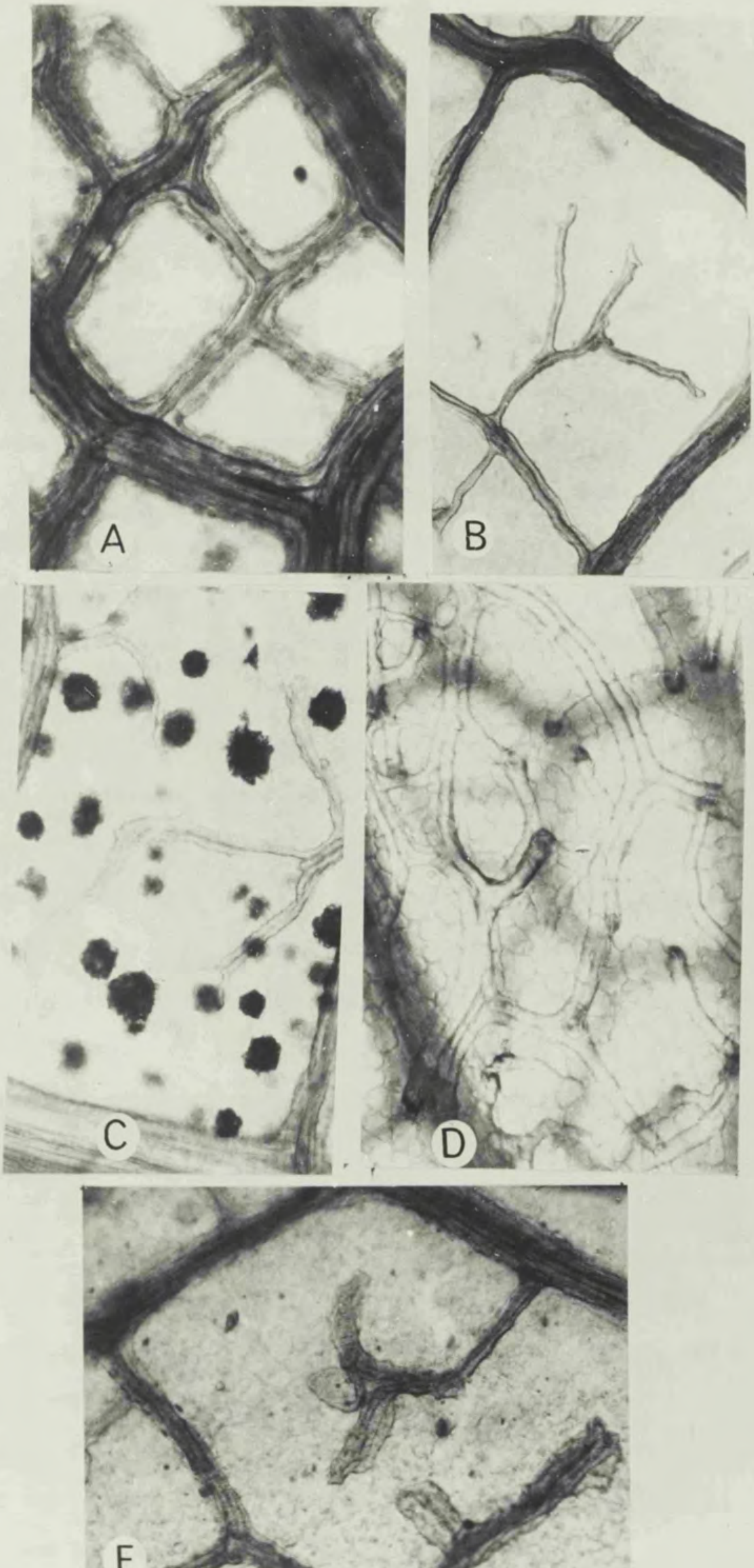


PLATE 5/8

CHAPTER 6

ANATOMY

6.1. Introduction

Anatomical characters are widely used in taxonomic and palaeobotanical studies. The importance of cuticular characters in taxonomic studies has been investigated by many authors (Stace 1963, 1965a, 1965b; Ferguson 1975; Dickison 1975; Wilkinson, 1978, 1979; Cutler 1979; Miranda & Chaphekar 1980; Barthlott 1981).

Metcalfe (1968) has mentioned that vegetative anatomy of flowering plants can be used for the identification of fragmentary material, preliminary identification of herbarium specimens, and the elucidation of the interrelationships of taxa at and above the species level.

Few papers have been published on the leaf anatomy of the family Combretaceae. Solereder (1908) and Metcalfe & Chalk (1950) summarized the available information. Very few papers, however, deal with the genera *Terminalia*, *Ramatuella*, *Buchenavia* and *Bucida*. Stace (1965b) published an extensive survey of the systematic anatomy of all genera of Combretaceae. He summarized several characters of diagnostic value and of taxonomic significance. He also provided a key to the epidermis of the genera of Combretaceae as well as keys to the species of many genera using cuticular characters only.

The leaf anatomy of only two species of *Terminalia* from America (*T. chicharronia* and *T. glabrescens*) have been previously studied, and no species of Combretaceae has been examined by SEM microscopy.

The aims of this study were to present a description of leaf anatomy of the genera *Terminalia* (in America), *Ramatuella*, *Buchenavia* and *Bucida* and to determine its taxonomic value.

6.2. Terminology

For terminology I have followed Stace (1965a), Esau (1977) and Wilkinson (1979).

6.3. Generic Descriptions

6.3.1. *Terminalia* (Plates 6/1, 6/2, 6/4, 6/5, 6/6 and Figure 6/1)

Epidermis: adaxial surface usually smooth, somestimes reticulate, usually without epicuticular wax; abaxial surface smooth, ridged, striate-reticulate, striate or reticulate, often with conspicuous wax. Epidermal cells of both surfaces polygonal, isodiametric or elongated, variable in size, but abaxial cells usually smaller and more variable; walls straight, curved or slightly to strongly undulated, with or without secondary anticlinal walls; inner periclinal walls usually smooth, but sometimes granulate, striate or perforate. Cells over primary and secondary veins modified on both surfaces (particularly on abaxial), narrowly elongated, rectangular or square, in more or less parallel rows, with pointed, oblique or truncate ends. Stomata either confined to abaxial surface or on both surfaces, almost always more numerous abaxially than adaxially. Stomata always anomocytic, usually longer than wide, 14-35 x 10-32 μm but sometimes rounded, or wider than long; guard cells kidney-shaped, slightly raised or superficial or sunken; pore elliptic or narrowly elongate; T-pieces present or not; stomatal ledge usually present; extra cuticular ridges sometimes present; giant stomata (water pores) present in most species. Trichomes always compartmented hairs only, more abundant abaxially, sometimes absent on adaxial surface and in the areoles of abaxial surface; hair bases small or relatively large, 5-50 µm in diameter, surrounded by 3-16 cells. Domatia present or absent, marsupiform of lebetiform.

Transverse section: lamina dorsiventral, 90-650 µm thick. Cuticle 1-25 µm thick, very thin to very thick on both surfaces, usually thicker adaxially than abaxially, usually smooth and flattened, distinguishable or indistinguishable from the rest of the outer wall of epidermal cells. Epidermal cells as wide as high (square) or wider than high (rectangular) or sometimes higher than wide (columnar), those of adaxial surface usually larger than those of abaxial surface; both adaxial and abaxial epidermises uniseriate. Hypodermis absent in all American species, 1-layered adaxially in T. laxiflora from Africa. Mesophyll usually one layer of tall adaxial palisade cells and 3-15 rows of compact or loose spongy tissue with isodiametric or slightly elongated lobed cells. Midrib raised to prominently raised abaxially and grooved (concave), flattened or raised adaxially, supplied with a single, circular, semicircular or U-shaped to crescentiform bicollateral vascular strand; vascular strands sometimes with very much incurved ends. Bundle sheath usually present, composed of an arc or an interrupted to closed ring of sclerenchymatous tissue. Vascular bundles of smaller veins usually embedded in mesophyll, occasionally vertically transcurrent. Ground tissue collenchymatous at periphery, parenchymatous towards the centre. Crystals always druses, in mesophyll, vascular bundles or ground tissue, but not in epidermal cells

Petiole: outline circular, elliptical or horseshoe-shaped, usually with short or long lateral wing-like projections. Vascular system usually of one main, central, bicollateral strand, circular or crescentiform with direct or strongly inrolled ends. Rib traces sometimes present, if so usually 2 and towards the adaxial side.

6.3.2. Ramatuella (plates 6/4E; 6/6B)

Epidermis: adaxial and abaxial surfaces smooth, without ornamentation or epicuticular wax. Epidermal cells adaxially isodiametric, with walls characteristically undulated in the outermost part only; inner periclinal walls often minutely perforate, or sometimes smooth; abaxial cells usually narrowly elongated in various directions, with relatively thin, straight to curved walls. Cells over primary and secondary veins usually rectangular or narrowly elongate, in parallel rows. Stomata on both adaxial and abaxial epidermises, usually fewer adaxially than abaxially, always anomocytic, 15-35 x 15-35 µm, rounded or elliptic or wider than long; guard cells kidney-shaped, superficial; pore elliptic; T-pieces always present, outer stomatal ledge always present and clear; extra cuticular ridges absent; giant stomata always present. Trichomes typical combretaceous hairs, sparse to very abundant abaxially, extremely sparse to very frequent adaxially; hair bases always small, 3-7 (10) µm diameter, surrounded by 3-6 (7) modified epidermal cells sometimes with thick walls. Domatia absent.

Transverse section; lamina dorsiventral, 200-450 µm thick. Cuticle thick or very thick, usually thicker adaxially than abaxially, (3) 5-25 µm thick, smooth and with a flat surface; cuticular flanges well developed adaxially, usually reaching mesophyll, abaxially less developed; cuticular ridges absent. Epidermal cells rectangular, or rectangular-squarish, adaxially larger than abaxially, uniseriate on both surfaces. Hypodermis absent. Mesophyll of one layer of tall (60-200 µm) palisade cells and 5-8 layers of loose and irregular spongy cells; large air spaces rarely present. Midrib usually flattened adaxially, slightly raised abaxially. Vascular strand bicollateral, circular or crescentiform, surrounded by a complete circle of sclerenchyma cells; bundle sheath extention sometimes present. Crystals druses, 15-45 μm diameter, sometimes sparse or absent.

6.3.3. Bucida (plates 6/3D; 6/7H)

Epidermis: adaxial and abaxial surfaces smooth, largely without ornamentation but with ridges round stomata; epicuticular wax rarely present. Epidermal cells usually isodiametric; anticlinal walls thin, usually conspicuously undulate on both epidermises; inner periclinal walls usually striate or smooth. Cells over primary and secondary veins elongated and narrow, with straight walls. Stomata on both adaxial and abaxial epidermises or confined to abaxial epidermis, anomocytic, 17-30 x 10-25 μm, usually elliptic, occasionally rounded; guard cells kidney-shaped, superficial or slightly sunken; pore elliptic or narrowly elliptic; T-pieces sometimes conspicuous; outer stomatal ledge usually absent or not conspicuous; extra cuticular ridges often present; giant stomata occasionally present. Trichomes typical combretaceous hairs, sparse adaxially, frequent to abundant on major veins abaxially; hair-bases small, 3-15 μm diameter, sparse on both surfaces. Domatia absent.

Transverse section: lamina dorsiventral, 170-370 μm. Cuticle 2-7 μm thick, adaxially thicker than abaxially, usually smooth. Cuticular flanges conspicuous but not long. Epidermal cells rectangular or square, adaxially larger than abaxially, always uniseriate. Hypodermis absent. Mesophyll of one layer of palisade cells (60-140) μm thick and 4-12 layers of spongy cells; large air spaces absent. Midrib usually flattened or grooved adaxially, slightly raised abaxially. Vascular strand bicollateral, circular or semicircular, surrounded by a thick bundle sheath of sclerenchyma cells; bundle sheath extention very common. Sclerenchyma cells very common in mesophyll and characteristically forming a subepidermal layer. Crystal druses, very common, 10-50 μm diameter.

Petiole: outline circular, without lateral wings. Vascular strand circular, with 2 lateral rib traces towards the adaxial surface.

6.3.4. Buchenavia (plates 6/2F; 6/3; 6/4F; 6/6F; 6/7A-D, F & G; 6/8 A & B and Figure 6/2 B, D & E)

Epidermis: adaxial surface smooth, usually without wax; abaxial surface smooth or ridged, usually with wax. Epidermal cells of both surfaces usually isodiametric, sometimes polygonal, 4-6-sided; walls straight to strongly undulated, inner periclinal walls smooth or sometimes granulate. Cells over primary, secondary and tertiary veins modified on both surfaces but more so abaxially, usually narrowly elongated in more or less parallel rows. Stomata confined to abaxial surface, sometimes very few present on adaxial surface particularly on or along the primary veins. Stomata always anomocytic, 15-40 x 13-40 µm, elliptic or rounded; guard cells reniform, superficial or sometimes sunken; pore usually elliptic; T-pieces sometimes present; stomatal ledge present but usually not conspicuous; extra cuticular ridges often present; giant stomata sometimes present. Trichomes typical compartmented hairs, present on both surfaces or sometimes absent adaxially; hair-bases usually small, 5-15 (35) µm diameter, surrounded by several modified epidermal cells. Domatia present or not, usually marsupiform, sometimes lebetiform.

Transverse section: lamina dorsiventral, 150-400 µm thick. Cuticle thin or thick on both surfaces, but adaxially thicker than abaxially, 1-2 µm thick, smooth and with a flat surface. Epidermal cells rectangular, square or columnar, adaxially larger than abaxially, uniseriate on both surfaces. Hypodermis absent. Mesophyll composed of 1 or sometimes 2 layers of palisade tissue and several layers of spongy tissue with isodiametric or elongated cells; large air spaces common in spongy layer. Midrib raised to prominently raised abaxially, grooved, flattened or raised adaxially, with a bicollateral crescentiform or circular vascular strand. Bundle sheath present or not; bundle sheath extention common. Crystals druses, (6) 10-50 µm diameter, sometimes absent.

Petiole: circular, oval or horseshoe-shaped, usually without lateral projections but sometimes with 2 short wing-like projections. Vascular system usually closed, sometimes crescentiform. Rib traces almost always present, usually 2.

6.4. Variation in anatomical characters

6.4.1. Cuticle

When viewed with the SEM, the cuticles appear smooth, ridged, striate, reticulate or irregularly folded. In most species examined the cuticle is flat and smooth and shows no surface sculpturing (plate 6/1D; 6/2C;6/3C). In some species, however, the cuticular ornamentation is clear. For example a striate pattern is found in *Terminalia myriocarpa* (plate 6/1B), *T. actinophylla* and *Buchenavia suaveolens*, although the striations show considerable variation in the species examined. Reticulate ornamentation is found in *Terminalia domingensis* (plate 6/1G), *T. neglecta*, *T. eriostachya* (plate 6/2D) and *T. bellirica* (plate 6/1E). Curved ridges of cuticle surrounding stomata ('extra cuticular ridges') are found in many species, e.g. *Terminalia argentea* (plate 6/1C), *T. bellirica* (plate 6/1A). *T. actinophylla* (plate 6/2A), *Bucida spinosa* (plate 6/3D) and *Buchenavia reticulata* (plate 6/3A).

6.4.2. Epicuticular wax

Most species have little or no wax. There is no wax seen in *Bucida* and *Ramatuella* but in *Terminalia* and *Buchenavia* wax is present in the form of plates, granules, scales, flakes and filaments. The pattern of distribution of wax particles may be a useful character. For example the cuticle of Terminalia neglecta has a few wax flakes on the guard cells but many over the anticlinal walls (plate 6/4A). Wax flakes in T. platyptera (plate 6/2B) are regularly and densely distributed on the whole surface, including stomata. While in T. australis wax is concentrated round the stomata only. The commonest type of wax in the species studied is wax flakes, but their size and distribution is very variable. It seems that wax morphology in the species examined is of little or no taxonomic value.

6.4.3. Epidermal cells

The taxonomic significance of the epidermal wall undulations at specific and generic levels has been emphasized by many authors (Barthlott 1981).

In Terminalia and Buchenavia the anticlinal walls, which usually show deeper undulation abaxially than adaxially are of considerable taxonomic value at the specific level and in many cases at the sectional level. Many species can be separated on the basis of the outline of their adaxial and abaxial epidermal cells because the undulation types are found to be constant in many species.

Four types of anticlinal walls have been recognized in species examined:

A - Straight or slightly curved, as in Terminalia biscutella (plate 6/6E). T. nipensis (plate 6/5C).

B - Curved or slightly undulated, as in Terminalia sections Actinophyllae (plate 6/6D) and Australes, and in Ramtuella (plate 6/4E; 6/6B).

C - Conspicuously but not deeply undulated, as in Terminalia sections Rhombocarpae and Terminalia, and in Bucida and most species of Buchenavia.

D - Deeply or strongly undulated as in Terminalia section Chuncoa (plate 6/5D) and in some species of Buchenavia (e.g. B. guianensis).

Despite the fact that the various types of anticlinal wall are characteristic of many species and sections, intermediates between two types (such as A and B, B and C, or C and D) can be found in a few species. For example, in Terminalia domingensis the wall of the abaxial epidermis varies from curved to slightly undulate and in T. catappa from curved to conspicuously undulate.

In the Aquifoliaceae, the anticlinal walls of epidermal cells of high mountain species in the tropics are usually straight or curved (Bass 1975). In Terminalia, however, there are species of relatively high altitude and with undulated anticlinal epidermal cell walls, e.g. Terminalia opacifolia (plate 6/5F) which grows on 1800 m altitude.

There are many examples in Terminalia showing no relation between wall undulations and the altitude, e.g. the epidermal walls are strongly undulated in T. dichotoma (plate 6/6C) and straight or curved in T. lucida although both species occupy lowland environments, and the walls are strongly undulated in T. opacifolia and straight to slightly undulated in T. guaiquinimae although both species come from the same locality at high altitude. Terminalia amazonia and T. glabrescens always have conspicuously or strongly undulated walls whether they grow in the lowlands or at higher altitudes.

The thickness of the anticlinal walls is of taxonomic value. Walls are very thick in all species of section Pachyphyllum (plate 6/5A) and in Ramatuella (plate 6/4E; 6/6B), thick in section Chicharronia, e.g. T. orientensis (plate 6/5B) and T. nipensis (plate 6/5C) and in some species of Buchenavia and thin in most other species of Terminalia, Bucida and Buchenavia, e.g. T. glabrescens (plate 6/5D).

The anticlinal walls are smooth in most species but they are pitted in section Pachyphyllum, e.g. Terminalia quintalata (plate 6/4D) and in Ramatuella. A characteristic alternation of buttresses and cavities along the anticlinal walls similar to that found in many gymnosperms (Barthlott 1981) was found in all species of section Pachyphylla (plate 6/5F) and in Ramatuella.

The nature of the inner periclinal walls is of taxonomic value in some species. They are smooth in most species examined (plate 6/4B), but perforate or heavily pitted walls are characteristic of T. quintalata (plate 6/4D; 6/6A). Striated walls were found in Terminalia actinophylla (plate 6/6D), Bucida buceras and Buchenavia suaveolens, and granulate periclinal walls were found in many species, e.g. Ramatuella virens (plate 6/4E) and Buchenavia suaveolens (plate 6/4F).

6.4.4. Stomata

Cutler (1979) mentioned that details of the stomatal aperture can be used to help in identification and classification.

In this study two types of stomata have been recognized:

Type A - Stomata usually elliptic or narrowly elliptic, often without T-pieces, and with a narrowly elliptic or elongate pore. The epidermal wall of the guard cells and the outer stomatal ledge are inconspicuous and the poral walls are thin. This type is found in most species examined, particularly those with thin leaves (plates 6/1B, C and F; 6/6C).

Type B - Stomata broadly elliptic, rounded or wider than long, with an elliptic or rounded pore and usually with T-pieces. The epidermal wall of the guard cells and the outer stomatal ledge are very conspicuous, and the poral walls of the guard cells are thick. This type is found in all species of sections Chicharronia (plates 6/4A; 6/5B) and Pachyphyllum (plate 6/5A) and a few species from other sections of Terminalia and in all species of Ramatuella and some species of Buchenavia, e.g. B. guianensis (plate 6/6F).

The number of stomata on the upper epidermis may vary from species to species and can be used to assist in the identification of some species of Terminalia and Ramatuella.

Stomata are always present on the intervenal areas of the abaxial epidermis, but adaxially their distribution can be classified into four groups:

A - Completely absent or extremely sparse on primary veins.

B - Sparse to frequent on primary veins, extremely sparse on secondary veins.

C - Frequent or abundant on primary veins, sparse to frequent on secondary veins, absent on intervenal areas.

D - Frequent to abundant on intervenal areas.

It is clear in Terminalia (particularly section Pachyphyllum) and Ramatuella that there is a tendency for stomata to occur adaxially to the same degree as abaxially. In all species of these two groups stomata are abundant adaxially on the primary and secondary veins. In Terminalia yapacana stomata always occur nearly equally on both epidermises, while in Ramatuella virens stomata were found to occur equally on both epidermises in eight specimens out of twelve; in the other four specimens stomata were rare on the adaxial epidermis. In Terminalia actinophylla stomata are abundant on both epidermises in most specimens examined, while in most species of Terminalia, and all species of Buchenavia and Bucida stomata are either confined to the abaxial epidermis or occur sparsely to frequently on the adaxial primary veins (table 6/1).

It is clear from table 6/2 that stomatal size and stomatal indices are of virtually no taxonomic value, although close species of sections often have similar size of stomata. Section Pachyphyllum has the largest size of stomata in Terminalia, while T. fagifolia has the smallest. Ramatuella has stomata of the same size as in section Pachyphyllum of Terminalia. Buchenavia species have slightly larger stomata than Terminalia and Bucida. The stomatal indices of Terminalia range from 7 to 36; T. eriostachya, T. arbuscula and T. subsericea have the lowest values (7-9), while T. actinophylla has the highest value (36). Buchenavia stomatal indices range from 4 to 28, while those of Bucida and Ramatuella range from 14 to 30. The stomatal index of a species varies from specimen to specimen and sometimes from place to place on the same specimens.

6.4.5. Trichomes and hair-bases (plates 6/1C and E; 6/5E; 6/6G and H)

Terminalia, Ramatuella, Bucida and Buchenavia have typical combretaceous hairs (plate 6/6H) where presence has no taxonomic value below the family level. But the type and distribution of hair-bases are of some taxonomic value. The hair-bases are of two types:

A - Small, usually 3-10 μm but sometimes up to 20 μm in diameter (including pore and poral rim), usually surrounded by 3-7 modified epidermal cells (plate 6/5E). This type is found in all species of Ramatuella and Bucida and in most species of Terminalia and Buchenavia.

B - Relatively large, usually over 20 μm and sometimes up to 50 μm in diameter, surrounded by 6-16 usually modified epidermal cells. This type is found only in a few species of Terminalia (plate 6/6G) and Buchenavia.

The distribution of hair-bases was found to be of little or no taxonomic value in most species, but in some species it is a diagnostic character, as in Terminalia eriostachya, T. fagifolia, T. argentea, T. steyermarkii and Buchenavia tomentosa. Four categories were recognized based on the distribution on the abaxial epidermis:

A - Hair-bases very sparse, if present confined to primary and secondary veins (e.g. Terminalia quintalata, T. yapacana, T. guiaquinimae, T. domingensis, T. nipensis, T. orientensis, T. pachystyla, Buchenavia suaveolens and most species of Bucida.

B - Hair-bases frequent on major veins, absent elsewhere (e.g. Ramatuella crispialata, Buchenavia congesta, B. pallidovirens, Terminalia lucida, T. nyssaefolia, T. obidensis and T. oblonga).

C - Hair-bases frequent to abundant on veins, sparse to frequent on intervenal areas as in most species of Terminalia and Buchenavia.

D - Hair-bases abundant to very abundant on intervenal areas as in *Terminalia argentea*, *T. fagifolia*, *T. glabrescens*, *T. steyermarkii*, *Ramatuella argentea* and *Buchenavia tomentosa*.

6.4.6. Venation

The occurrence and prominence of the higher-order venation and areolation are useful characters for the identification of some species. Four categories were recognized:

A - Higher-order venation and areolation slightly to prominently raised as in *Terminalia chicharronia*, *T. maestyrensis*, *Buchenavia reticulata* and *B. tomentosa*.

B - Higher-order venation and areolation present but not raised (some species of *Terminalia*, *Buchenavia* and *Bucida* table 6/1).

C - Higher-order venation present but areolation usually wanting or incomplete (most species of *Bucida* and some species of *Terminalia* and *Buchenavia*.

D - Only primary, secondary and a few tertiary veins present (all species of *Ramatuella*, most species of *Terminalia* and some of *Buchenavia*.)

6.4.7. Domatia

The presence of domatia is characteristic of some species of *Terminalia* and *Buchenavia*, but domatia are absent in *Ramatuella* and *Bucida*. The shape of domatia has been considered of taxonomic value in the Combretaceae (Stace 1965b) but in American *Terminalia* and *Buchenavia* species it seems to be of limited importance. In *Terminalia amazonia*, for example, lebetiform and marsupiform domatia can be found. In *Buchenavia parvifolia* domatia may be absent, a tuft of hairs or marsupiform. In *Buchenavia*, *B. fanshawei* is the only species characteristically to possess lebetiform domatia.

6.4.8. Transverse section (figure 6/1 and plate 6/7)

Leaves of the four genera examined are almost always dorsiventrally organized, with only adaxial palisade tissue. But sometimes a more or less centric arrangement can be found in *Terminalia fagifolia* and *T. acuminata*.

In most species examined which have thick leaves (such as species of sections Pachyphylla and Chicharronia of Terminalia and species of Ramatuella) it is found that the lamina thickness is mainly a result of an increase in the number of rows of spongy layer cells. In thin leaved species the spongy layer is composed of 4-7 rows of cells while in thick or very thick leaved species it is composed of 8-15 rows. The increase in the number of rows of spongy cells is usually accompanied by an increase in the size of the spongy cells, e.g. Terminalia steyermarkii which has a spongy layer (300-400 μm) 6-7 times thicker than the palisade layer (50-70 μm). All members of section Diptera, which have relatively thin leaves, have the spongy layer thinner than the palisade layer.

In some species the thickness of the lamina is not only due to the increase in thickness of the spongy tissue but also due to an increase in the height of the palisade cells, as in Ramatuella obtusa, and the thickness of the epidermis cells (particularly the adaxial cells) as in Terminalia quintalata (figure 6/1E) and Buchenavia sericocarpa (plate 6/7G), which characteristically have a palisade-like adaxial epidermis. A few species of Terminalia which occur outside America, for example T. laxiflora (figure 6/1D), have an adaxial hypodermis of large clear cells lacking chloroplasts. This hypodermis, which in general is a feature of xeromorphic plants, may serve the same function as a very thick adaxial epidermis.

Based on the cuticular membrane thickness four categories were recognized:

A - Cuticle very thin, up to 2 μm as in all species of section Australes and most species of section Terminalia, e.g. T. arbuscula.

B - Cuticle thin, 2-5 μm as in most species of Terminalia, Buchenavia and Bucida.

C - Cuticle thick, 6-10 μm as in most species of Ramatuella and some species of Terminalia and Buchenavia.

D - Cuticle very thick, over 10 μm, e.g. Terminalia guiaquinimae,

T. quintalata, T. steyermarkii, Ramatuella argentea and R. virens.

It is noted that mountain and high altitude species have usually thickly coriaceous leaves with a thick cuticle, while lowland and rainforest species have usually thin leaves with a thin cuticle. However, Ramatuella, which is a lowland rainforest genus, has a very thick lamina and cuticle.

Sclerenchyma cells are common in midrib and mesophyll of all the genera examined. They are of three types: phloem fibres, xylem fibres and bundle sheath extentions. Phloem fibres are very common in midribs of most species examined. Their amount and manner of distribution often vary within the same species. However, they are characteristic of Bucida and some species of Terminalia and Buchenavia, in which there is a thick and continuous ring of sclerenchyma cells surrounding the vascular strands. However, in several species of Terminalia and Buchenavia phloem fibres are either completely absent or there are only a few cells scattered around the vascular strands.

Xylem fibres in large amounts in the vascular strands are generally rare. They are found in only a few species, e.g. Terminalia yapacana.

Sclerified bundle sheath extentions are characteristic of Bucida, common in Buchenavia and frequent or absent in Terminalia and Ramatuella. In all species of Bucida sclerenchyma cells branch off from bundle sheath extentions and extend horizontally beneath the epidermis, forming a characteristic interrupted subepidermal layer of sclerenchyma cells (figure 6/7H). In several species of Buchenavia and Terminalia sclerenchyma cells occur irregularly in the mesophyll.

6.4.9. Petiole (figure 6/2 and plate 6/8)

The importance of the vascular structure of the petiole as a taxonomic character has been discussed by Howard (1979). He mentioned Terminalia as an example of a petiole with a closed vascular system and with no rib traces.

In this work and from the general features of the T.S. of the petiole the following types were recognized:

A - Outline circular or semicircular without lateral wing-like projections; vascular system a single crescentiform bundle without lateral rib traces, e.g. *T. reitzii* (figure 6/2A).

B - Same as above but with 2 lateral rib traces, e.g. *Buchenavia capitata* (figure 6/2B).

C - Outline same as above but the vascular system composed of two medullary strands (a crescentiform ventral strand and a flat or curved dorsal strand) with two lateral rib traces, e.g. *Terminalia oblonga* (figure 6/2C).

D - Outline same as above but the vascular system is a complete or sometimes slightly dissected medullated cylinder with two rib traces, e.g. *Buchenavia pallidovirens* (figure 6/2D) and *Bucida buceras*.

E - Outline circular or elliptic with two lateral wing-like projections; vascular system is a complete medullated cylinder, with two lateral rib traces, e.g. *Buchenavia macrophylla* (figure 6/2E) and *Ramatuella argentea*.

F - Outline as in E but the vascular system is a crescentiform strand usually with inrolled ends and without rib traces, e.g. section *Chicharronia* (*Terminalia domingensis*, figure 6/2F).

G - Outline same as above but with two rib traces, e.g. *Terminalia quintalata* (figure 6/2G), *Ramatuella virens*.

epidermal

6.4.10. Key to American species of *Terminalia* based on cuticular characters only

1 - Domatia present 2

1 - Domatia absent 5

  2 - Hair-bases large, abundant to very abundant on abaxial surfaces; domatia usually marsupiform, densely pubescent, present only in the axil of the primary veins 3

  2 - Hair-bases small, usually confined to the major veins; domatia often lebetiform, sparsely pubescent or glabrous, present in the axil of primary, secondary, tertiary or higher-order veins. . . 4

3 - Walls of abaxial and adaxial epidermis curved or slightly undulated . . . . *T. acuminata*

3 - Walls of abaxial and adaxial epidermis strongly undulated . . . . *T. glabrescens*

4 - Walls of adaxial epidermis moderately to strongly undulated . . . . *T. amazonia*

4 - Walls of adaxial epidermis weakly undulated . . . . *T. catappa* & *T. latifolia*

5 - Walls of abaxial epidermis straight or curved to slightly undulate 6

5 - Walls of abaxial epidermis moderately to strongly undulated 11

6 - Stomata confined to abaxial epidermis 7

6 - Stomata on both adaxial and abaxial epidermises 8

7 - Walls of abaxial epidermis straight or curved; hair-bases frequent to very frequent on major veins, sparse elsewhere; areolation not conspicuous . . . . *T. australis*

7 - Walls of abaxial epidermis slightly undulated; hair-bases abundant to very abundant on major veins, frequent to very frequent elsewhere; areolation conspicuous . . . . *T. eichleriana*

8 - Stomata adaxially frequent to abundant, rarely absent in the areoles; hair-bases always small and absent in the areoles .... *T. actinophylla*

8 - Stomata adaxially absent in the areoles; hair-bases large or small, frequent to very abundant in the areoles 9

9 - Hair-bases usually large; higher-order veins and aerolation usually conspicuous . . . . *T. fagifolia*

9 - Hair-bases always small; higher-order veins and areolation usually inconspicuous 10

10 - Hair-bases usually very abundant adaxially, rarely sparse in the areoles; walls of adaxial epidermis straight . . . . *T. argentea* & *T. phaeocarpa*

10 - Hair-bases frequent or abundant on major veins, rare elsewhere; walls of adaxial epidermis curved to slightly undulated . . . . *T. triflora*, *T. reitzii* & *T. uleana*

11 - Cuticle very thin to thin 12

11 - Cuticle thick to very thick 19

12 - Stomata confined to abaxial epidermis 13

12 - Stomata on both adaxial and abaxial epidermises 17

13 - Hair-bases large 14

13 - Hair-bases small 15

14 - Walls of adaxial epidermis straight; higher-order venation and areolation often raised; hair-bases abundant to very abundant . . . . _T. eriostachya_

14 - Walls of adaxial epidermis undulated; higher-order venation not raised; hair-bases sparse, usually confined to primary and secondary veins . . . . _T. arbuscula_

15 - Higher-order venation and areolation usually present and conspicuous 16

15 - Higher-order venation and areolation usually absent, if present then inconspicuous . . . . _T. januariensis_

16 - Walls of adaxial epidermis straight or slightly curved . . . . _T. lucida_

16 - Walls of adaxial epidermis moderately to strongly undulated . . . . _T. dichotoma_

17 - Higher-order venation and areolation very conspicuous; all features of stomata very conspicuous; walls of adaxial epidermis straight; hair-bases sparse . . . . _T. chicharronia_

17 - Higher-order venation and areolation often absent or inconspicuous, features of stomata scarcely visible but T-pieces sometimes conspicuous; walls of adaxial epidermis slightly or moderately undulated; hair-bases frequent or abundant on veins 18

18 - Cuticle very thin; walls of adaxial epidermis usually curved to slightly undulate; hair-bases sparse and often confined to midrib . . . . _T. guyanensis_

18 - Cuticle thin-thick; walls of adaxial epidermis undulated; hair-bases frequent to abundant on major veins, sparse elsewhere . . . . T. oblonga

19 - Hair-bases very abundant, particularly abaxially . . . . T. steyermarkii

19 - Hair-bases extremely sparse, if present confined to midribs and secondry veins 20

20 - Stomata nearly equally frequent on both abaxial and adaxial epidermises . . . . T. yapacana

20 - Stomata usually confined to abaxial surfaces, if adaxially present confined to midrib and secondary veins 21

21 - Adaxial antclinal walls very thick and moderately to strongly undulated; periclinal walls granulate or perforate . . . . T. quintalata & T. guiaquinimae

21 - Adaxial anticlinal walls usually thin and straight to slightly undulate; periclinal wall smooth . . . . T. chicharronia

6.5. Discussion

Terminalia, Ramatuella, Bucida and Buchenavia are closely related genera which are also anatomically very similar. Bucida can be separated from the other three genera on the basis of its distinctive subepidermal sclerenchyma, but otherwise shows close similarity to Buchenavia and various species of Terminalia.

The four species of Bucida examined are anatomically very similar or uniform and not separable on cuticular characters. Also all species of Ramatuella are very similar and not or hardly separable on anatomical characters, although there is some variation in the distribution of hair-bases and stomata between species.

The variation shown by Terminalia covers most of that of Buchenavia and Ramatuella. Ramatuella differs in anatomical characters from Buchenavia and Bucida, but closely resembles those of Terminalia section Pachyphyllum. This fact supports the similarity in gross morphology and pollen structure between the two taxa.

The leaf anatomy of Buchenavia and Bucida, on the other hand, closely resembles that of other, less xeromorphic sections of Terminalia, e.g. sections Chuncoa, Oblonga, Terminalia.

This pattern of variation supports the idea that Terminalia resembles an ancestral group which gave rise to Ramatuella, Bucida and Buchenavia.

In Terminalia leaf anatomy and particularly cuticular characters are of high taxonomic value at specific levels and show considerable variation between species. Hence most morphologically distinct species are separable on cuticular characters alone (see key, section 6.4.10.). Also several sections can be identified by their leaf anatomy. Leaf anatomy can help in identification of sterile material of closely related species. For example, Terminalia amazonia and T. glabrescens can be separated by their hair-bases and T. quintalata and T. yapacana by the degree of distribution of stomata on the adaxial leaf surface. Also leaf anatomy provides useful criteria for establishing synonymy between closely related taxa and helps the data offered by external morphology and other sources.

Buchenavia also shows the same type of variation as in Terminalia. Most of the species can be separated on cuticular characters alone (Stace 1965b). Cuticular characters are very similar in some species, e.g. B. capitata, B. kleinii, B. parvifolia and B. oxycarpa, but in many others they are distinct and characteristic, for example B. sericocarpa, which has palisade like epidermal cells, and B. suaveolens, which has cells round the stomata differing from the rest of epidermal cells in the nature of the inner periclinal walls and degree of staining (plate 6/4F). Large stomata and thick cuticle are characteristic of *B. nitidissima* and *B. guianensis*, and large hair-bases of *B. tomentosa*.

Key to Table 6/1 (see also text)

Domatia: A. absent B. Present

Hair-bases:

Type: A. small B. large

Distribution: A. glabrous to extremely sparse B. frequent on major veins C. abundant on veins, sparse to frequent on intervenal areas D. very abundant on intervenal areas.

Adaxial epidermis:

Cuticular thickness: A. very thin B. thin C. thick D. very thick

Undulation: A. straight B. curved - slightly undulate C. conspicuously (moderately) undulate D. strongly or deeply undulate

Venation: A. areolation raised B. areolation conspicuous but not raised C. areolation absent D. only primary, secondary and few tertiary veins present

Abaxial epidermis: same categories as in Adaxial epidermis.

Stomata:

Distribution on adaxial epidermis: A. absent B. frequent on primary veins. Absent on secondary veins C. abundant on primary veins, frequent on secondary veins. D. frequent to abundant on intervenal areas.

Type: A. stomata elliptic to narrowly elliptic; features of stomata scarcely visible B. stomata often rounded; features of stomata very conspicuous.

Table 6/1. Summary of major epidermal characters of 47 species of Terminalia (from America), 6 of Ramatuella, 4 of Bucida and 17 of Buchenavia.

Character / Species	domatia	Hair-bases		Adaxial epidermis			Abaxial epidermis			Stomata	
		type	distribution	cuticular thickness	undulation	venation	cuticular thickness	undulation	venation	distribution on adaxial epidermis	type
1. Terminalia actinophylla	A	A	B-C	C	A-B	C	C	A-C	C-B	C-D	A
2. T. acuminata	B	B	C	B	B	D-C	B	B	D	C	A
3. T. amazonia	B	A	B-C	C	D-C	C-D	B	D-C	D	C	A
4. T. arbuscula	A	B	C	A	B	B	A	D	B	A	A
5. T. argentea	A	A	D	C	A	D	C	A	D	C	A
6. T. aroldi = 13	A	A	A	B	A-B	D	B	B-C	C-B	B	B
7. T. australis	A	A	B-C	A	B	B-C	A	B	B	A	A
8. T. biscutella = 5	A	A	B-C	B	A	D	A	A	D	B	B
9. T. brasiliensis = 19	B	B	C	B-C	D	C-D	B	D	C	B	A
10. T. bucidoides = 33	A	A	B-C	B	B	B-C	B	B	B-C	B	A
11. T. camoxa	A	A	A	A	C	D	A	D	D	B	A
12. T. catappa	B	A	C	A	B	B-C	A	B-C	B-C	B-C	A
13. T. chicharronia	A	A	C-B	B-C	A	B	A-B	C	A	B	B
14. T. dichotoma	A	A	C	D	C	B-A	C	D	B-A	A	A
15. T. domingensis = 13	A	A	A	C	B-C	C	C	C	B-C	B	B
16. T. eichleriana	A	A	D-C	B	A-(B)	B-C	A	A-B	B	A	A
17. T. eriostachya	A	B	C	C	A	C-D	B	B	C	A	A-B
18. T. fagifolia	A	B	D	C	A	C	A	A-B	A-B	B	A
19. T. glabrescens	B	B	D	B-C	D	D	B	D	C-D	B	A
20. T. grandialata = 24	A	A	B	C	B	C-D	B	B	C-D	A	A
21. T. guaiquinimae	A	A	A	D	B	D	C	C	D	C	B
22. T. guyanensis	A	A	C	B	A-B	C	A	C	B-C	B	B
23. T. hylobates = 37	A	A	C	B	A	B	A	A	B	C	A

24. T. januariensis	A	A	C-B	B	C	D-C	A	C	D-C	A	A
25. T. latifolia	B	A	C	A	B-C	C	A	C	D	B-C	B
26. T. lucida	A	A	A-B	B-C	A-B	C	A	C	B-C	A	A
27. T. maestyrensis = 13	A	A	C	B	C	B	A	C-D	A	B	B
28. T. mameluco = 33	A	A-(B)	B-A	B	B	B-C	B	C-B	B	B	A
29. T. neglecta = 13	A	A	B-C	B	B	B-C	B	B-C	B	B	B
30. T. nipensis = 13	A	A	A	C	A	D	C-B	A-C	D	B	B
31. T. nassaefolia = 26	A	A	B	B-C	B	C	A	B-C	B	A	A
32. T. obidensis = 33	A	A	B	B	B	B	A	B	B	B	B
33. T. oblonga	A	A	B	B	B	B	A	B-C	C	B	B
34. T. opacifolia = 21	A	A	A	D	D	D	D-C	D	D	C	B
35. T. orientensis = 13	A	A	A	C-D	A-C	D	C	C	C-D	B	B
36. T. pachystyla = 13	A	A	A	D	A-B	D	C	C	C-D	B	B
37. T. phaeocarpa	A	A	C	C	A	B	A	A	B	C	A
38. T. quintalata	A	A	A	D	B-C	D	D	B	D	C	B
39. T. reitżii	A	A	B-C	B	B	D	A	A-B	C-D	A	A
40. T. riedelii	A	A	C	B	C	D-C	A	C	D	A	A
41. T. steyermarkii	A	A	D	C-D	C	D	B-C	B-C	D	C	B
42. T. subsericea = 5	A	A	C-D	C	A	D	B	A	D	C	A
43. T. tarapotensis = 33	A	A	B-C	B	B	B	A	B	(B)-C	B	B
44. T. triflora	A	A	C	A	B	D	A	A-B	D-C	B	A
45. T. uleana	A	A	C	A	A-B	C	A	A-B	C	B	A
46. T. virgata = 21	A	A	A	D	B	D	C	C	D	C	B
47. T. yapacana	A	A	A	C	B	D	C	B-C	D	D	B
48. Ramatuella argentea	A	A	D	C	B	D	C	A-B	D	C	B
49. R. crispialata	A	A	B-C	C	B	D	B	A-B	D	C	B
50. R. latifolia	A	A	B	B-C	B	D	B	A-B	D	C	B
51. R. maguirei	A	A	B	C	B	D	B-C	A-B	D	C	B
52. R. obtusa	A	A	B-C	C	B	D	B	A-B	D	C	B
53. R. virens	A	A	B-C	(C)-D	B	D	D	A-B	D	D-C	B

54. *Bucida buceras*	A	A	A	B-C	C	C	B	C	C	B	A
55. *B. ophiticola*	A	A	A	B-C	B	D	B	C	C	A	B
56. *B. spinosa*	A	A	A	C-B	C	D	B	C	C-B	B	A
57. *B. subinermis*	A	A	A	C-B	C-D	C	B	C-D	B	B	A
58. *Buchenavia capitata*	B	A	B-C	A-C	B	C	A-B	C-D	C-B	B	A
59. *B. congesta*	A	A	B	B-C	D	D	B	C-B	C-D	B	B
60. *B. grandis*	A	A	B-C	B-C	B	C	B	C-B	B-C	B	A
61. *B. guianensis*	A	A	A-B	C-D	D	C	C	D	B-A	B	B
62. *B. hoehneana*	A	A	B-C	B-C	B	D-C	B	C	C	B	A
63. *B. igaratensis* = 64	B	A	B-C	B-C	A-B	C	B	B	B	A	A
64. *B. kleinii*	B-A	A	B-C	B	B-C	B	A	B	B	B	A
65. *B. macrophylla*	A	A	B-C	B	C	D	A	D	C-B	B	A
66. *B. nitidissima*	A	A	A	C-D	B	D	B	D	D	B	A-B
67. *B. ochroprumna*	B	A	B-C	B	B	D	B	D	C	B	A
68. *B. pallidovirens*	A	A	B	C	B-A	C	B	D	B	B	B
69. *B. parvifolia*	B	A	B-C	B	B	D	B	C-D	C	B	A
70. *B. rabelloana* = 69	A	A	B-C	B-C	B	D	B	C-D	D-C	B	A
71. *B. sericocarpa*	B-A	A	B-C	B-C	B	D	B	C-B	D-C	B	A
72. *B. suaveolens*	A	A	A	B-C	A	C	B	A-B	B	B	A
73. *B. tomentosa*	A	B	C-D	B	A	C	A	C	A	B	A
74. *B. viridiflora*	A	A	C	B	B	C-D	B	B	C	B	A

Table 6/2. Dimensions of stomata, stomatal index, lamina and cuticle thickness, shape of epidermal cells and shape of adaxial midrib of species of Terminalia, Ramatuella, Bucida and Buchenavia

co = columnar; F = flattened; G = grooved; PR = prominently raised; R = raised; re = rectangular; sq = square; SR = slightly raised.

Character / Species	Thickness of lamina	Stomatal index	Width of stomata (averages between extremes)	Length of stomata (averages between extremes)	Thickness of adaxial cuticle	Thickness of abaxial cuticle	Shape of adaxial epidermal cells	Shape of midrib(adaxial)
1. T. actinophylla	240	36	20-21-22	18-20-22	5	5	re	R
2. T. acuminata	100	21	10-11-12	15-17-18	2-4	2-3	re	SR
3. T. amazonia	140-230	21	12-15-17	18-23-27	2-10	2-5	re	F-SR
4. T. arbuscula	90-110	8	12-14-17	22-25-27	1-2	1	re	F-G
5. T. argentea	200-240	16	13-15-17	18-20-22	7-8	5-6	re-sq	R-PR
6. T. australis	200-225	21	8-10-12	19-20-22	1	1	re-sq	PR
7. T. bucidoides = 21	170-190	21	8-10-11	18-20-22	3	1	re	SR
8. T. catappa	200	12	10-13-15	15-22-25	1-2	1-2	re	G
9. T. chicharronia	350	21	20-22-25	20-22-25	3-4	1-2	sq-re	G
10. T. dichotoma	250-270	16	10-12-15	20-23-25	12	5-7	re	SR
11. T. eichleriana	120-150	25	10-13-15	14-17-20	3	1-2	re	F
12. T. eriostachya	320-340	7	16-18-20	17-20-24	6-8	4-5	re	G
13. T. fagifolia	170	21	10-13-16	13-15-18	5-6	1-2	sq-re	SR
14. T. glabrescens	240-260	19	20-25-30	20-25-33	5	2-3	re	SR
15. T. grandialata = 18	220	13	10-12-15	20-23-25	5-7	2-3	sq-re	SR
16. T. guaiquinimae	500-580	16	25-27-30	20-25-28	20-25	5-6	sq-co	F
17. T. guyanensis	150-180	14	14-15-18	19-22-24	2-3	1-2	sq-re	R
18. T. januareiensis	200-210	11	10-13-15	19-23-25	2-3	1-2	re	SR
19. T. latifolia	210	11	12-15-17	20-23-24	1-2	1-2	re	G
20. T. lucida	200-210	21	11-13-20	28-30-32	4-6	2	re	SR

21. T. oblonga	180-250	18	18-22-25	22-25-30	5-6	2	re	R
22. T. opacifolia = 16	350	17	23-27-32	24-27-32	11-13	9-11	co	F
23. T. orientensis = 9	600-650	21	25-28-30	25-27-30	15-17	9-10	sq	F
24. T. phaeocarpa	160-180	20	12-14-16	14-15-17	3	1	re	R
25. T. quintalata	300-350	14	27-30-32	25-28-30	14-16	12-15	co	F
26. T. reitzii	100-150	15	8-13-15	15-18-22	2-3	1-2	re	R
27. T. riedelii	150-180	11	15-18-20	15-18-22	2-4	1-2	re	SR
28. T. steyermarkii	500-550	13	25-31-35	25-31-35	8-12	5-10	co	F
29. T. subsericea = 5	150	9	8-11-15	15-19-22	7	5	re	SR
30. T. triflora	170-200	11	10-13-15	18-20-21	1	1	re	SR
31. T. virgata	500	20	25-30-32	25-29-34	20-25	8-10	sq-co	F
32. T. yapacana	350-400	33	25-28-31	25-30-35	6-9	5-7	re	F
33. Ramatuella argentea	200-250	17	15-21-23	15-22-25	10-12	8	re	F
34. R. crispialata	400-450	21	28-31-35	26-30-35	6-7	3	re	F
35. R. latifolia	250-300	30	22-26-32	20-26-30	5-8	4	re	F
36. R. maguireii	250	23	20-25-28	20-25-30	5-7	4-5	re	F
37. R. obtusa	400	21	27-30-33	28-31-35	5-7	4	re	F
38. R. virens	350-400	22	24-27-32	25-29-33	12-25	10-25	re	F
39. Bucida buceras	170-220	23	15-21-25	20-24-27	3-5	2-3	re	F
40. B. ophiticola	350-370	14	10-15-18	20-22-25	3-5	2-3	sq	F-G
41. B. spinosa	300-350	22	17-20-25	17-22-25	3-7	3-5	sq-re	F
42. B. subinermis	280-330	17	15-20-25	20-26-30	3-7	4-5	re	F
43. Buchenavia capitata	150-200	26	14-18-22	20-25-30	3-7	2-4	re	F
44. B. congesta	200-250	22	18-24-27	20-30-33	3-5	2-4	re	SR-R
45. B. grandis	200-300	12	17-25-30	15-25-30	5-7	3-5	sq-re	R
46. B. guianensis	200-300	20	25-30-37	25-30-35	8-12	7-10	re	R
47. B. hoehneana	250-350	15	20-25-32	25-29-35	3-5	2-4	re	F
48. B. igaratensis = 49	270-300	17	20-23-25	25-30-37	6-8	3-5	sq	F
49. B. kleinii	220-260	17	15-20-25	20-24-30	3-5	1-2	re	F
50. B. macrophylla	180-220	10	18-20-25	22-30-35	2-3	1-2	re	F

51. <u>B. nitidissima</u>	300-400	16	30-33-40	25-35-50	8-12	4-6	sq-re	F
52. <u>B. ochroprumna</u>	170-250	28	15-18-22	18-20-25	2-5	2-4	re	F
53. <u>B. oxycarpa</u>	180-220	10	15-22-25	18-24-28	6-9	5	re	F-SR
54. <u>B. pallidovirens</u>	300-350	23	27-29-33	25-34-40	7-10	3-5	sq	R
55. <u>B. parvifolia</u>	100-170	14	17-20-25	18-22-27	4-5	2-3	re	F
56. <u>B. rabelloana</u> = 55	300	17	15-18-20	19-25-28	6-10	3-5	re	F
57. <u>B. serioccarpa</u>	200-250	04	13-16-23	18-20-24	3-7	3-5	co	G
58. <u>B. suaveolens</u>		07	18-20-25	20-23-27				
59. <u>B. tomentosa</u>	200-250	19	22-25-30	25-28-33	5	2	sq-re	SR
60. <u>B. viridiflora</u>	200-350	17	22-25-30	20-27-33	3-5	2-5	re	F-SR

Figure 6/1: Drawings of leaf lamina T.S. of Terminalia.

A. T. hylobates, showing palisade tissue thicker than spongy tissue.

B. T. domingensis showing bundle sheath extension, and palisade tissue much thinner than spongy tissue. D. T. laxiflora showing adaxial hypodermis. E. T. quintalata showing columnar epidermal cells.

F. T. fagifolia showing undifferentiated mesophyll.

C. T. triflora showing crystals in mesophyll.

Figure 6/2: Drawings of petiole T.S.

A. Terminalia reitzii showing a single crescentiform vascular system. B. Buchenavia capitata, showing crescentiform vascular system with two rib traces. C. T. oblonga showing two main strands and two rib traces. D. B. pallidovirens showing circular vascular system. E. B. macrophylla petiole with wing-like projections. F. T. domingensis showing 2 adaxial wing-like projections and a thick ring of schlerenchyma cell surrounding the vascular strand. G. T. quintalata showing inrolled vascular system and long lateral wings.

Plate 6/1: SEMs of intact leaf surfaces of Terminalia. Scale bar for A-E = 20 μm, F =5μm, G = 100 μm.

A. T. bellirica, abaxial surface, showing stomata surrounded by curved cuticular ridges (extra cuticular ridge). B. T. myriocarpa, abaxial surface, showing striate pattern of cuticular ornamentation.

C. T. argentea, abaxial surface, showing trichomes and stomata surrouned by cuticular ridges. D. T. perrieri, abaxial surface, showing smooth surface, small particles of wax and no cuticular ridges

E. T. bellirica, adaxial surface, showing striate-reticulate ornamentation. F. T. australis, abaxial surface, showing an elongate stoma with long and narrow ledge and abundant wax. G. T. domingensis, adaxial surface, showing reticulate ornamentation.

Figure 6/1

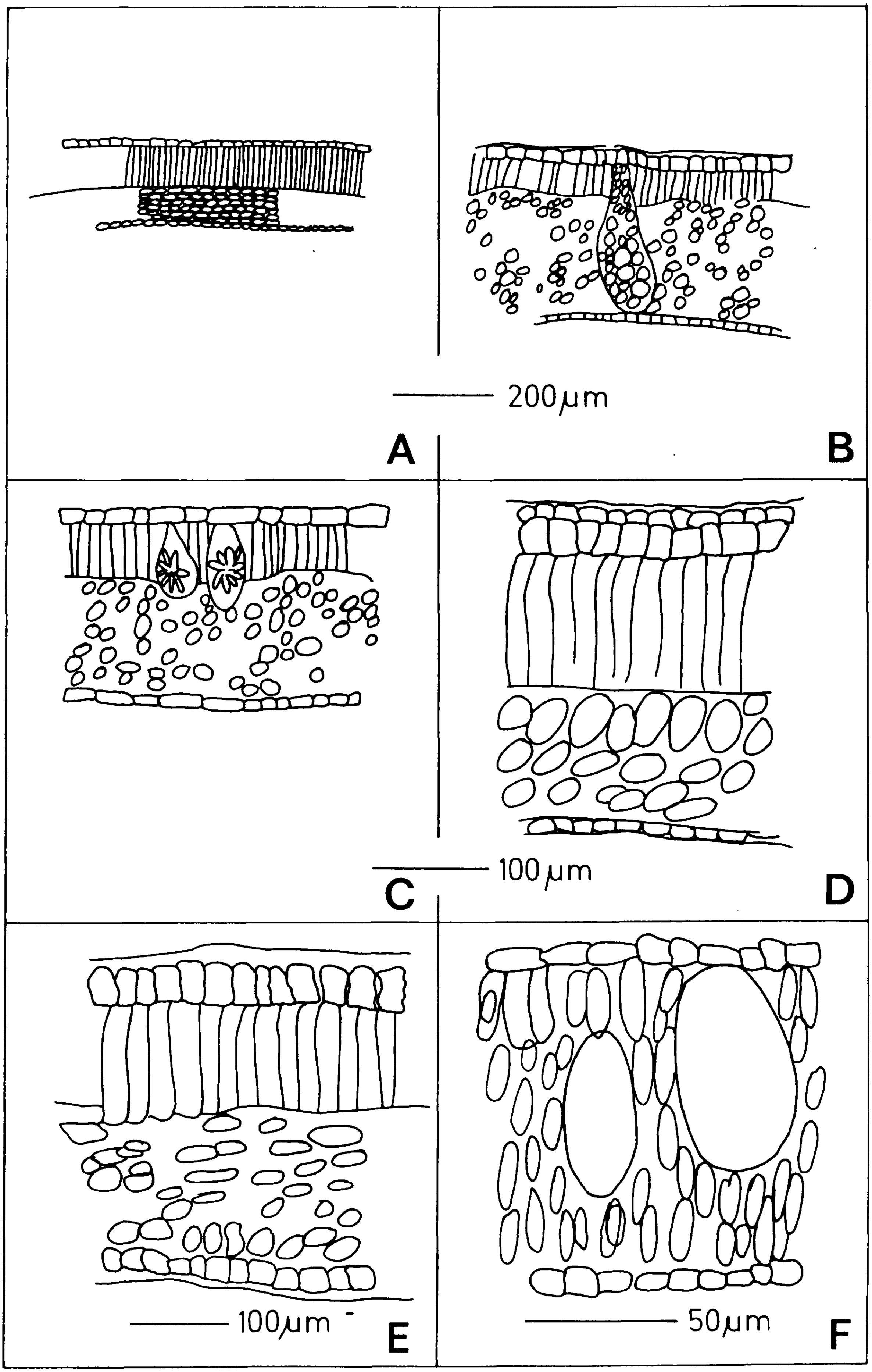
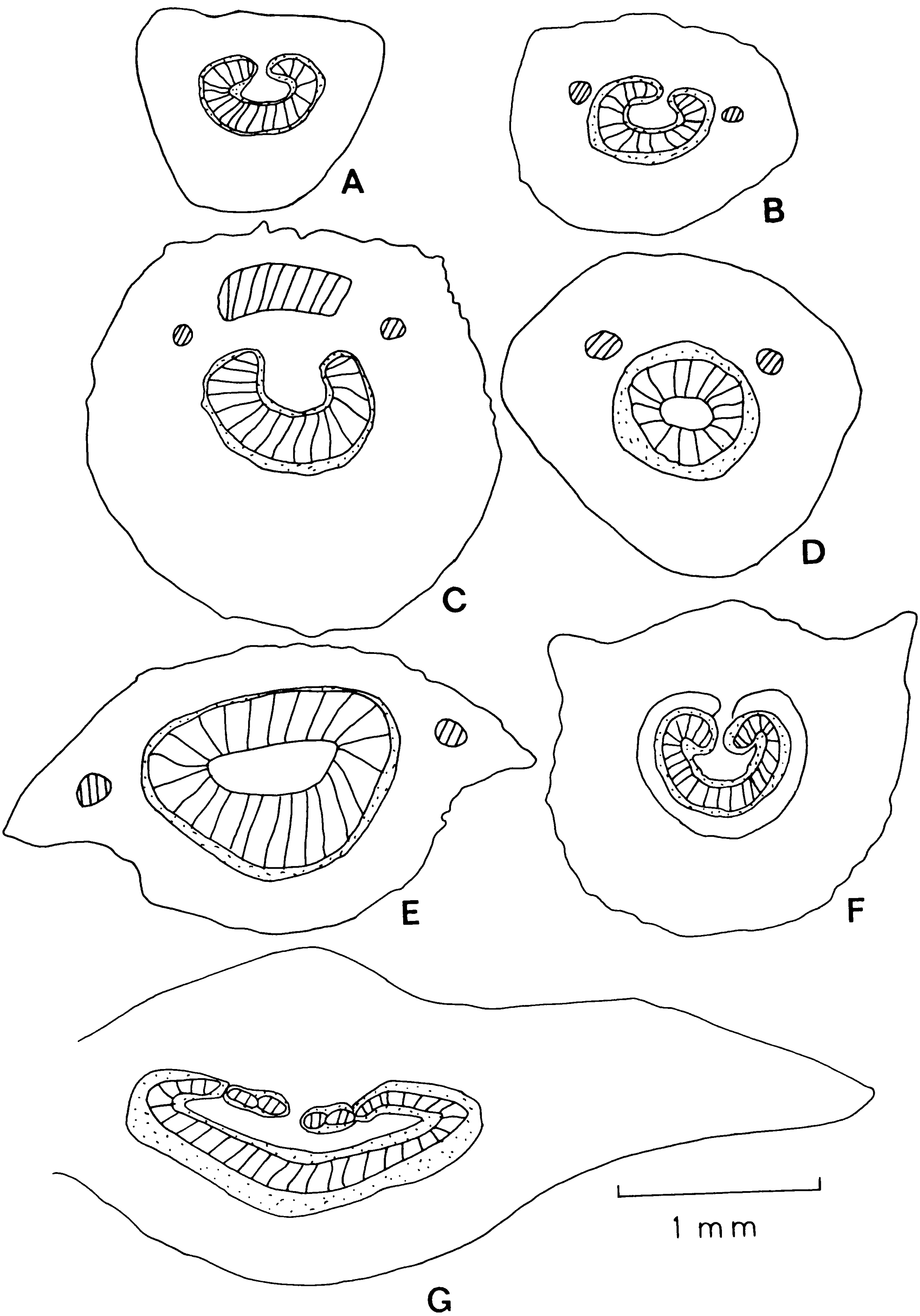


Figure 6/2



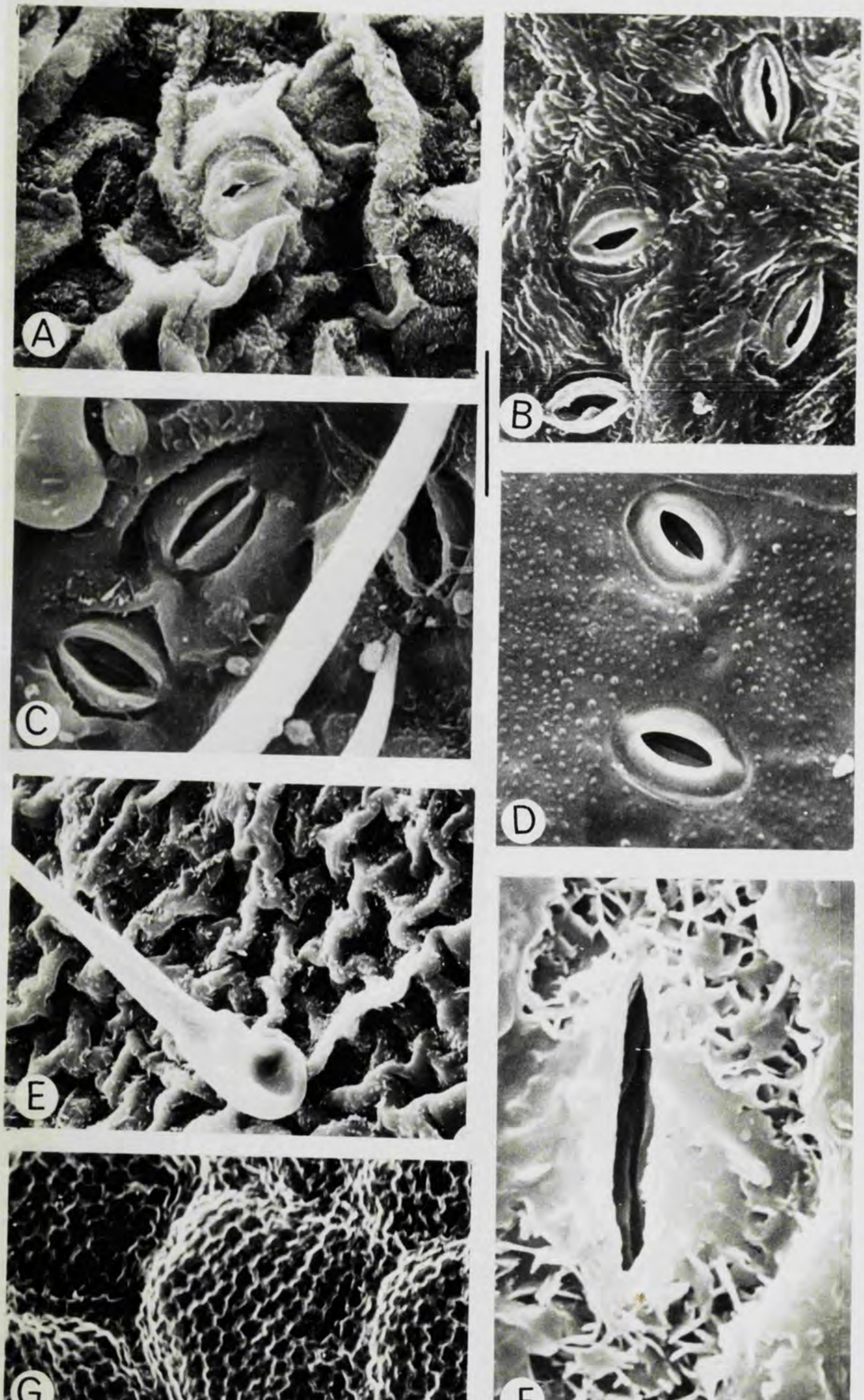


PLATE 6/1

Plate 6/2. SEMs of intact abaxial leaf surfaces of Terminalia and Buchenavia. Scale bar for A-D =µ10 M, E-F = 400 µm.

A. T. actinophylla, showing convex outer walls. B. T. platyptera, showing abundant epicuticular wax. C. T. nitens, showing rounded and sunken stomata. D. T. eriostachya, showing slightly raised stomata. E. T. acuminata, showing marsupiform domatia. F. B. fanshawei, showing lebetiform domatium.

Plate 6/3: SEMs of intact leaf surfaces of Buchenavia and Bucida. Scale bar = 10 µm.

A. B. reticulata, abaxial surface, showing stomata with raised ledge, cuticular ridges and abundant wax. B. B. pallidovirens, abaxial surface, showing round and sunken stoma. C. B. capitata, abaxial surface, showing smooth surface and stoma with thick and elongate ledge. D. Bucida spinosa, abaxial surface, showing smooth surface and stoma with stomatal ledge and cuticular ridges. E. Buchenavia reticulata, adaxial surface, showing surface sculpturing and scales of wax. F. Buchenavia fanshawei, abaxial surface, showing curvature of outer walls.

Plate 6/4: SEMS of cuticularséprations of Terminalia, Ramatuella, and Buchenavia. Scale bar = 10 µm.

A & B. T. neglecta, abaxial epidermis (A. from outside, B. from inside, showing imperforate walls. C & D. T. quintalata, abaxial epidermis (C. from outside, D. from inside), showing perforate anticlinal and periclinal walls. E. R. virens, adaxial epidermis from inside, showing granulate periclinal walls. F. B. suaveolens, abaxial epidermis from inside, showing granulate periclinal walls.

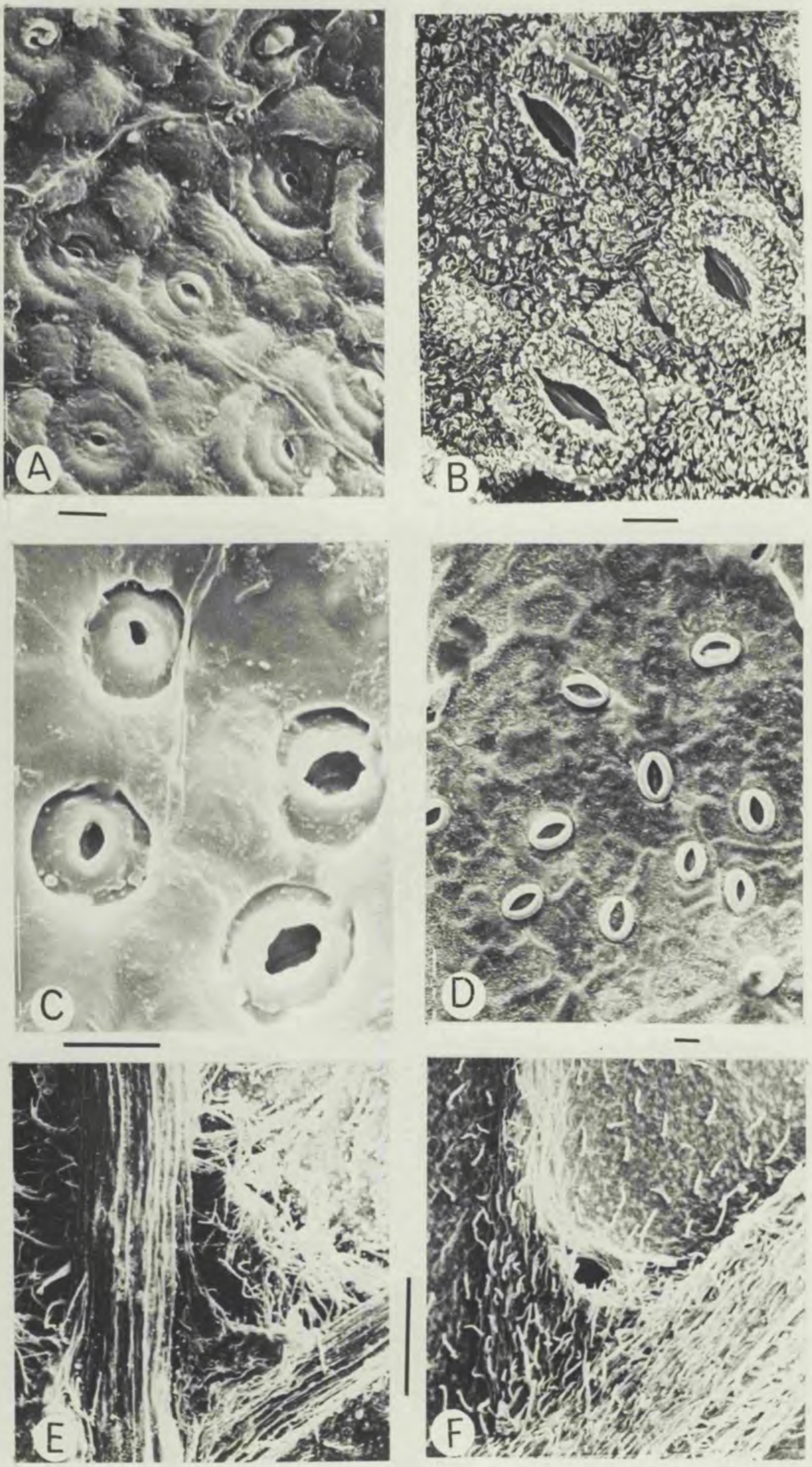


PLATE 6/2

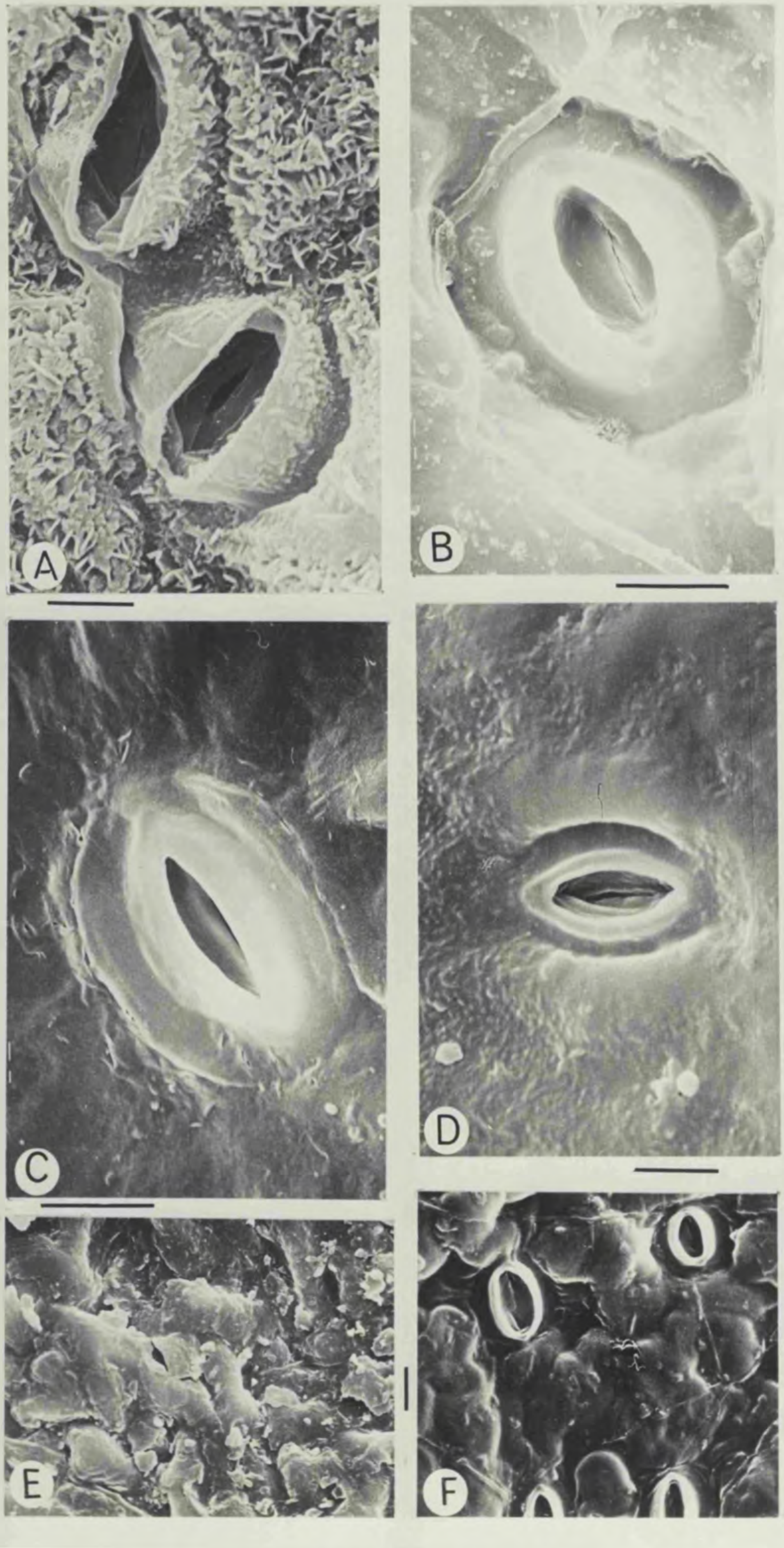


PLATE 6/3

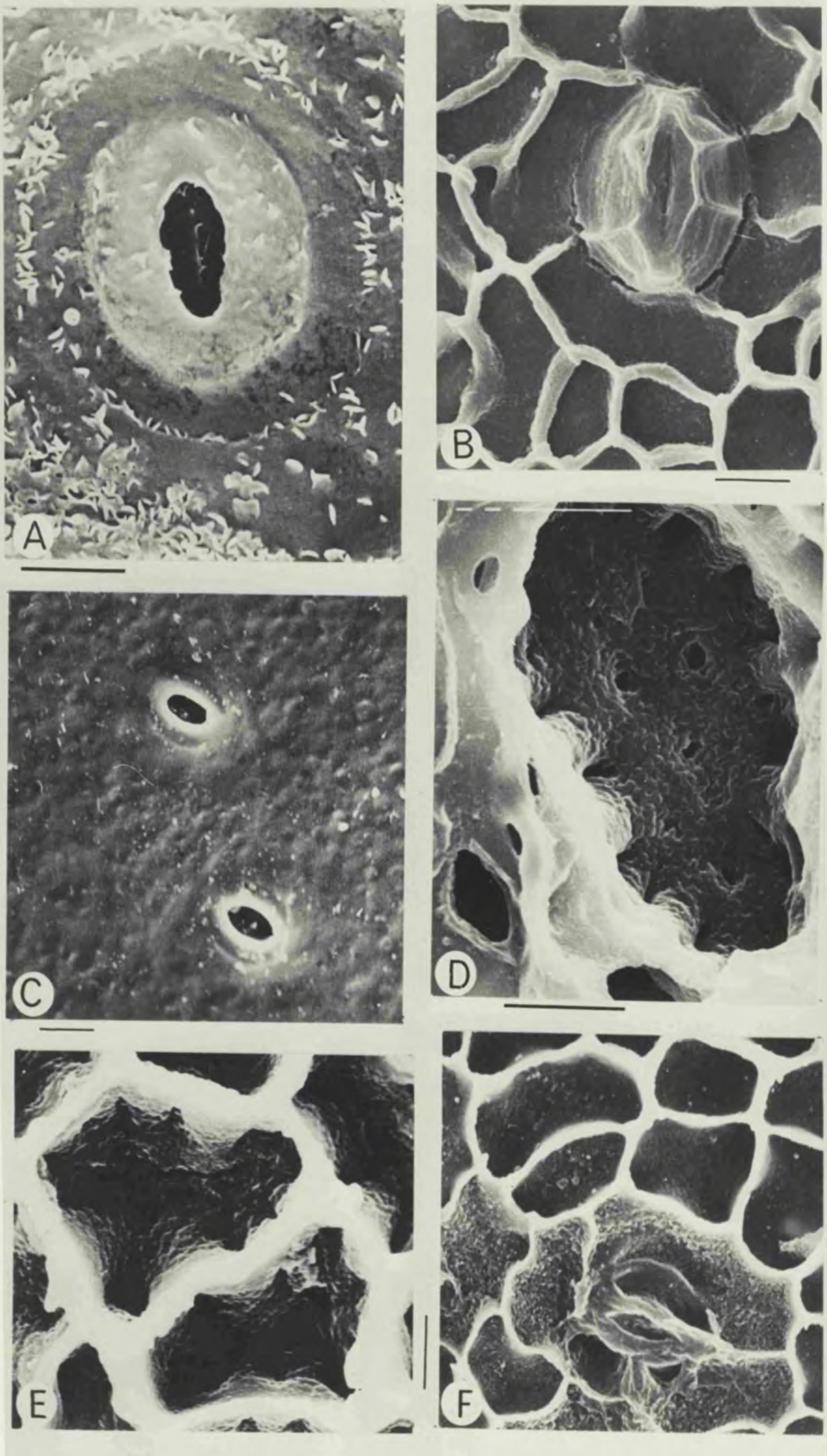


PLATE 6/4

Plate 6/4

Plate 6/5: Light micrographs of leaf cuticles of Terminalia.

Scale bar = 10 µm.

A. *T. virgata*, abaxial epidermis, showing very thick anticlinal walls. B. *T. orientensis*, abaxial epidermis, showing details of stomata and undulated walls. C. *T. nipensis*, adaxial epidermis, showing straight walls. D. *T. glabrescens*, adaxial epidermis, showing strongly undulated walls. E. *T. guyanensis*, adaxial epidermis, showing small hair bases (compare size of cells and wall thickness with C). F. *T. opacifolia*, adaxial epidermis, showing alternating buttresses and cavities along anticlinal walls. G. *T. neglecta*, abaxial epidermis, showing midrib cells.

Plate 6/6: Light micrographs of leaf cuticles of Terminalia, Ramatuella and Buchenavia. Scale bar = 15 µm.

A. *T. quintalata*, abaxial epidermis, showing perforate walls. B. *R. virens*, adaxial epidermis, showing stomata and perforate walls. C. *T. dichotoma*, abaxial epidermis, showing narrowly elliptic stoma with inconspicuous epidermal walls of the guard cells (Type A stoma). D. *T. actinophylla*, adaxial epidermis, showing anticlinal walls of Type B. E. *T. biscutella*, adaxial epidermis, showing anticlinal walls of Type A. F. *B. guinanensis*, abaxial epidermis, showing stomata of Type B. G. *T. fagifolia*, abaxial epidermis, showing large hair-bases (Type B). H. *T. eichleriana*, adaxial epidermis, showing typical combretaceous hair.

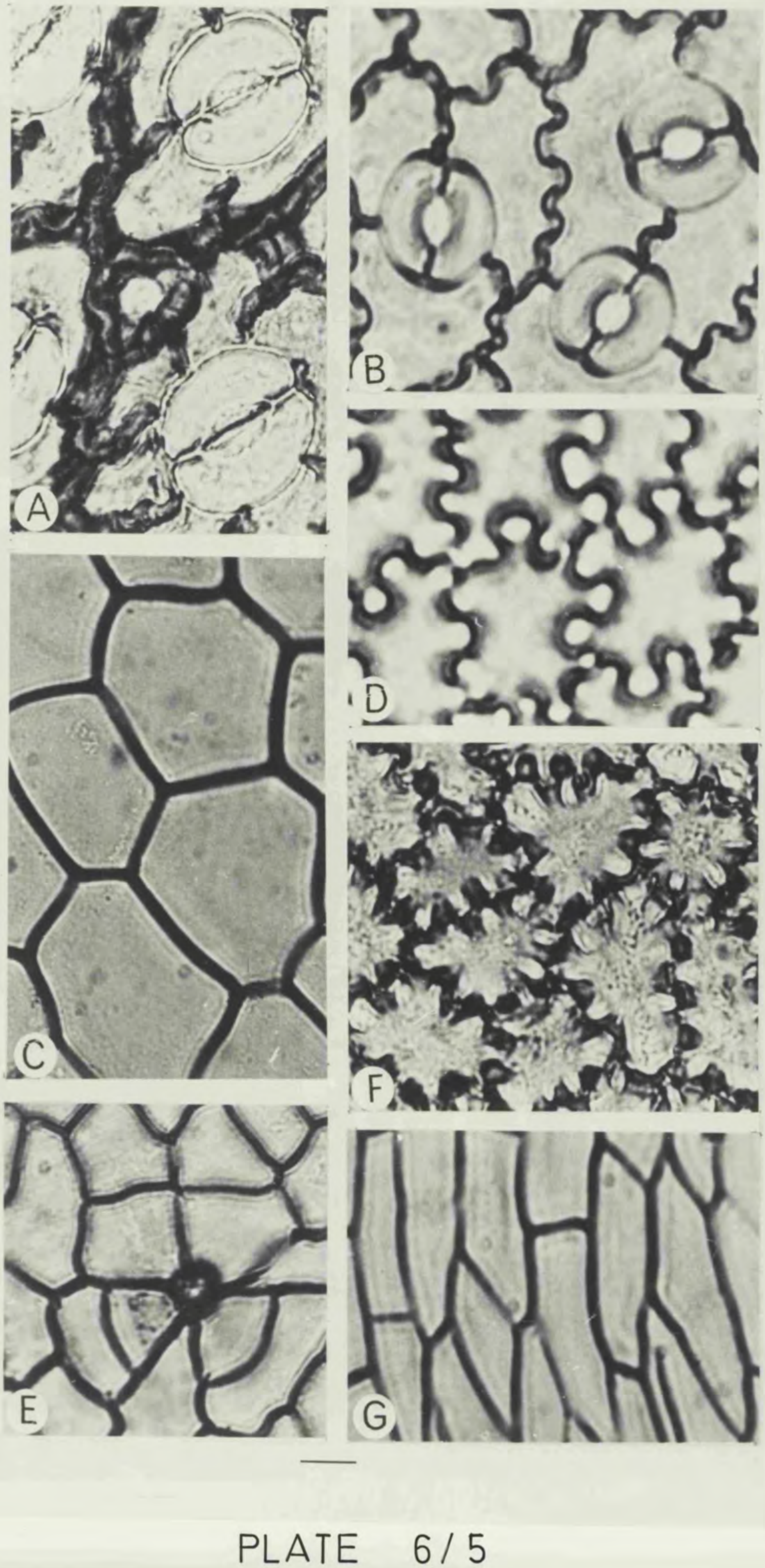


PLATE 6/5

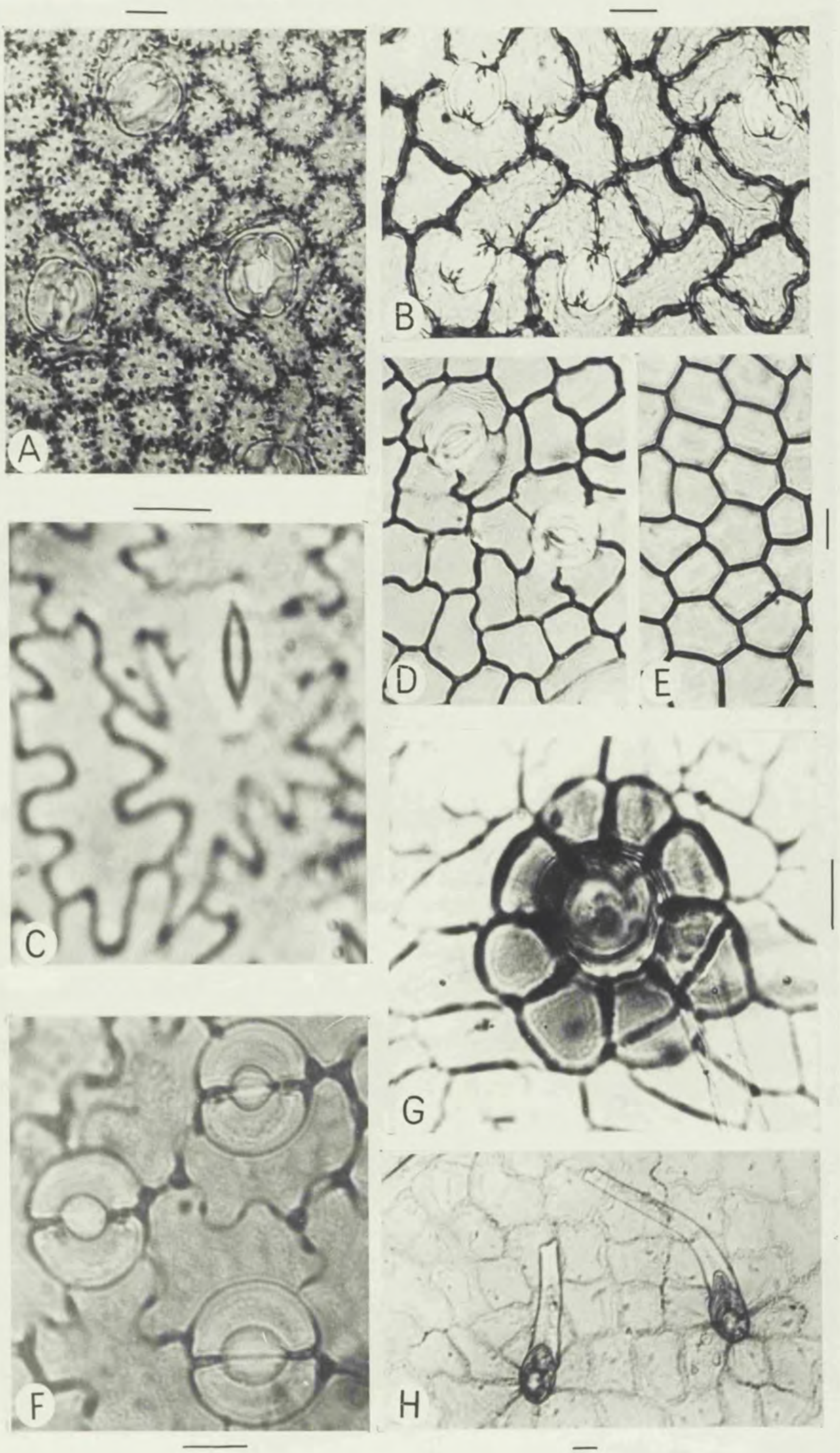


PLATE 6/6

Plate 6/7: Leaf T.S. of Buchenavia, Terminalia and Bucida, A-E midrib, F-H lamina. Scale bar = 100 µm.

A. B. macrophylla, showing vascular system of two segments and no ring of sclerenchyma cells. B. B. pallidovirens, showing raised adaxial surface and an interrupted ring of sclerenchyma round the vascular system. C. B. nitidissima, showing thick cuticle and few sclerenchyma cells. D. B. seriococarpa, showing vascular system surrounded by a ring of sclerenchyma cells. E. T. dichotoma, showing a thick ring of sclerenchyma cells surrounding the vascular system.

F. Buchenavia capitata, showing bundle sheath extension.

G. B. sericocarpa, showing palisdade-like epidermal cells.

H. Bucida subinermis, showing subepidermal layer of sclerenchyma cells and large amount of sclerenchyma in mesophyll.

Plate 6/8: Petiole T.S. of Buchenavia and Terminalia.

Scale bar = 250 µm.

A. B. rabelloana, showing crescentiform vascular strand with two rib traces. B. B. tomentosa showing circular vascular strand.

C. T. argentea, showing a circular strand with no rib traces.

D. T. hylobates, showing crescentiform strand with slightly inrolled ends, and one lateral rib trace.

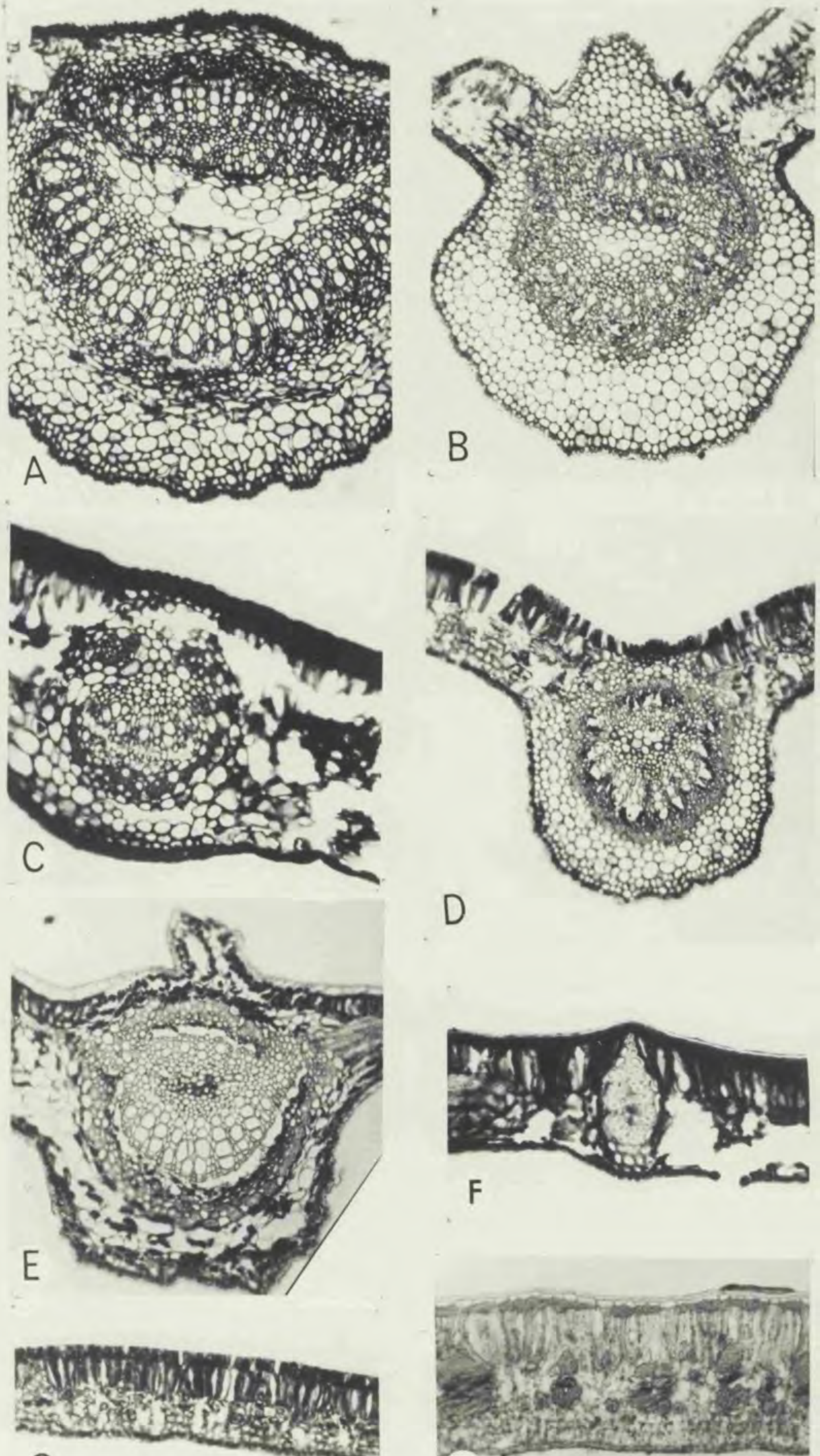


PLATE 6/7

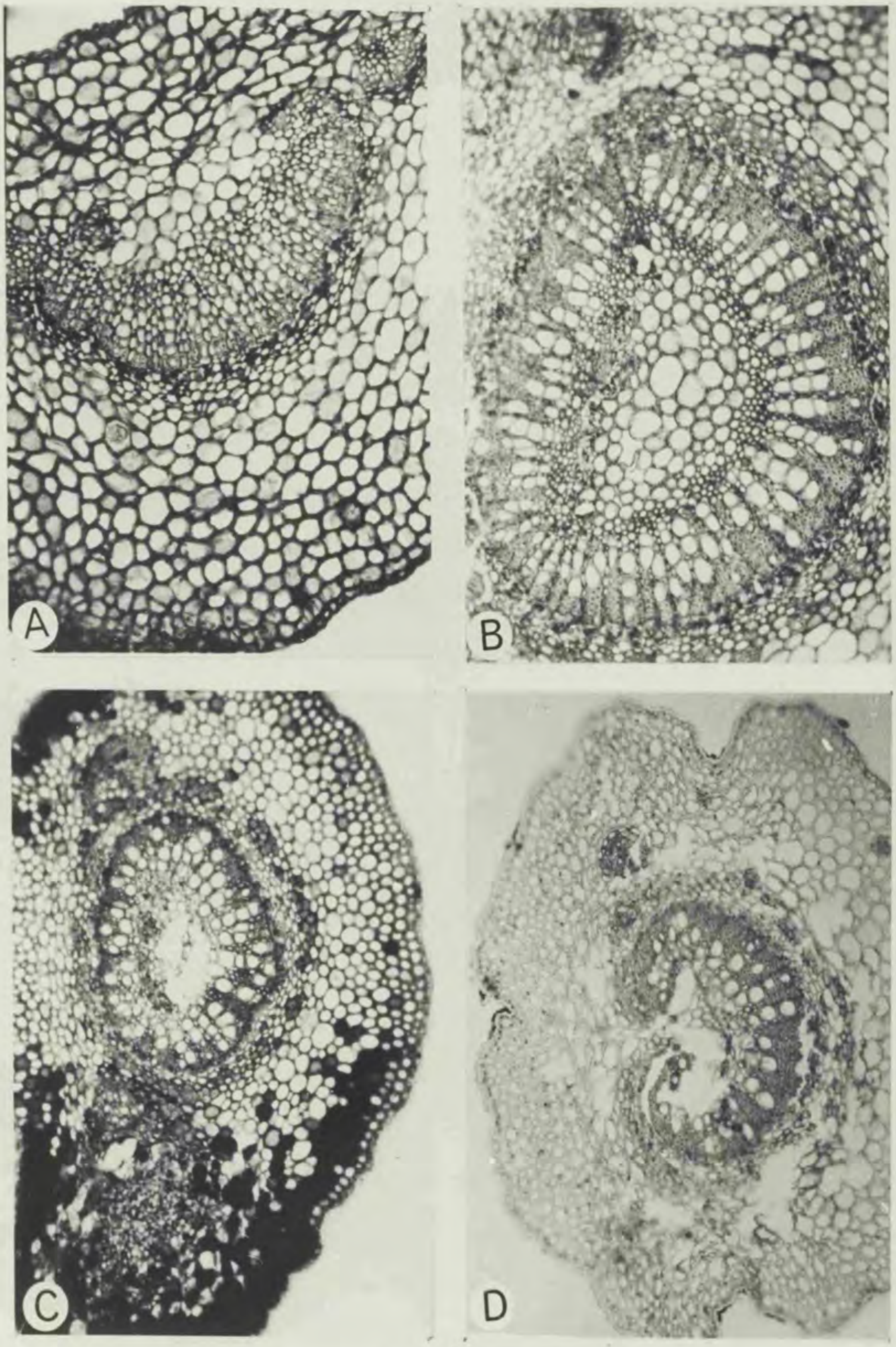


PLATE 6/8

CHAPTER 7

POLLEN MORPHOLOGY

7.1. Introduction

Pollen morphology has long been known as an important criterion in determining the natural relationships of plant genera and families. The diagnostic value of pollen morphological characters such as size, shape, number of endo and ecto apertures, ornamentation of the exine and many other features have been considered by many authors (Erdtman 1952, 1969; Faegri & Iversen, 1964; Ornduff, 1966; Clarke & Kupicha, 1976; and Hideux & Ferguson 1976).

Van Campo (1976) demonstrated that pollen grains may vary considerably not only at all taxonomic levels but also in a single individual, sometimes even in a single stamen. On the other hand, in the Umbelliferae, for example, there is a considerable degree of similarity in the pollen of many very different genera and only five pollen-types have been recognized from studying over 2000 species of the family (Cerceau-Larrival, 1971; Cerceau-Larrival & Ronald, 1976).

Evolutionary trends in the pollen grains of several families of angiosperms have been discussed by many authors. Punt (1976) reviewed most of these trends. One of the best papers concerned with the evolutionary significance of the exine surface is by Walker (1976), in which he reviewed the pollen wall architecture in 36 families of primitive flowering plants (Ranalean complex).

Walker (1976) says "in the search for ancestral angiosperm pollen in the fossil record workers should concentrate on looking for pollen which may have all or some of the following characters: large size, boat shaped form, psilate surface, atectate exine structure, a monosulcate aperture and probably no endexine". He also emphasized that verrucate, echinate and reticulate exine surfaces are derived from psilate surfaces. However, Punt (1976) considered recticulate exine surfaces as primitive and psilate and pilate exine surfaces as derived. He also mentioned that the trend is from small size to large size pollen.

Muller & Leenhouts (1976), on the other hand, found in the genus Dimocarpus (Sapindaceae) that the ornamentation characters of the exine are more variable, and of secondary importance for the recognition of evolutionary trends.

References to pollen morphology in the Combretaceae are very few. Erdtman (1952) gave a brief illustrated description for the family, mentioning only two examples (Laguncularia racemosa and Quisqualis indica). From the very little material examined (about 10 species from 4 genera), he reported that the family Combretaceae has tricolporate, prolate spheroidal to prolate pollen grains with well defined and lalongate endoapertures (ora). He also mentioned that pollen grains similar to those above have been found in Combretum and Terminalia. The pollen grains of Buchenavia, Bucida and Ramatuella have not been previously investigated.

This study was undertaken to fulfil the following aims:

1. to describe the pollen morphology of the genera Terminalia, Ramatuella, Bucida and Buchenavia;

2. to assess the taxonomic importance of pollen morphology in the above genera;

3. to describe the fundamental pollen-types in the Combretaceae and to elucidate their evolutionary significance.

7.2. Terminology

The terminology of pollen grains is complex. This is mainly because of the absence of internationally accepted standard terms, although the ICP (International Conference on Palynology) working group on Terminology have recently made some proposals (Nilsson & Muller, 1978).

In this work terminology in general follows that of Erdtman (1952), but in some cases I have followed Faegri & Iversen (1964) and Reitsma (1970).

7.3. Results - Pollen descriptions

7.3.1. Terminalia (Plates 7/1 A-C; 7/2; 7/3 A, B & G, Figure 7/1)

Pollen grains heterocolporate, with six colpi and three endoapertures, prolate spheroidal to prolate, (9-) 19.75 (-35) x (9-) 18 (-30) µm; p/E ratio (0.86-) 1.10 (-1.47). Outline in polar view circular or tending to hexagonal or less frequently triangular or 3-lobed, the lobes slightly convex; in equatorial view usually elliptical or sometimes circular. Ectoapertures long colpi, (8-) 15 (-30) x (0.5-) 2.5 (-3) µm, usually approximately $\frac{2}{3}$ the length of the polar axis but sometimes as long as the polar axis; ends acute or rounded; sides elliptical; membrane smooth or granular. Endoapertures colpi, or lalongate or lolongate pori 0.9-4 x 0.6-2 µm, well defined, usually protruding sometimes sunken; margin entire or irregularly crenate. Ornamentation psilate, punctate or verrucate.

Variations in surface sculpturing, pollen grain size and shape

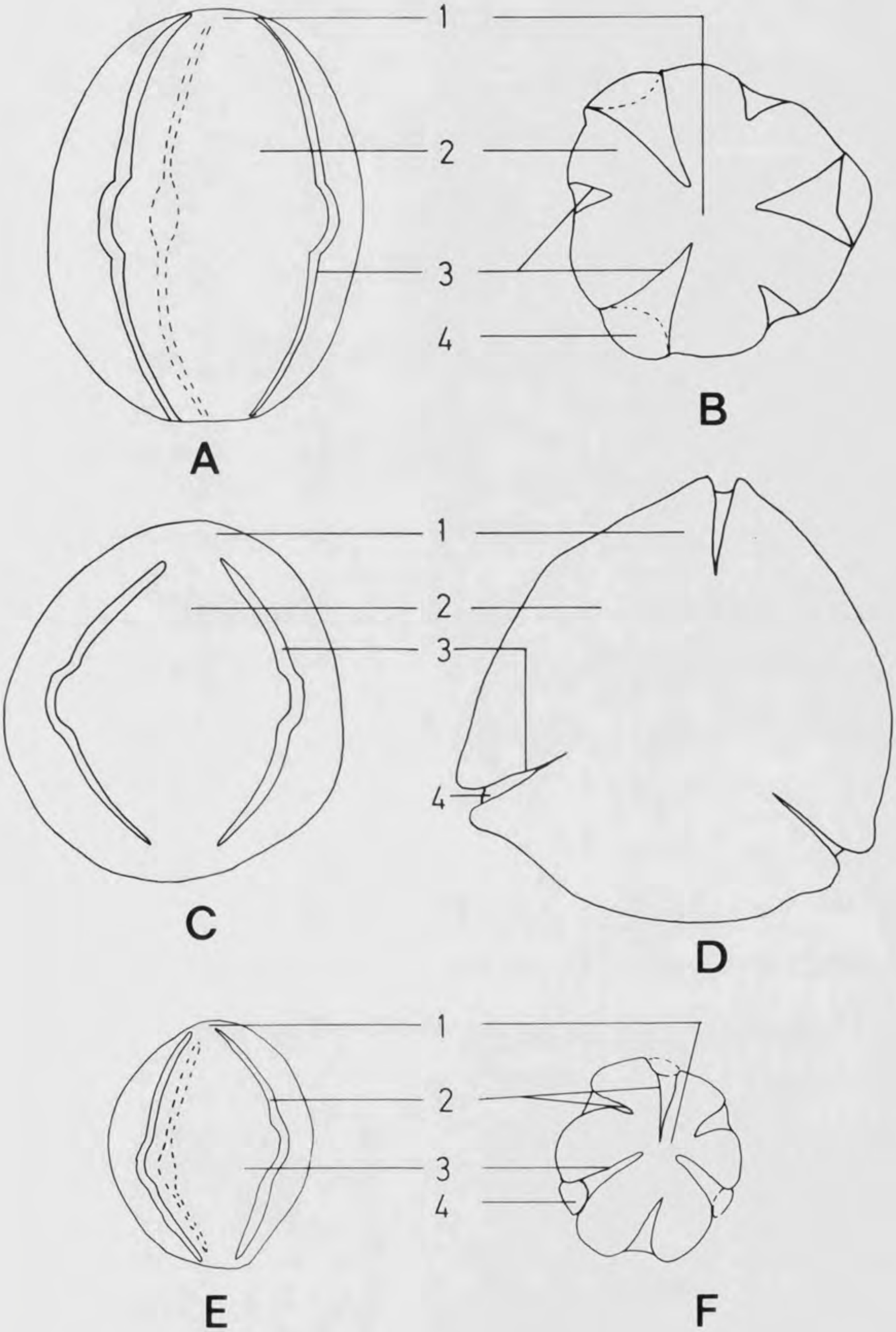


Fig. 7/1: Diagram of typical _Terminalia_, _Buchenavia_ and _Bucida_ pollen grains. A, C and E equatorial view; B, D and F polar view respectively. 1. apocolpium 2. mesocolpium 3. colpus. 4. limit of endoaperture appear to represent a continuous range but it is easy to recognize two main pollen types.

Type I: Terminalia type (Plates 7/1 A-C; 7/2; 7/3 G. Figure 7/1)

Ornamentation psilate or psilate-punctate or psilate-perforate or sparsely fossulate; ectocolpi very long to medium; endoapertures variable in shape and size, colpi or lalongate pori or lolongate pori. Pollen size and shape variable. Found in most species of Terminalia.

Type II: Vicentia type: Plate 7/3 A & B)

Ornamentation verrucate or verruculate; ectocolpi medium; endoapertures usually indistinct or small pori. Pollen relatively small; shape in polar view usually circular. Found only in Terminalia acuminata (section Vicentia).

7.3.2. Ramatuella (Plate 7/3 E)

Pollen grains heterocolporate with six colpi and three endoapertures, prolate spheroidal, (16-) 18.3 (-20) x (15-) 17.33 (-20) µm; P/E ratio (1.00-) 1.05 (-1.33). Outline in polar view hexagonal or circular or 3-6-lobed, with convex lobes; in equatorial view elliptic or subcircular. Ectoapertures long colpi, usually as long as the polar axis but sometimes slightly shorter, (10-) 13 (-17) x 1.5- 2 (-3) µm, with elliptic sides and acute to acuminate ends; membrane granulate. Endoapertures lolongate pori 1-3 x 1-2 µm. Ornamentation psilate to psilate punctate with shallow depressions.

Pollen type in this genus is of the Terminalia type.

7.3.3. Bucida (Plate 7/3 C,D; Figure 7/1)

Pollen grains heterocolporate with 6 colpi and 3 endoapertures, prolate spheroidal, (13-) 17.9 (-23) x (13-) 17.17 (-23) μm; P/E ratio (1.0-) 1.03 (-1.08). Outline in polar view hexagonal to circular or sometimes 3-small lobed, with slightly convex lobes; in equatorial view elliptic. Ectoarpertures long colpi, usually as long as the polar axis but sometimes shorter, (10-) 12 (-16) x (0.8-) 1.5 (-2.5) μm, with elliptic sides and acute-acuminate ends; membrane smooth-granular. Endoapertures lolongate pori or colpi, 1.5-5 x 1-2 μm, well defined. Ornamentation psilate or psilate punctate, usually with shallow depressions. Pollen grains in this genus are of the Terminalia type.

7.3.4. Buchenavia (Plates 7/1 D-F; 7/3 F; 7/4; 7/5 G. Figure 7/1)

Pollen grains 3-colporate, oblate spheroidal to prolate spheroidal, (13-) 18.60 (-42) x 13-) 18.26 (-41) μm; P/E ratio (0.88-) 1.01 (-1.33). Outline in polar view trangular, or sometimes subcircular; mesocolpia almost always convex; in equatorial view circular to broadly elliptical. Ectoapertures medium colpi, (5-) 11 (-20) x (0.5-) 1.0 (-1.5) μm, usually $\frac{1}{2}$ to $\frac{2}{3}$ the length of the polar axis, with elliptic sides and acute ends; margins irregularly papillate-spinulate. Endoapertures circular or lolongate pori diameter 0.3-1.0 μm. Ornamentation usually densely and shortly echinate - baculate or occasionally verrucate; echina length 0.25-0.75 μm.

Only one pollen type recognized in this genus, designated here as Buchenavia type.

7.3.5. Other genera of Combretaceae

The genera Combretum, Quisqualis, Conocarpus and Anogeissus were found to have pollen of the Terminalia type, and Thiloa has pollen of the

Vicentia type. In addition three extra pollen types were found among the other genera of the family are designated here as follows:

Pteleopsis type:

Pollen grains heterocolporate, with 6 colpi and 3 endoapertures, prolate spheroidal to subprolate, 16-22 x 15-20 µm; ectoaperatures long colpi; endoapertures short colpi or pori; outline in polar view usually circular-hexagonal; ornamentation reticulate.

Pteleopsis and *Lumnitzera* belong here.

Laguncularia type: (Plate 7/5 F)

Pollen grains tricolporate, prolate spheroidal, 18-28 x 18-30 µm; ectoapertures medium colpi; endoapertures pori; outline in polar view triangular; ornamentation psilate.

Only *Laguncularia* is of this type.

Strephonema type: (Plate 7/5 H)

Pollen grains tricolporate, prolate spheroidal to subprolate or prolate, 30-34 x 14-22 µm; ectoapertures medium colpi, usually bounded by margo; endoapertures pori; outline in polar view circular or circular-triangular; ornamentation distinctly reticulate.

Only*Strephonema* is of this type.

7.3.6. Key to genera based on pollen types

1. Pollen grains heterocolporate (6-colpi)
   2. Ornamentation reticulate . . . . (*Pteleopsis* type)
      Pteleopisis and *Lumnitzera*
   2. Ornamentation psilate or verrucate
      3. Ornamentation psilate . . . . (*Terminalia* type)
         Terminalia, *Ramatuella*, *Bucida*, *Concocarpus*, *Anogeissus*, *Combretum* and *Quisqualis*

3. Ornamentation verrucate . . . . (Vicentia type)

Terminalia (sect. Vicentia) and Thiloa

1. Pollen grains tricolporate (3-colpi)

4. Ornamentation reticulate . . . . (Strephonema type)

Strephonema

4. Ornamentation psilate or echinate-baculate

5. Ornamentation psilate . . . . (Laguncularia type)

Laguncularia

5. Ornamentation echinate-baculate . . . . . . (Buchenavia type)

Buchenavia

7.4. Discussion

The pollen grains of 47 species of Terminalia (including representatives of all American species and almost all sections in the world), 15 species of Buchenavia, 4 species of Bucida and 2 species of Ramatuella were examined by light microscopy and in most cases scanning electron microscopy (SEM) as well. Representatives of the genera Strephonema, Laguncularia, Conocarpus, Anogeissus, Combretum, Thiloa, Quisqualis Lumnitzera and Pteleopsis were also examined in less detail for comparison. A list of the specimens studied is given in Appendix 3. P/E ratios, shape and size details for the various species are illustrated in Tables 7/1 and 7/2 and displayed graphically for Terminalia in Figures 7/2 and 7/3 and for Buchenavia in Figure 7/4.

The material was difficult to manipulate not only because of the small flowers and tiny anthers, but also because of the small pollen grains, particularly in Buchenavia and Bucida in which they usually do not exceed 20 μm (Table 7/2).

It is well known in many families that species cannot be distinguished by pollen grains alone. Since this is also true in most genera of Combretaceae attention was focused on the generic and higher levels.

7.4.1. General morphology

Shape and size (Fig. 7/1 and Plate 7/1)

In Terminalia, Ramatuella and Bucida equatorial outlines vary within and between species from spheroidal to prolate spheroidal to subprolate to prolate, but they are usually prolate spheroidal (Plate 7/1 A & C). However, a few grains with oblate spheroidal shape sometimes can be found in species of Terminalia (Table 7/1). While the polar view is usually circular - hexagonal, sometimes it is 3-lobed as in Terminalia eriostachya (Plate 7/1 B), or trigonal with slightly concave sides as in T. januariensis, or circular as in Terminalia platyptera (Plate 7/5 A).

In Buchenavia the equatorial outlines vary within a species or between species from prolate spheroidal to oblate spheroidal (Plate 7/1 D; 7/4 C). The polar view is usually triangular with convex sides and with apertures situated at the angles (Plate 7/1 E & F).

The pollen in most species of the four genera mentioned above is small (in the sense of Erdtman, 1952), with an average usually less than 20 µm. The polar axis is usually longer than the equatorial axis but in Buchenavia it is often shorter. The size range of the longst axis is 9-35 µm in Terminalia, 13-42 µm in Buchenavia, 13-23 µm in Bucida and 16-20 µm in Ramatuella, Although the pollen grains of most species of Terminalia are larger than those of the other genera, T. yapacana, T. acuminata and T. actinophylla have the smallest pollen in the whole group, and Buchenavia ochroprumna sometimes has pollen grains larger than those of any species of Terminalia. In four species of Terminalia (T. australis, T. guaiquinimae, T. oblonga and T. quintalata) the pollen is medium sized (i.e. more than

25 μm across according to Erdtman). But these four species merely represent the top end of a continuous range.

Generally the variation in pollen size and shape in this group is of no taxonomic importance.

Similar shape and size of pollen to that in Terminalia were also found in the genera Conocarpus, Anogeissus, Pteleopsis, Combretum, Thiloa and Laguncularia but relatively larger pollen grains were found in Lumnitzera littorea (30-45 μm), and Quisqualis indica (40-55 (60) μm).

Apertures:

The pollen grains of Terminalia, Ramatuella, Bucida and Buchenavia are basically 3-zonoaperturate. In some pollen grains of Terminalia dichotoma one aperture can be situated outside the equatorial zone. In T. acuminata and sometimes in some species of Buchenavia the apertures are very small and not very distinct. In other genera of the subtribe Terminaliinae (e.g. Anogeissus leiocarpus) 4-zoneaperturate pollen grains can be found.

The ectoapertures are always colpi. The length of the ectocolpi varies from species to species and within the same species, but it is usually very long to medium. In some species (e.g. T. fagifolia and T. yapacana) the ectocolpi of compound apertures are longer than the ectocolpi of simple apertures, while in some other species they are equal or shorter. Therefore syncolpate (Plate 7/2 D) or syncolporate (Plates 7/3 G and 7/4 A) pollen grains can be found in many species. Also within the same species some grains have ectocolpi which are contiguous at the pole, sometimes only 2 ectocolpi anastomating at the pole (e.g. T. brasiliensis) and sometimes 4 (e.g. T. virgata). The width of the ectocolpi also varies within and between species.

In Buchenavia, Laguncularia and Strephonema there are three ectoapertures, while in Terminalia, Ramatuella, Bucida and other genera there are 6. The aperture membrane is usually smooth but sometimes is beset with small granules (e.g. T. hylobates) (Plates 7/2 A and 7/5 B).

Pp. 161-169
do not exist

In all species of _Buchenavia_, _Bucida_, _Ramatuella_ and most species of _Terminalia_ the ectoapertures are bounded by the same sexine element of the surface ornamentations. But in other genera (e.g. _Strephonema_) the ectoapertures are often surrounded by an obvious margo of closed zone (Plate 7/5 H). However, in some species of _Terminalia_ and _Conocarpus_ (Plate 7/5 E) this zone can be found only in the region of endoapertures.

Although the endoapertures vary in shape and size in most species of the genera examined, they are generally larger than the maximum width of the ectoapertures. However, small endoapertures (usually circular pori) occur in _Terminalia acuminata_ and some species of _Buchenavia_ (e.g. _B. macrophylla_) (Plate 7/4 C & D).

In _Terminalia_ the shape of the endoapertures has significant diagnostic value, enabling some species to be easily distinguished, for example _T. platyptera_ (Plate 7/2 E), _T. januariensis_ and _T. guyanensis_ by having a colpus, _T. hylobates_ (Plate 7/2 A) by having irregular and sunken pori, _T. catappa_ (Plate 7/2 C) and _T. dichotoma_ by having lalongate and protruding endoapertures, and _T. eriostachya_ (Plate 7/2 B), _T. chicharronia_ and _T. arbuscula_ (Plate 7/2 F) by having lolongate pori.

Generally the endoapertures in _Terminalia_ can be classified into four types:

1 Endoapertures very small or indistinct

2 Endoapertures medium or short colpi

3 Endoapertures lalongate or irregular pori

4 Endoapertures lolongate pori

In types 2-4 the endoapertures are sometimes protruding.

In _Bucida_, _Ramatuella_ and _Buchenavia_ the endoapertures are usually lolongate pori (type 4 above). Endoapertures similar to those in _Terminalia_ can be found in other genera of the family e.g. _Conocarpus_, _Anogeissus_, _Combretum_ _Strephonema_ etc.

Ornamentation

The ornamentation of the pollen grains in the Combretaceae shows a considerable variation which can be of great diagnostic value at generic levels. But at specific levels the surface sculpturing is of very little taxonomic value within the material studied. However, 2 distinct types of ornamentation (psilate and verrucate) were found in Terminalia. Reticulate ornamentation is found in Lumnitzera, Pteleopsis and Strephonema, echinate or echinulate in Buchenavia, verrucate in Thiloa, and psilate in the other seven genera examined.

The surface of the exine in Terminalia, Ramatuella and Bucida is randomly variable. Psilate (smooth) (Plates 7/2 B & E; 7/5 A), psilate and punctate, punctate (Plates 7/2 C & F; 7/5 C), sparsely and minutely perforate, psilate and slightly microrugulate (Plate 7/5 D) occur in various species or within a species or even within the same flower (e.g. T. yapacana has some pollen with psilate ornamentation and some with punctate ornamentation).

7.4.2. Pollen morphology and taxonomy

The pollen morphology of Terminalia acuminata has considerable taxonomic value; the verrucate tectum distinguishing this species and its section from all other Terminalia species and sections examined. Although the rest of the species of Terminalia examined have more or less similar pollen grains, the relation between some species based on the shape of endoaperture and the exine surface can be deduced. For example T. catappa, T. dichotoma, T. lucida and T. arbuscula have very similar pollen grains. The endoapertures in all of them are bounded by a protruding zone of the ectoapertures and the tecta are psilate-punctate, tending to become slightly micro-rugulate. On the other hand T. phaeocarpa, T. hylobates and T. argentea have very similar pollen which is characterized by sunken endoapertures, granulate membrane of the ectoapertures and psilate-minutely perforate tecta. Close similarity is also present between pollen of T. guyanensis and T. januariensis and between all members of section Chicharronia. The similarity between species of these groups agrees with the similarity in their macromorphology.

The pollen grains of Ramatuella are uniform throughout the genus and very similar in all features to that in Terminalia.

In all species of Bucida examined the pollen grains are also uniform in all featurs, although in Bucida buceras some variation in the exine surface sometimes can be found. However, palynological evidence supports its close relation to Terminalia.

Buchenavia has very distinct pollen grains which differ from those in all the other genera. The echinulate ornamentation which is more or less uniform throughout the genus is apparently unique in the Combretaceae. In all species examined the closest exine ornamentation to that in Buchenavia is that in Terminalia acuminata. However Buchenavia differs from Terminalia by having 3 ectocolpi pollen, a character which is found in only 2 other genera, Laguncularia (tribe Lagunculariеae) and Strephonema (subfamily Strephonematoideae). These two genera differ from Buchenavia by having psilate and reticulate pollen grains respectively.

Pollen morphological evidence suggests an affinity of Terminalia with Conocarpus and Anogeissus from the same subtribe Terminaliinae on one hand, and with Pteleopsis (subtribe Pteleopsidinae) and Combretum from subtribe Combretinae on the other hand.

The palynological information available now does not support Vollesen's (1981) proposal that the Terminalia and Pteleopsis should be united. On the contrary, the exine sculpture of pollen of Pteleopsis shows affinity with that in the subtribe Combretinae. It would be revealing to study the pollen of more species of Pteleopsis and Combretum.

The similarity between the pollen grains of most genera of the subtribe Terminaliinae and their affinity with pollen of the genera of subtribes Combretinae and Pteleopsidinae may support Exell & Stace's (1966) classification of Combretaceae, in which these three substribes were united into the tribe Combreteae.

The unique pollen grain type (Strephonema type) which characterizes all species of the genus Strephonema supports its recognition by Engler & Diels (1899) as a separate subfamily.

However, in general the six main pollen types recognized are not at all correlated with known or suspected intergeneric relationships in the family.

7.4.3. Evolutionary trends

The P/E ratio of the pollen grains of Terminalia varies between prolate spheroidal and prolate, and in Buchenavia from prolate spheroidal to oblate spheroidal. In Bucida and Ramatuella it is almost always prolate spheroidal. Transitions between prolate spheroidal and prolate pollen is present in species of Terminalia.

In Terminalia (Table 7/1), from the 36 species studied, 19 have prolate spheroidal pollen, 7 prolate spheroidal-subprolate pollen, 6 subprolate pollen, 3 subprolate-prolate pollen, and 1 species has usually prolate pollen. This series of transitions suggests a trend towards the prolate shape.

In Buchenavia (Table 7/2), from the 15 species examined, 6 have prolate spheroidal pollen, 6 prolate spheroidal-oblate spheroidal pollen, and 3 species have oblate spheroidal pollen. This may suggest a trend towards the oblate shape. In all genera examined the spheroidal-prolate or spheroidal shape is considered the primitive or basic shape, and the prolate and oblate shapes are considered derived. This trend is in agreement with the ideas of Punt (1976) and Walker (1976).

As mentioned before, the pollen grains of Terminalia and related genera are small, but it seems that pollen size (in some genera) is correlated with flower size. Species with larger flowers (usually with larger anthers) have larger pollen grains, e.g. Quisqualis indica and Lumnitzera littorea, and vice versa, e.g. T. acuminata and most species of Buchenavia. However, the marked increase in pollen size in the four species of Terminalia noted previously (Table 7/1) is not correlated with any increase in flower size.

Long ectoapertures are considered primitive by many authors (Punt, 1976; Walker, 1976; Muller & Leenhouts, 1976) and this trend seems to be of relevance in the Combretaceae. Most species of the genera studied have pollen with long ectoapertures but in some species of Terminalia, Buchenavia and Strephonema the shortening in the ectocolpi is clear. Good examples can be found in Buchenavia macrophylla (Plate 7/4 C) and Strephonema pseudocola (Plate 7/5 H).

Reduction in size of endoapertures also can be observed in Buchenavia macrophylla and species of Terminalia.

The exine surface of most genera examined is psilate (Plates 7/2; 7/3 C-E; 7/5 A-E) and unspecialized. A trend from psilate to scabrate to verrucate (Plate 7/3 A & B) is clear in Terminalia, and to echinate (Plate 7/4) in Buchenavia. A tendency for the psilate exine to become punctate (Plate 7/5 A-C) or minutely perforate was also observed in some species of Terminalia.

The evolutionary trends in the exine surface of pollen of other genera of the family, particularly those genera which have pollen with reticulate ornamentation, could not be elucidated because of the very limited pollen morphological data available.

Table 7/1: Measurements and morphology of *Terminalia* pollen.
Minimum, mean and maximum values.

Species	Polar axis = P			Equatorial axis = E			P/E Ratio			Shape	Notes
1. *T. actinophylla*	12	14.8	16	12	13.96	15	0.92	1.06	1.15	Prolate spheroidal	one grain oblate spheroidal
2. *T. acuminata*	12	13.72	17	10	11.28	16	0.93	1.21	1.30	Subprolate	3 grains oblate spheroidal
3. *T. adamantium*	18	19.84	22	16	18.36	20	1.00	1.08	1.10	Prolate spheroidal	
4. *T. amazonia*	14	18.68	23		17.38	20	1.00	1.07	1.25	Prolate spheroidal to subprolate	
5. *T. arbuscula*	16	18.73	22	14	15.22	20	1.00	1.23	1.26	Subprolate	
6. *T. argentea*	17	20.72	25	15	17.92	20	1.05	1.15	1.29	Subprolate	
7. *T. australis*	22	26.98	31	22	25.68	28	1.00	1.05	1.16	Prolate spheroidal	
8. *T. bipleura* = 16	14	16.8	20	13	16.04	18	0.94	1.04	1.23	Prolate spheroidal to subprolate	2 grains oblate spheroidal
9. *T. biscutella* = 6	15	17.84	20	15	15.96	17	1.00	1.11	1.13	Prolate spheroidal	
10. *T. camuxa*	15	18.00	20	15	17.04	19	1.00	1.05	1.25	Prolate spheroidal to subprolate	
11. *T. catappa*	17	19.96	22	17	17.76	20	0.94	1.12	1.15	Prolate spheroidal	2 grains oblate spheroidal
12. *T. chicharronia*	20	21.9	23	17	17.95	20	1.00	1.22	1.35	Subprolate - prolate	
13. *T. dichotoma*	18	18.9	20	16	17.45	19	1.00	1.08	1.17	Prolate spheroidal	
14. *T. domingensis* = 12	20	22.35	25	16	16.8	20	1.10	1.33	1.47	Prolate	
15. *T. eichleriana*	19	20.20	21	15	16.52	18	1.00	1.22	1.33	Subprolate	
16. *T. eriostachya*	20	21.76	25	17	17.84	20	1.05	1.21	1.35	Subprolate - prolate	
17. *T. fagifolia*	15	17.44	21	13	16.64	18	0.94	1.04	1.2	Prolate spheroidal	1 grain oblate spheroidal
18. *T. glabrescens*	14	15.44	18	13	14.76	16	1.00	1.04	1.15	Prolate spheroidal	
19. *T. guaiquinimae*	24	30.30	35	23	28.80	33	0.96	1.05	1.20	Prolate spheroidal to subprolate	
20. *T. guyanensis*	16	18.84	21	14	16.04	19	1.00	1.17	1.40	Subprolate - prolate	
21. *T. hylobates*	19	22.66	35	17	19.83	24	0.90	1.14	1.50	Subprolate	
22. *T. januariensis*	20	23.3	27	18	19.36	22	1.1	1.20	1.31	Subprolate	
23. *T. lucida*	15	16.32	20	15	15.88	17	0.94	1.02	1.17	Prolate spheroidal	1 grain oblate spheroidal
24. *T. mameluca*	17	20.19	24	17	19.38	23	1.00	1.04	1.2	Prolate spheroidal	
25. *T. neglecta* = 12	17	17.5	19	14	15.55	17	1.05	1.12	1.28	Prolate spheroidal to subprolate	
26. *T. nipensis* = 12	17	17.7	19	16	17.15	18	0.94	1.03	1.11	Prolate spheroidal	
27. *T. oblonga*	25	29.52	32	23	26.6	31	1.00	1.10	1.55	Prolate spheroidal	
28. *T. gracifolia* = 19	15	17.16	20	15	16.36	21	0.89	1.04	1.25	Prolate spheroidal to subprolate	1 grain oblate spheroidal
29. *T. quintalata*	23	25.92	28	23	25.24	28	1.00	1.02	1.08	Prolate spheroidal	
30. *T. reitzii*	16	18.44	20	15	17.88	20	1.00	1.03	1.26	Prolate spheroidal to subprolate	
31. *T. riedelii*	17	18.08	20	16	17.48	20	1.00	1.03	1.11	Prolate spheroidal	
32. *T. steyermarkii*	20	23.11	25	20	22.22	25	1.00	1.04	1.08	Prolate spheroidal	
33. *T. tararotensis* = 27	15	18.04	25	15	17.52	22	0.86	1.02	1.12	Prolate spheroidal	3 grains oblate spheroidal
34. *T. triflora*	18	20.08	22	16	19.52	21	0.90	1.02	1.12	Prolate spheroidal	1 grain oblate spheroidal
35. *T. virgata* = 19	14	17.24	19	13	16.92	19	1.00	1.01	1.11	Prolate spheroidal	
36. *T. yapacana*	9	12.64	15	9	11.96	15	1.00	1.05	1.11	Prolate spheroidal	

Table 7/2: Measurements and morphology of Buchenavia, Bucida and Ramatuella pollen.

Minimum, mean and maximum values.

Taxa	Polar axis = P			Equatorial axis = E			P/E Ratio			Shape
1. Buchenavia callistachya = 14	15	15.62	16	15	15.5	16	1.00	1.00	1.06	prolate spheroidal
2. B. capitata	13	17.32	22	13	16.23	20	1.02	1.06	1.12	prolate spheroidal
3. B. grandis	17	19.95	20	17	18.63	20	0.94	1.07	1.15	prolate spheroidal
4. B. guianensis	15	17.85	18	15	16.86	19	0.94	1.03	1.13	prolate spheroidal
5. B. igaratensis = 6	13	17.00	19	13	16.00	18	1.00	1.06	1.13	prolate spheroidal
6. B. kleinii	16	16.95	18	16	16.81	18	0.88	1.00	1.06	prolate spheroidal - oblate spheroidal
7. B. macrophylla	17	18.69	20	17	18.00	19	1.00	1.03	1.17	prolate spheroidal
8. B. megalophylla	17	18.27	19	17	18.27	19	0.94	1.00	1.05	prolate spheroidal - oblate spheroidal
9. B. ochroprumna	16	21.8	42	20	21.59	41	0.90	1.00	1.1	prolate spheroidal - oblate spheroidal
10. B. oxycarpa	18	20.66	24	19	21.33	26	0.90	0.96	1.00	oblate spheroidal
11. B. pallidovirens	18	19.5	20	18	19.66	22	0.95	0.99	1.00	oblate spheroidal
12. B. reticulata	16	18.33	20	15	17.83	19	1.00	1.02	1.2	prolate spheroidal - oblate spheroidal
13. B. suaveolens	16	18.00	21	16	17.66	20	1.00	1.01	1.06	prolate spheroidal - oblate spheroidal
14. B. tomentosa	15	18.20	22	15	18.66	23	0.9	0.97	1.1	oblate spheroidal
15. B. viridiflora	20	20.68	22	20	20.88	22	0.99	1.00	1.05	prolate spheroidal - oblate spheroidal

16. *Bucida buceras*	13	16.33	20	13	16.06	20	1.00	1.01	1.07	prolate spheroidal
17. *B. ophiticola* = 18	17	18.07	20	15	17.00	18	1.00	1.06	1.13	prolate spheroidal
18. *B. spinosa*	14	18.07	25	14	17.7	23	1.00	1.05	1.08	prolate spheroidal
19. *B. subinermis* = 16	15	18.57	23	15	17.95	22	1.00	1.03	1.06	prolate spheroidal
20. *Ramatuella argentea*	17	18.6	20	15	17.1	20	1.00	1.08	1.33	prolate spheroidal
21. *R. virens*	16	18.0	20	16	17.57	19	1.00	1.02	1.05	prolate spheroidal

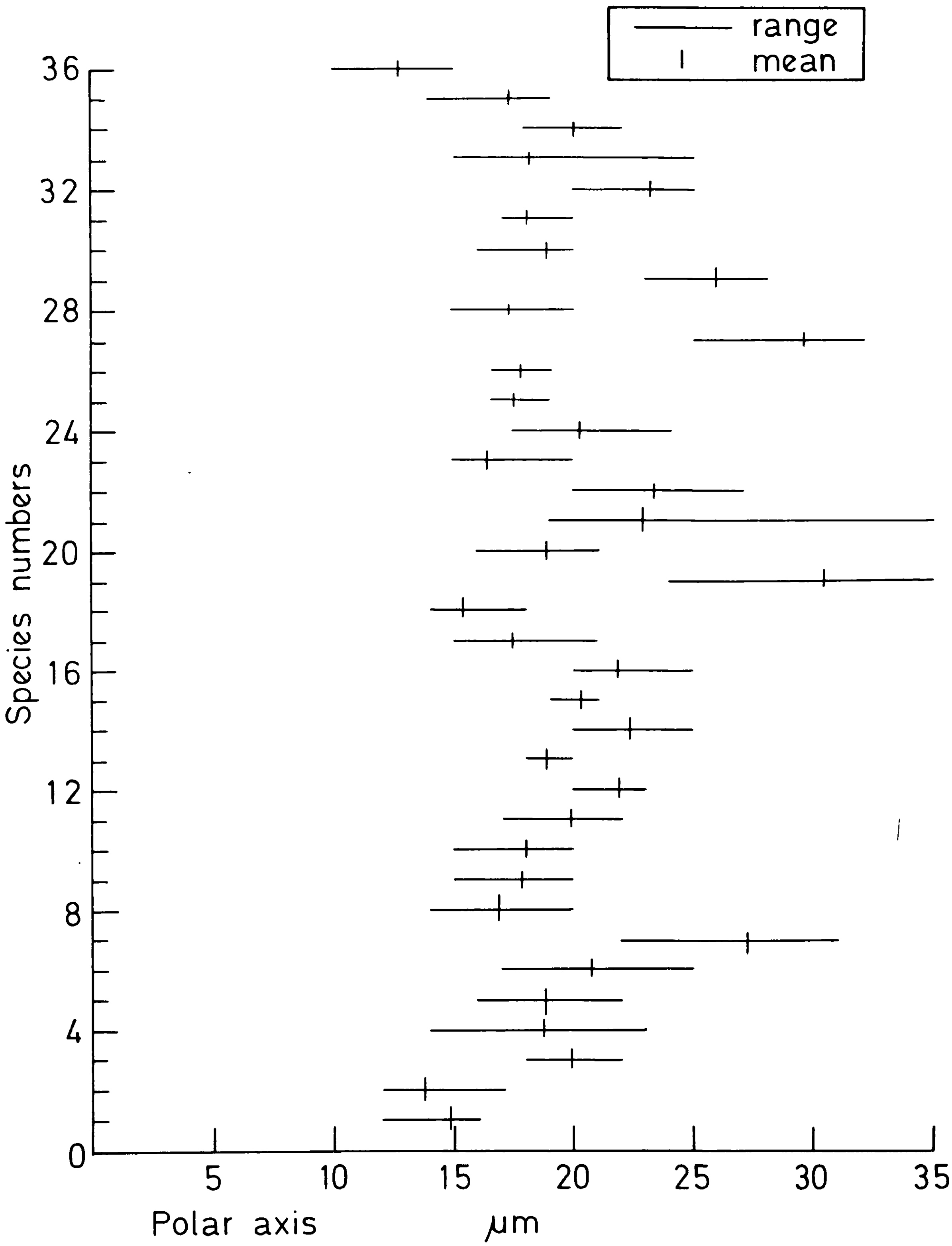


Fig. 7/2: Variation in the length of the polar axis in *Terminalia* pollen

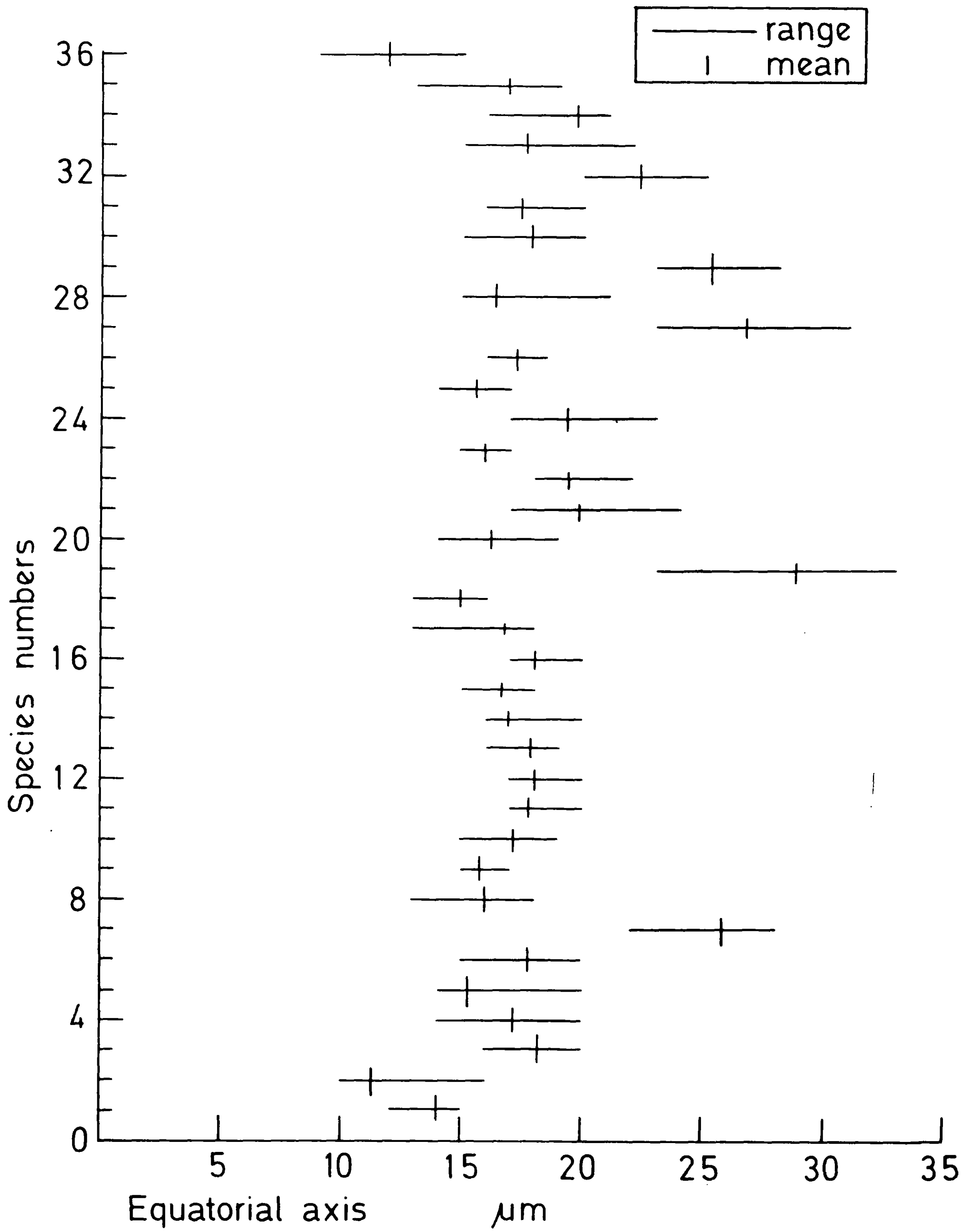


Fig. 7/3: Variation in the length of the equatorial axis in

<u>Terminalia</u> pollen

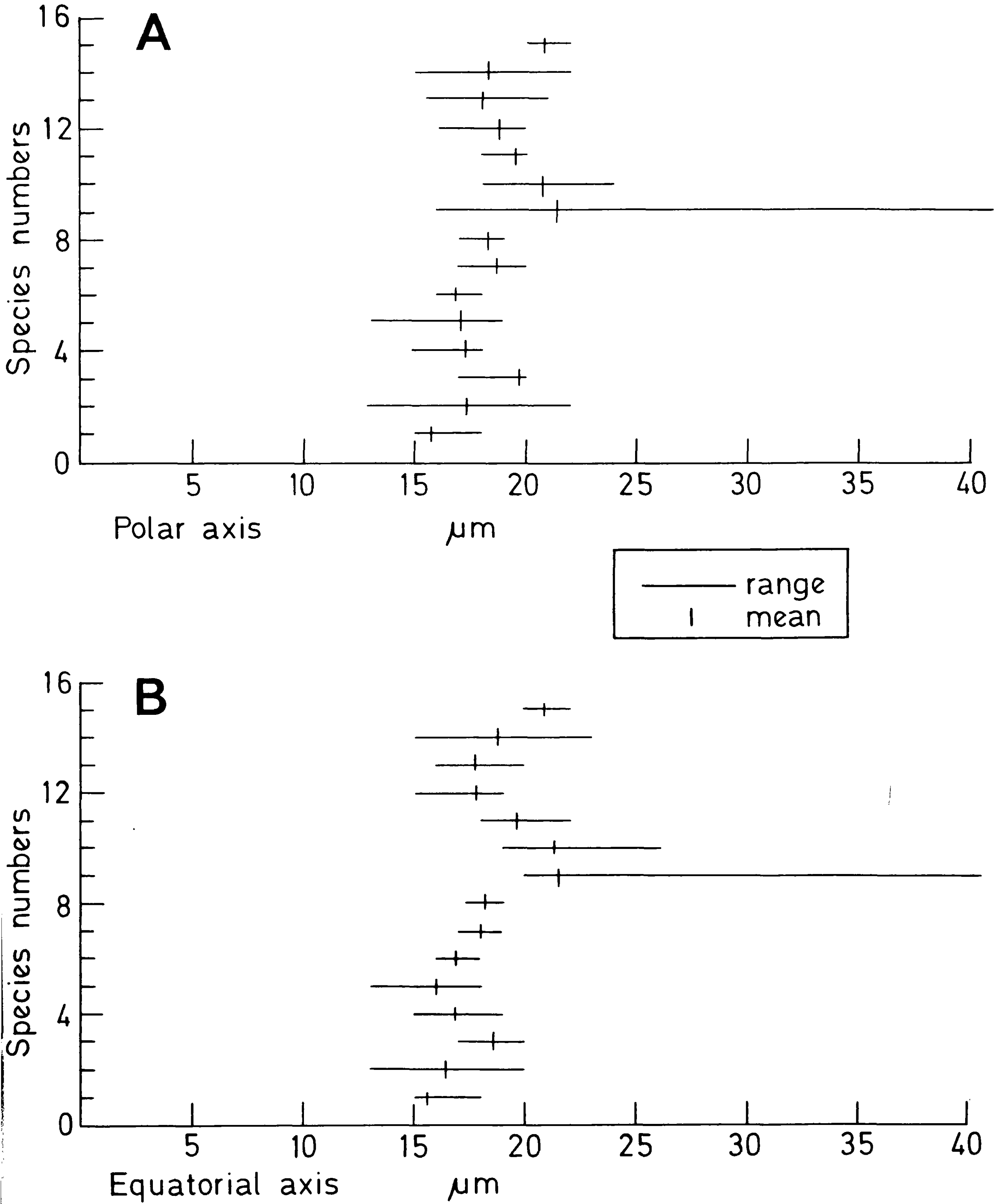


Fig. 7/4 A and B. Variations of the polar axis and equatorial axis respectively in <u>Buchenavia</u> pollen

Plate 7/1: Light micrographs showing general pollen morphological features in *Terminalia* and *Buchenavia* Scale bar = 10 µm.

A. and B. *T. eriostachya*, A equatorial view, B polar view. C. *T. catappa* equatorial view. D. *B. macrophylla*, equatorial view. E. and F. *B. ochroprumna* polar view, E. high focus, F. low focus.

Plate 7/2: SEM micrographs showing apertures of *Terminalia* pollen Scale bar = 5 µm.

A. *T. hylobates*, showing lalongate endoaperture. B. *T. eriostachya*, showing lolongate endoaperture. C. *T. catappa*, showing protruding lalongate endoaperture. D. *T. opacifolia*, showing syncolpate ectoapertures. E. *T. platyptera*, showing colpus endoaperture. F. *T. arbuscula*, showing protruding lalongate endoaperture.

Plate 7/3: SEM micrographs showing pollen of *Terminalia*, *Bucida*, *Ramatuella* and *Buchenavia*. Scale bar = 5 µm.

A. and B. *T. acuminata* showing *Vicentia* type, A. equatorial view, B. subequatorial view, C. *Bucida buceras*. D. *B. spinosa*. E. *Ramatuella virens*. F. *Buchenavia viridiflora*, subpolar view, compare with Plate 4A. G. *T. lucida*, subpolar view, showing syncolporate pollen.

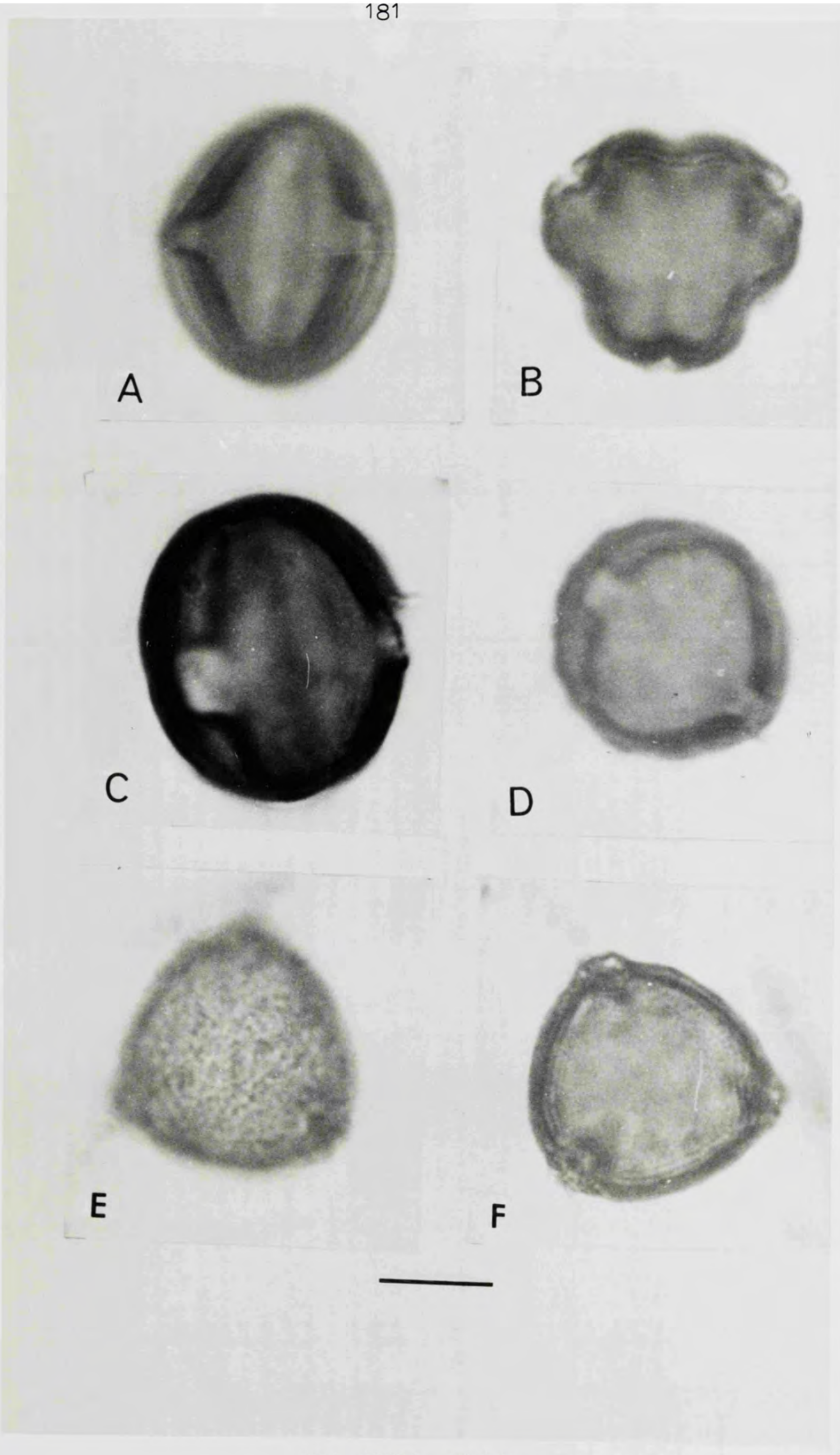


PLATE 7/1

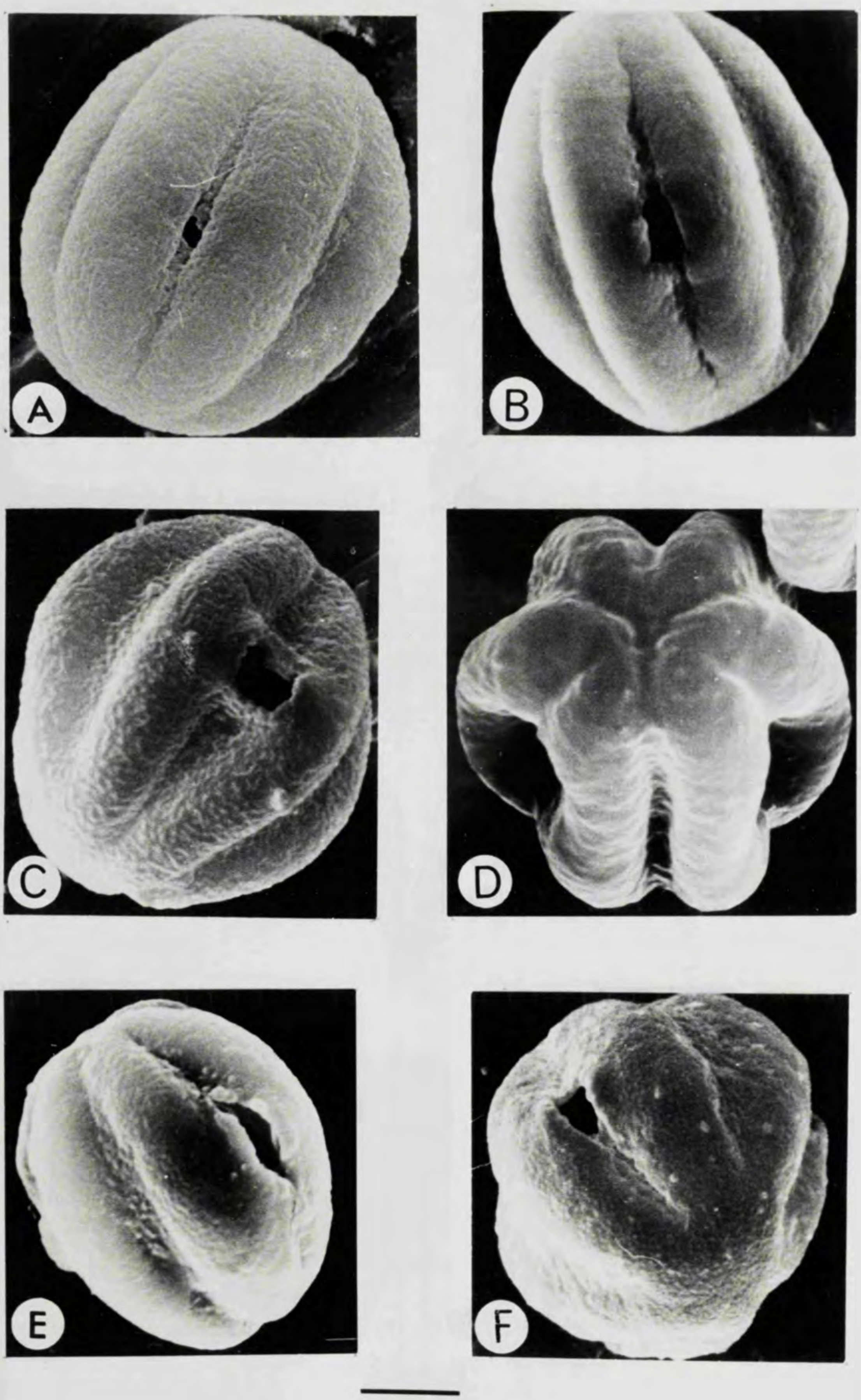


PLATE 7/2

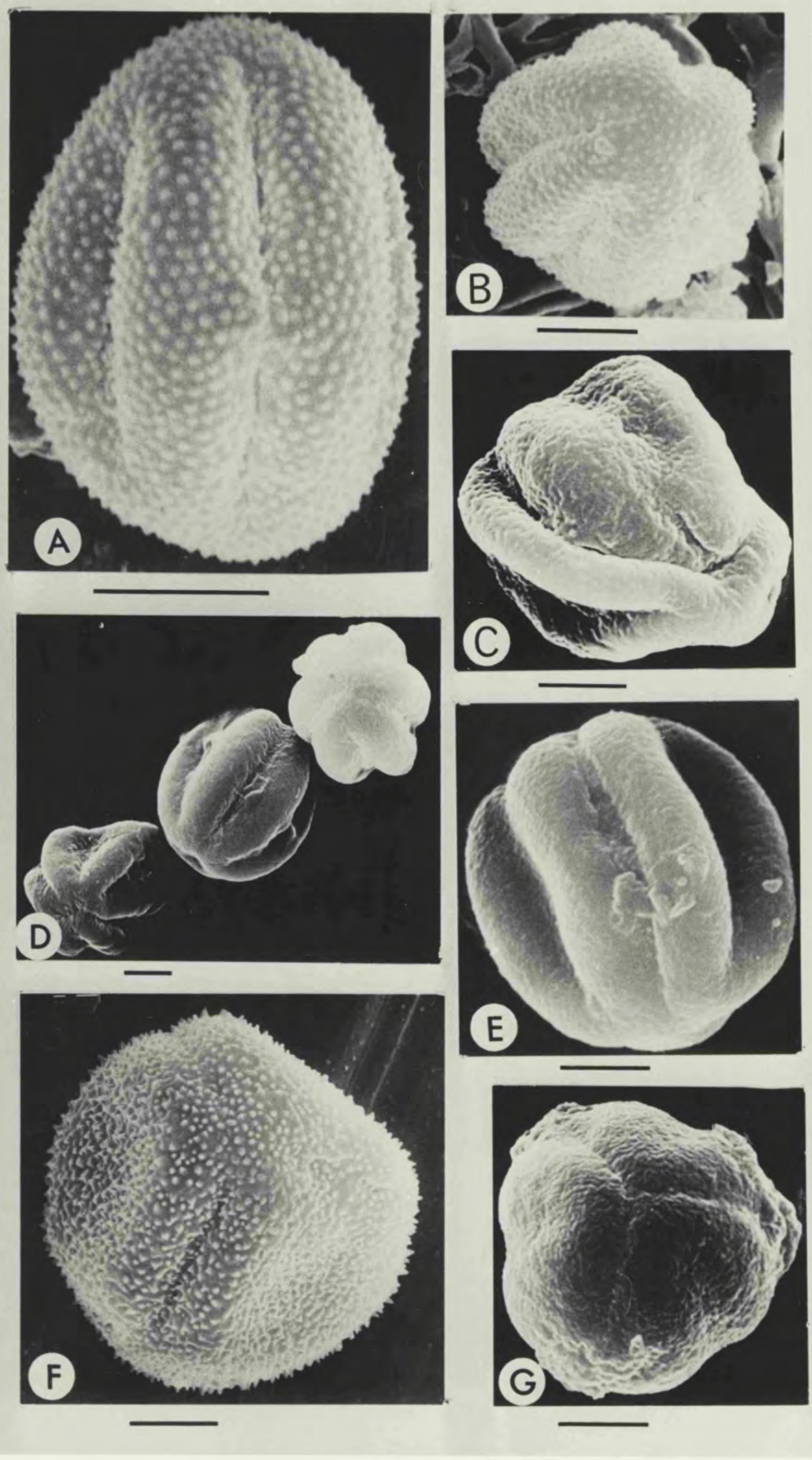


PLATE 7/3

Plate 7/4: SEM micrographs showing general features, ornamentation and apertures of Buchenavia pollen. Scale bar = 1 μm.

A. B. pallidovirens, polar view showing syncolporate pollen.

B. B. callistachya, equatorial view. C. B. macrophylla, equatorial view showing short ectoaperture and a small pore. D. Same species, showing detail of exine sculpture. E. and F. B. ochroprumna, E. equatorial view, showing irregular shape with a crack in the wall. F. Details of exine surface showing echinate ornamentation.

Plate 7/5: SEM micrographs showing general features, apertures and ornamentation of Combretaceae pollen. Scale bar = 1 μm.

A. Terminalia platyptera, polar view, showing smooth ornamentation.

B. T. hylobates, showing granulate membrane of ectoaperture.

C. T. neglecta, showing punctate ornamentation. D. T. domingensis, showing slightly microrugulate ornamentation. E. Conocarpus erecta showing endoapertures bounded by margo. F. Laguncularia racemosa, showing laguncularia type. G. Buchenavia megalophylla, showing a lolongate endoaperture. H. Strephonema pseudocola, showing reticulate ornamentation, note the exine in the ectoaperture region.

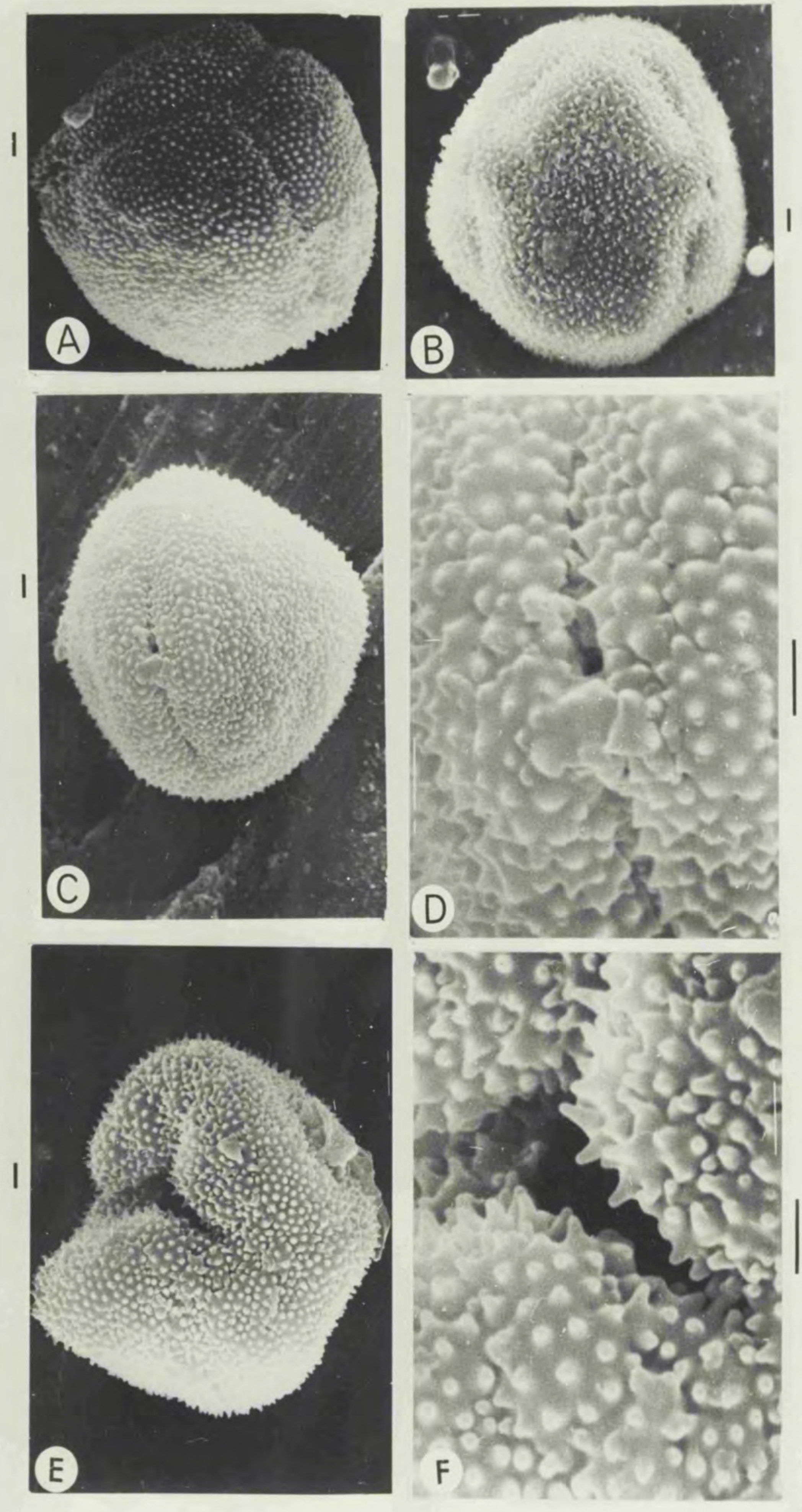


PLATE 7/4

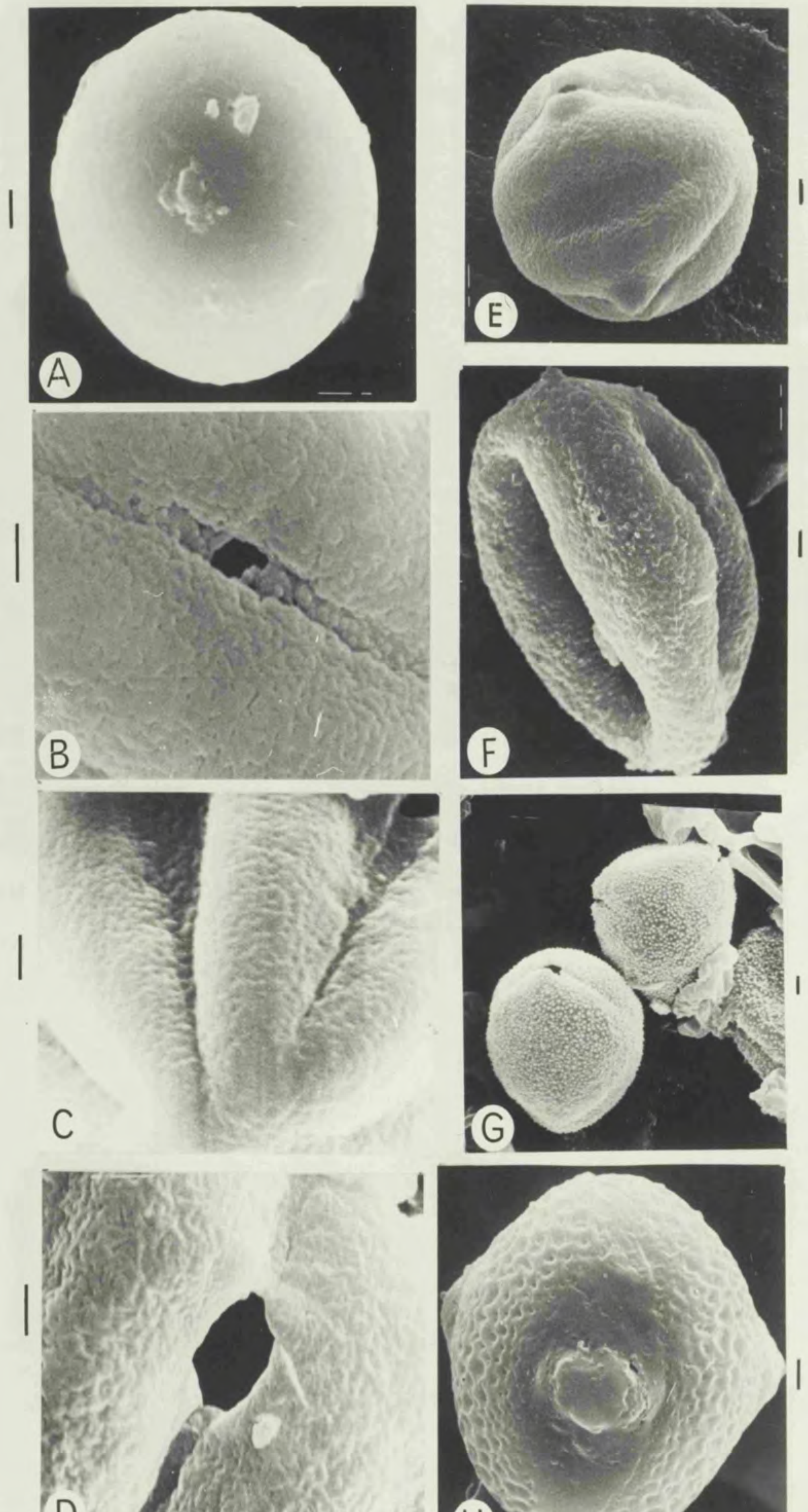


PLATE 7/5

PLATE 7/5

CHAPTER 8

TAXONOMY AT THE GENERIC AND SECTION LEVELS

8.1. Introduction

The species of Terminalia fall in my classification into 22 sections, of which 11 occur in America (Table 8/1). All American species have been fully investigated by me, but species from outside America have been studied in less detail.

The description presented for the non-American sections of Terminalia is largely based on the representative species available at BM and K, but information about other species, not deposited in BM and K, is also included based on the literature.

An attempt has been made to present a natural key in which the closely related sections can be keyed out as much as possible near to each other.

In preparing this chapter and Chapter Nine I have consulted the following references: Stafleu (1967), Stafleu & Cowan (1976-1983), Farr, Leussink & Stafleu (1979), Stearn (1966) and Royal Botanic Gardens, Kew (1980).

8.2. Terminalia

8.2.1. General description of the genus Terminalia

Terminalia L. Syst. Nat. ed. 12, 2: 674 (1767) et Mant.

Pl. : 21 (1767) nom. cons.

Type species: T. catappa L.

Syn. : Adamaram Adans., Fam. Pl. 2 : 445 (1763), pro parte, excl. Hort. Malab. 4 : t.5 (1682).

Panel Adans., Fam. Pl. 2 : 447 (1763), pro parte, excl. type.

Myrobalanifera Houtt., Nat. Hist. 2, 2 (Handl. Pl. - Kruidk, 2) : 485, t. 10, fig. 2 (1774).

Tanibouca Aublet, Hist. Pl. Guiane 1 : 448, t. 178 (1775).

Kniphofia Scop., Introd. Hist. Nat. 327 (1777), non Moench (1794, nom.cons.).

Aristotelia Comm. ex Lam., Encycl. 1 : 349 (1785), in syn.

Resinaria Comm. ex Lam., Encycl. 1 : 349 (1785), in syn.

Chuncoa Pavōn ex A. L. Juss., Gen. Pl. 76 (1789).

Badamia Gaertner, Fruct. sem. pl. 2 : 90, t.97, fig. 1 (1790), non Badhamia Berkeley (1853, Myxomycetes).

Myrobalanus Gaertner, Fruct. sem. pl. 2 : 90, t. 97, fig. 2 (1790).

Catappa Gaertner, Fruct. sem. pl. 2 : 206, t.127 (1791).

Gimbernatea Ruiz. Lopez & Pavōn, Fl. Peruv. Prodr. 138, t. 36 (1794).

Fatrea A. L. Juss., Ann. Mus. Hist. nat. 5 : 223 (1804).

Pentaptera Roxb., Hort.Bengal. : 34 (1814), nom.nud.

Ramatuella Kunth, Nov. Gen. Sp. 7 : 253 (1825).

Vicentia Allemão Pl. Novas Brasil (844).

Chicharronia A. Rich. in R. de la Sagra, Hist. Phys. Cuba Bot. Pl. Vasc. : 529, t. 43 (1846).

Terminaliopsis Danguy, Bull. Mus. Hist. Nat. Paris 29 : 108 (1923).

Trees or shrubs, deciduous or evergreen. Branching usually sympodial. Leaves usually spirally arranged, often crowded at the ends of the branches, sometimes on short spur-shoots (in Africa), rarely opposite (in Asia) or alternate, petiolate or subsessile; petiole slender or stout, often biglandular; lamina chartaceous to thickly coriaceous, usually entire, sometimes subserrate or subcrenate (in Africa and Madagascar), often with 2 or more glands at or near the base, glabrous or hairy. Domatia often present. Venation brochidodromous or eucamptodromous-brochidodromous or eucamptodromous, or rarely craspidodromous. Inflorescences usually axillary spikes, sometimes capitate-subcapitate or paniculate, rarely terminal, often andromonoeceous. Flowers small, actinomorphic, usually pentamerous, sometimes tetramerous; upper receptacle campanulate, infundibuliform or cupuliform with well developed lobes, hairy or glabrous; petals absent; stamens usually 10, sometimes 8, rarely 4-5 (in Madagascar), exserted, usually conspicuously so; anthers versatile; disk intrastaminal, usually densely pilose; style simple and free, hairy or glabrous, exserted; ovary completely inferior, unilocular, usually with 2 pendulous ovules. Fruit very variable in size and shape, (1) 2-5 (6) winged, or unwinged and drupe-like with a fleshy or leathery mesocarp.

Geographical range: Tropical Central and South America, West Indies, Africa, Madagascar, the Mascarenes, Asia from Pakistan through India, Indo-China and S. E. Asia to Fiji Islands and Australia (Map 8/1).

8.2.2. Key to the sections of Terminalia

1 - Fruit terete, ridged or narrowly winged, if narrowly winged then the wing stiff and rarely exceeding 5 mm wide 2

1 - Fruit distinctly winged 5

  2 - Fruit usually large, 3-17 cm long, compressed, ovoid or ellipsoid, often narrowly angled or winged but the wing becoming gradually broader towards the apex . . . . 1. Section Terminalia

  2 - Fruit usually small, 0.5-3(4.5) cm long, globose, cylindrical, broadly ellipsoid-ovoid, or flattened, completely wingless or uniformly circumalate 3

3 - Fruit usually globose or terete, not compressed, usually completely wingless; leaves often broadly elliptic and with long petiole . . . . 2. Section Myrobalanus

3 - Fruit ellipsoid-ovoid or flattened, circumalate or not winged; leaves obovate to spathulate or narrowly elliptic and usually with short petiole 4

Fruit usually circumalate, suborbicular or ovoid, 1-5 x 0.8-3 cm; leaves medium-sized (3-20 x 2-7.5 cm), not on spur-shoots, with usually 7-20 pairs of secondary veins; inflorescences usually long . . . . 3. Section Catappa

Fruit not winged, only sometimes obscurely ridged, ellipsoid to ovoid, 0.6-2 x 0.4-1.1 cm; leaves small (0.5-5 x 0.5-2.5 cm), often on spur shoots, with 3-7 pairs of secondary veins; inflorescences short . . . . 4. Section Fatrea

5 - Fruit distinctly stipitate, usually with persistent style 6

5 - Fruit sessile, rarely with very short pseudostipe, usually without persistent style 9

6 - Leaves in fascicles on short spur shoots 7

6 - Leaves not in fascicles on short spur shoots 8

7 - Branchlets usually bearing spines; fruit usually longer than broad, often small . . . . 5. Sect. Abbreviata

7 - Branchlets usually without spines; fruit usually suborbicular or broader than long, occasionally obovate, often large . . . . .6. Section. Discocarpae

8 - Bark on young branchlets peeling off in cylindric or hemi-cylindric papery flakes leaving a reddish-brown or brown newly exposed surface . . . . 7. Section Psidioides

8 - Bark on young branchlets not peeling off as above . . . . 8. Section Platycarpae

9 - Inflorescences paniculate 10

9 - Inflorescences simple 12

10 - Flowers tetramerous; stamens 8 . . . . 9. Section Vicentia

10 - Flowers pentamerous; stamens 10 11

11 - Fruit with 5(6) equal wings, often large, 1-few per spike. . . . . 10. Section Pentaptera

11 - Fruit with 1-4 wings, usually small, numerous per spike . . . . .11. Section Myriocarpae

12 - Fruit 2- or occasionally 3-winged 13

12 - Fruit with 4 or 5 equal or unequal wings 20

13 - Fruit always longer than broad; body narrower than wing 14

13 - Fruit broader than long, or if occasionally slightly longer than broad then the body more conspicuous and much wider than wing 15

14 - Leaves 15-30 (50) cm long, with 8-30 pairs of secondary veins; flowers 8-15 mm long; fruit 3-10 x 2-6 cm .12. Section. Archipelagi

14 - Leaves up to 10 cm long, with 3-6 pairs of secondary veins; flowers 4-7 mm long; fruit 1-3(4) x 1-2 cm .13. Section Circumalata

15 - Inflorescence a long spike 16

15 - Inflorescence capitate, subcapitate or slightly elongate . . . 18

16 - Body of fruit orbicular or suborbicular, wider than wing . . . . 14. Section Rhombocarpae

16 - Body of fruit elliptic or trigonal, ridged or slightly to strongly keeled or rarely bulged, always narrower than wing 17

17 - Leaves coriaceous to thickly coriaceous; venation typically brochidodromous, often prominently raised; margin usually revolute; fruit small, up to 2 x 4 cm (endemic to West Indies) . . . . , . 15. Section Chicharronia

17 - Leaves chartaceous to subcoriaceous; venation usually euchamptodromous-brochidodromous, not raised; margin not revolute; fruit usually large 2-6 x 2-12 cm . . . . 16. Section Oblongae

18 - Inflorescences capitate, with few flowers; fruit 2-winged

. . . . 17. Section Australes

18 - Inflorescences slightly elongate, with numerous flowers, if sometimes capitate then fruit 3-winged 19

19 - Fruit very large, 4-10 cm wide, always with 2 wings . . . . 18. Section Diptera

19 - Fruit small or very small up to 1 x 3 cm, with 2 or 3 wings . . . . 19. Section Actinophylla

20 - Leaves chartaceous or subcoriaceous, with eucamptodromous venation; fruit 5-winged, 3 rudimentary and 2 normally transversely spreading . . . . 20. Section Chuncoa

20 - Leaves thickly coriaceous, with weak brochidodromous venation; fruit with 4 or 5 equal wings 21

21 - Inflorescence usually a long spike, sometimes short or subcapitate, with perfect flowers usually towards the base; fruits numerous, scattered along the rachis . . . . 21. Section Pachyphylla

21 - Inflorescences usually short or subcapitate, with perfect flowers usually towards the apex; fruits crowded into spherical capitula . . . . 22. Section Ramatuella

8.2.3. The sections of Terminalia

1. Section Terminalia, sectio typica generis.

Type species: Terminalia catappa L., the type of the genus.

Syn: Adamaram Adans., Fam. Pl. 2 : 445 (1763), pro parte, excl. Hort. Malab 4. t. 5 Based on Hort Malab iv. t. 3, 4, 35 (1682) of which 3 and 4 are Terminalia catappa L.

Kniphofia Scop., Introd. Hist. Nat. 327 (1777), Non Moench (1794, nom. cons.). Based on Adamaram in Hort. Malab. (Terminalia catappa L.).

Badamia Gaertner, Fruct. som. pl. 2 : 90, t. 97 (1790), non Badhamia Berkeley 1853 (Myxomycetes). Based on Bad amia commersonii Gaertner (= Terminalia catappa)

Section Catappa C. B. Clarke, Fl. Brit. Ind. 2 : 444 (1878) pro parte incl. type (T. catappa).

Section Eucatappa Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 9 (1900), pro parte incl. type.

Medium or large-sized trees. Leaves spirally arranged, often crowded at the tips of the branchlets; petiole often short-medium and stout, eglandular or with two often inconspicuous glands; lamina chartaceous to coriaceous, usually large, obovate; apex rounded or obtuse rarely shortly acuminate; base subcordate to rounded or attentuate. Domatia usually present. Venation brochidodromous or eucamptodromous - brochidodromous; secondary veins 8-40 pairs, moderate or thick, usually raised below; tertiary veins regularly or irregularly percurrent; higher order venation distinct or not. Inflorescence long to very long 8-50 cm; peduncle 2-6 cm long; rachis (3)6-30(45). Flowers usually medium, pentamerous; male flowers numerous; hermaphrodites few and usually towards the base of the inflorescence; steamens 10; style glabrous. Fruit large (2) 3-17 x (1.5) 2-8 x 1-6 cm usually compressed, ellipsoid or ovoid, usually angled or sometimes narrowly winged; wing if present very stiff and gradually becomes broader towards the apex.

Geographical range: Asia (from Pakistan throughout India to South-East Asia), New Guinea to Fiji Is., Australia, Madagascar and Mauritious, and West Indies (Map 8/2).

29 species.

The section is very common in Asia and Australia. T. catappa (a native species of tropical Asia) is commonly planted in Africa and naturalized in America. But in West Indies the section is represented by two wild species, T. latifolia and T. arbuscula.

This section is one of the largest and most heterogeneous sections of Terminalia. The variability within the section extends to all features of the species. There are no characters unique to the section.

2. Section Myrobalanus (Gaertner) DC., Prod. 3 : 12 (1828).

Based on Myrobalanus (incl. Badamia) Gaertner, Fruct. 2 : 90. t. 97 (1790).

Lectotype: Myrobalanus bellirica Gaertner selected by Exell, ING 1979 = Terminalia bellirica (Gaertner) Roxb., Pl. Corom. 2: 54, t. 198 (1805).

Syn: Panel Adans., Fam. pl. 2 : 447 (1763), pro parte quoad Hort. Malab. 4. t. 10 (1687) (= T. bellirica fide Exell 1931).

Myrobalanifera Houtt., Hand Pl. Kruidk. 2 : 485 t. 10 (1774). Based on Myrobalanifera citrina Houtt. (= Terminalia chebula Retzius fide Exell in ING 1979.

Section Catappa C. B. Clarke, Fl. Brit. Ind. 2 : 444 (1878), pro parte excl. type (T. catappa).

Section Belericae Engler & Diels in Engler, Mon. Afr. Pflan. 4: 8 & 30 (1900). Lectotype: Terminalia bellirica, designated here as it gives rise to the sectional name.

Series F of Exell, Fl. Males. 4 : 550 (1954).

Subgroup A1 of Capuron, Combret. Arbust. Arbor. Madag. : 22 (1967), pro parte.

Medium or large size trees. Leaves spirally arranged along the branchlets or crowded at the ends of the branchlets; petiole often long, moderate, eglandular; lamina chartaceous to subcoriaceous, usually medium-sized, variable in shape but often broadly elliptic to oblanceolate; apex rounded to obtuse or sometimes acuminate; base rounded or obtuse or cuneate. Domatia absent or sometimes present. Venation usually eucamptodromous; secondary veins 6-13 pairs, moderate, not raised below; tertiary veins percurrent; higher order-venation often distinct. Inflorescence medium or long, (3) 5-15 cm long, andromonoecious. Peduncle 2-5 cm long. Flowers small to large, pentamerous or occasionally tetramerous (in Madagascar); stamens (8) 10 (12); style glabrous or hairy. Fruit usually small-medium, 1-3 x 0.5-2.5 cm, globose to subglobose or broadly ellipsoid or cylindrical, completely wingless, but often with five ridges, often densely pubescent.

Geographical range: Asia (from west Pakistan throughout India to South-East Asia), Australia and Madagascar (Map 8/3).
14 species.

The affinities of the section are with sections Terminalia and Catappa. The section is very closely related to section Terminalia, and sometimes when the fruits are glabrous the two sections are not separable from each other. [illegible]

3. Sect. Catappa (Gaertner) DC., Prod. 3 : 10 (1828).

Based on Catappa Gaertner, Fruct. sem. pl. 2 : 206 t. 127 (1791).

Type: Catappa benzoin Gaertner, loc. cit. (based on Terminalia angustifolia Jacq., which is an illegitimate name change for Croton bentzoë L.) = Terminalia bentzoë (L.) L.f., Suppl. Pl. : 434 (1781).

Syn.: Aristotelia Comm. ex Lam., Encycl. 1 : 349 1785, in syn. Based on Terminalia mauritiana Lam. = T. bentzoë (L.) L.f.

Resinaria Comm. ex Lam., loc. cit. Based on T. mauritiana Lam.

Subgenus Catappa (Gaertner) Eichler in C. Martius, Fl. Bras. 14, 2: 82 (1867).

Sect. Eucatappa Engler & Diels in Engler, Mon. Aft. Pflanz. 4 : 28 (1900), pr parte excl. type (T. catappa).

Terminaleopsis Danguy, Bull. Mus. Hist. Nat. Paris, 29 : 108 (1923). Type Terminaliopsis tetrandra Danguy

Subgroup A1 of Capuron, Combret. Arbust. Arbor. Madag. : 22 (1967), pro parte.

Small to large-sized trees. Leaves spirally arranged, dispersed along the branchlets or crowded at their apices; petiole short or medium, usually biglandular; lamina papyraceous to coriaceous, usually small to medium sized, narrowly elliptic to obovate or spathulate; apex rounded or acuminate or apiculate; base usually cuneate, sometimes decurrent into the petiole. Domatia usually present. Venation brochidodromous or eucamptodromous-brochidodromous or eucamptodromous; secondary veins (6) 8-16(20) pairs often narrowly spaced, usually slightly raised beneath; tertiary veins randomly reticulate or percurrent; higher order venation sometimes distinct. Inflorescence usually short to medium 2-17 cm, andromonoecious. Flowers small, pentamerous occasionally tetramerous (in Madagascar); stamens 10 (occasionally 8 or 4 in Madagascar); style glabrous. Fruit usually compressed, suborbicular or ovoid, 1-5 x 10.6-3 cm, usually uniformly cirumalate or circumridged.

Geographical range: Madagascar, Mauritius, South-East Asia, Philippines, Indonesia, New Guinea to Fiji Island, and Australia (Map9~~1~~4).

55 species.

Comments: Section Catappa is the largest section of the genus Terminalia. It is very closely related to sections Terminalia and Myrobalanus and sometimes it is hardly separable from them (particularly in Australia).

In South-East Asia and Malaysia the affinities of the section are with section Terminalia while in Madagascar and Australia the affinities are with section Myrobalanus. However, it differs from section Myrobalanus by its strongly compressed uniformly circumalate fruits and from Terminalia by its smaller size and different shape of leaves.

4. Sect. Fatrea (A. L. Juss.) Exell, Kirkia 7, 2 : 229 (1970).

Based on Fatrea A. L. Juss., Ann. Mus. Par. 5 : 223 (1804).

Type: Fatrea buxifolia A. L. Juss., Dict. Sci. Nat. 16 : 206 (1820).

Syn: Sect. Myrobalanus sensu Engl. & Diels in Engler, Mon. Afr. Pflanz. 4 : 9 (1900), non DC.

Group B ('Fatrea') of Capuron, Combret. Arbust. Arbor. Madag. : 78 (1967).

Shrubs or small trees. Leaves spirally arranged or alternate often on spur shoots; petiole short, eglandular; lamina chartaceous, small or very small; obovate-elliptic to obovate; apex often obtuse-rounded; base cuneate; upper surface and lower surface usually glabrous. Domatia absent. Venation weakly brochododromous; secondary veins 3-7 pairs, usually diverging at narrowly acute angle; intersecondary veins common; tertiary veins ramified. Inflorescence very short to slightly elongate 0.2-3.5(6) cm long. Flowers pentamerous, hermaphrodite, laxly arranged on the rachis; stamens 10. Fruit ellipsoid-ovoid, not or obscurely ridged, or rarely very narrowly winged, 0.6-1.8(24) x 0.4-1.1 cm, almost always pedicelate.

Geographical range: Madagascar and Eastern Africa (Map 8/3).
12 species.

The affinity of the section is with sections Catappa/Abbreviatae although its fruits have similarity with those of Myrobalanus.

Under his section Fatrea, Exell (1970) mentioned Terminalia fatraea (Poir) DC. as the type species of the section but in ING he stated Fatraea buxifolia (which is not mentioned in IK) as the type species of the genus Fatraea Thouars.

5. Sect. Abbreviatae Exell, Bol. Soc. Bret., Sér. 2, 42 : 30 (1968).

Type: T. prunioides Lawson, in Oliv., Fl. Trop. Afr., 2 : 415 (1971)

Syn. Sect. Platycarpae Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 17 (1900), pr parte excl type.

Subgroup A2 Capuron, Combret. Arbust. Arbor. Madag., 52 (1967), pro parte.

Shrubs or small trees. Branchlets often bearing spines. Leaves in fascicles on short spur shoots; petiole usually short or very short, eglandular; lamina chartaceous, usually small or very small, broadly to narrowly obovate; apex obtuse-rounded or emarginate; base cuneate. Domatia absent. Venation brochidodromous; secondary veins 2-7 pairs; tertiary veins randomly reticulate, not raised. Inflorescence medium, to 8 cm long; peduncle 1-3 cm long. Flowers pentamerous, hermaphrodite, usually glabrous or nearly so except pubescent in T. polycarpa; stamens 10. Fruit 2-winged, stipetate, always longer than broad usually 1.5-6.5 x 1-3 cm.

Geographical range: Southern and eastern Africa and Madagascar. South Africa, Botswana, Namibia, Mozambique, Zimbabwe, Zambia, Angola, Malawi, Tanzania, Uganda, Kenya, Somali Republic, Ethiopia and Sudan (Map 8/4). 7 species in Africa and 3 species in Madagascar.

The section is closely related to sections Fatrea and Discocarpae.

6. Sect. Discocarpae Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 26 & 31 (1900).

Lectotype: Terminalia orbicularis Engler & Diels in Engler, op. cit. : 26 t. 15 fig. A. (1900), designated here, equivalent name to Discocarpae.

Syn: Subgroup A2 of Capuron, Combret. Arust. Arbor. : 52 (1967), pr parte quoad T. neotaliata Capuron

Shrubs or trees. Leaves spirally arranged on stunted spur shoots; petiole short or long, 1-6 cm long, eglandular; lamina chartaceous, oblanceolate or elliptic or suborbicular; apex obtuse-rounded or emarginate or shortly acuminate; base obtuse or rounded or cuneate. Domatia sometimes present. Venation brochidodromous; secondary veins 3-6 pairs, weak or moderate; tertiary veins randomly reticulate, not conspicuous. Inflorescence medium, 3-6 cm long; peduncle about 1 cm long. Flowers pentamerous or tetramerous; stamens 10 or 8; style glabrous or hairy. Fruit 2-winged, suborbicular 5-10 x 4-9 cm; body fusiform, sparsley puberulous, with short persistent style and relatively long stipe (up to 10 mm long); wings developed beyond the persistent style at apex and beyond the insertion of the stipe.

Geographical range: Eastern Africa and Madagascar (Map 8/5).

5 species.

The affinities of the section are with sections Abbreviatae and Platycarpae.

7. Sect. Psidioides Exell, Bol. Soc. Bot., Sér. 2, 42 : 30 (1968).

Type: T. sericea Buchell ex DC., Prod. 3: 13 (1828)

Syn. : Sect. Platycarpae Engler & Diels pro parte, excl. type.

Shrubs or small trees. Bark on young branchlets peeling off in cylindrical or hemicylindrical flakes, leaving a reddish brown or brown newly exposed surface. Leaves spirally arranged, not in fascicles terminating short spur shoots, sometimes crowded at or near the ends of the branchlets; petiole very short to medium, 0.1-3 cm long, eglandular; lamina medium to large, chartaceous or subcoriaceous, obovate or oblanceolate or elliptical-oblong; apex acute to rounded or shortly acuminate or mucronate; base acute to cuneate. Domatia absent. Venation often brochidodromous; secondary veins (5) 8-14 pairs, moderate, slightly raised below; intersecondary veins usually present; tertiary veins randomly reticulate. Inflorescence 6-14 cm long; peduncle 1.6-5 cm long; flowers pentamerous, stamens 10; style hairy or glabrous. Fruit 2-winged, medium, usually 3-7.5 x 16.-4.3 cm, always longer than broad, elliptic or oblong in outline; body fusiform, with conspicuous persistent style at apex and distinct stipe at base; wings narrow and long, never developed beyond the insertion of the stipe.

Geographical range: Southern Africa (Map 8/3).

6 species.

The section is closely related to section Platycarpae.

8. Sect. Platycarpae Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 17 (1900), emend. Exell. Bol. Soc. Brot., Sēr. 2, 42 : 31 (1968).

Lectotype: Terminalia brownii Fresen., Menckenb. 2 : 152, t. 9, fig. 1 (1837), selected by Exell (1968) but simply as the first species in Engler & Diels' section. Redesignated here, as it is a common and representative species.

Syn. : Sect. Stenocarpae Engler & Diels op. cit. : 11 (1900). lectotype: T. macroptera Guill. & Perr., Fl. Senegamb. Tent. 1, 276, t. 63 (1832), selected by Exell 1968 but simply because it is the first in the section. Redesignated here as it is a well-known and representative species.

Small to large trees, or shrubs. Leaves spirally arranged or alternate, not borne in fascicles on short spur shoots; petiole short to long, often eglandular; lamina thinly to thickly chartaceous, usually large or medium, usually obovate-oblong to oblanceolate or elliptic or oblong; apex often obtuse, or sometimes acuminate; base acute to rounded. Domatia absent. Venation eucamptodromous; secondary veins 7-20 pairs, often raised below, intersecondary veins common; tertiary veins irregularly or regularly percurrent; higher order venation randomly reticulate. Inflorescence long, up to 22 cm; peduncle 1-5 cm long. Flowers pentamerous; stamens 10, style hairy or glabrous. Fruit large to very large, always longer than broad, (3) 5-12 x 2-6 (8), elliptic or oblong or oblong-elliptic, 2 winged; wings narrow, 5-10 times longer than broad, 0.5-1.3 x 4-12 cm, thickly chartaceous; body fusiform, 0.7-2 cm dia., always conspicuously pedicelate and with a long persistent style at apex.

Geographical range: Africa (central, eastern, southern and south western Africa) (Map 8/5).

9. Sect. Vicentia (Allemão) Engler & Diels in Engler, Mon. Afr. Pflanz. 4, 29 (1900).

Based on Vicentia Allemão, Pl. Novas Brasil (1844)

Type: Terminalia acuminata (Allemão) Eichler, the only species in the section.

Trees. Leaves alternate; petiole relatively long, biglandular; lamina chartaceous, usually medium sized, oblong to elliptic oblong or ovate-oblong; apex often long acuminate; base acute; upper surface nearly glabrous; lower surface densley rufous pubescent particularly on the primary and secondary veins. Domatia present, hairy. Venation eucamptodromous. Inflorescence axillary panicle. Flowers small, hermaphrodite, tetramerous; stamens 8; style glabrous. Fruit 3-4(or 5)-winged, body very narrow.

Geographical range: South America (Brazil) (Map 8/4).

This section has some affinities with sections Myriocarpae and Pentaptera from Asia.

10. Sect. Pentaptera C. B. Clarke in Hoocker f., Fl. Brit. Ind. 2 : 447 (1878).

Based on Pentaptera Roxb., Hort. Bengal : 34 (1814).

Type: Pentaptera angustifolia Roxb. (= Terminalia arjuna (Roxb.) Wight & Arn., Prod. Fl. Pen. Ind. Or. 1 : 314 (1934), non T. angustifolia Roxb. Hort. Bengal: 33 (1814).

Syn.: Subgenus Pentaptera (Roxb.) Eichler in C. Martius, Fl. Braz. 14, 2 : 82 (1867).

Large trees, leaves subopposite or subopposite and alternate; petiole short or medium, biglandular; lamina usually oblong or ovate-oblong, medium to large, thickly chartaceous; apex usually obtuse-rounded, occasionally acute; base usually obtuse. Domatia absent. Venation eucamptodromous; secondary veins 8-16 pairs, tertiary veins percurrent but not raised. Inflorescence panicle. Flowers pentamerous, hermaphrodite; stamens 10. Fruit large, 2.5-6 cm long, with five (rarely six) equal wings, wings narrow, always longer than broad; body highly schlerenchymatous and hard to cut in section.

Geographical range: Asia (from Pakistan throughout India to Burma and Thailand (Map 8/4).

5 species.

The affinities of the section are with sections Myriocarpae, Vicentia and Myrobalanus.

11. Sect. Myriocarpae Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 29 (1900).

Lectotype: Terminalia myriocarpa Van Heurck & Muell. Arg. in Van Heurck Obs. Bot. : 215 (1870), designated here, a representative and widespread species.

Syn. : Subgenus Monoptera Eichler in C. Martius, Fl. Braz. 14 : 82 (1867).

Lectotype: Terminalia monoptera Roth, Nov. Pl. Sp. : 382 (1821), designated here as it gives rise to the name of the subgenus.

Sect. Monoptera Engler & Diels in Engler, Mon. Afr. Pflanz. 4: 29 (1900). Type: T. paniculata Roth, the only species mentioned under the section.

Sect. Polyanthae Engler & Diels in Engler. Op. Cit. : 30 (1900).

Lectotype: T. polyantha Presl, Abh. Königl. Böhm. Gesel. Wiss. Ser. V, 6 : 573 (1851), deisngated here as it gives rise to the name of the section.

Series A. subseries (a) of Exell, Fl. Males. 4 : 550 (1954).

Sect. Chuncoa (Pavon ex A. L. Juss.) C. B. Clarke, Fl. Br. Ind. 2 : 448 (1878), pro parte excl. type.

Large or small trees. Leaves alternate or subopposite; petiole often short and biglandular but sometimes eglandular; lamina chartaceous or subcoriaceous, variable in shape and size, apex usually acute; base often obtuse-rounded to subcordate, occasionally cuneate. Domatia absent. Venation eucamptodromous; secondary veins usually numerous, up to 35 pairs, often parallel; tertiary vein obliquely and irregularly percurrent. Inflorescence panicle, 4-17 cm long. Flowers pentamerous, hermaphrodite; stamens 10, style glabrous. Fruit small, 2-20 x 6;14 mm, with 3-5 wings, if 3-4 wings then 0-2 rudimentary, if 5 wings 2-3 rudimentary; body very small.

Geographical range: India, China, IndoChina, Malaysia, Philippines, Solomon Islands and New Britain (Map 8/5).

7 species.

The affinities of the section are with sections Pentaptera and Myrobalanus.

12. Sect. Archipelagi Alwan sect. nov.

Type: Terminalia archipelagi Coode, Kew, Bull. 23 : 299 (1969).

Arbor grandis vel media. Folia spiraliter ordinata ad ramulorum apices congesta. Venatio eucamptodroma; venae secondarii infra prominentes, 10-30 paribus. Inflorescentiae spicatae. Flores 8-16 x 8-10 mm; staina 10, exserta, 10-15 mm longa; stylus 13-30 mm longus. Fructus circumalatus, longior quam latus, alis 8-25 mm latis.

Medium to large-sized tree. Leaves spirally arranged, crowded at the apices of the twigs; petiole short or medium, 0.3-3 cm long, eglandular or biglandular; lamina large or very large, subcoriaceous to coriaceous, obovate or obovate-oblanceolate; apex obtuse-rounded base acute-cuneate. Domatia present or absent. Venation eucamptodromous; secondary veins numerous, usually 10-30 pairs; tertiary veins percurrent. Inflorescence axillary spike, to 15 cm long. Flowers large, 8-16 x 8-10 mm, pentamerous; stamens 10, 10-15 mm long; style 13-25 (30) mm long. Fruit circumalate, longer than broad, elliptic or oblong in outline; body ridged, trigonal or slightly keeled, ellipical, with persistent style; wing always longer than broad, 8-25 mm wide.

Geographical range: New Britain, Solomon Is. & Fiji Is. (Map 8/4).

4 Species: T. archipelagi, T. rerei, T. capitanea, T. crebrifolia.

The affinities of this section are with sections Catappa. The section is distinct in having large leaves with numerous secondary veins, large flowers with long style, and distinctly winged fruits with keeled body which terminates in a persistent style.

13. Sect. Circumalatae Engler & Diels in Engler, Mon. Afr. Plfanz. 4 : 28 (1900).

Lectotype: Terminalia circumalata F. Muell., Fragm. 3 : 91 (1862) (= T. canescens (DC.) Radlk., Th. Dur. Ind. Gen. Phan. 500 (1888) fide Byrnes 1977), designated here as it gives rise to the sectional name.

Shrubs or rarely trees. Leaves spirally arranged, usually crowded at the ends of the branchlets; petiole very short or long, eglandular or inconscpicuously biglandular; lamina subcoriaceous to coriaceous, concolorous, small or medium, usually narrow, narrowly obovate to obovate or obanceolate or narrowly oblong; apex obtuse or acute; base attentuate, usually decurrent on the petiole. Domatia present. Venation weakly brochidodromous; secondary veins 3-6 pairs, weak, not raised; tertiary veins if conspicuous then randomly reticulate. Inflorescence medium to long spike, andromonoecious, with few male flowers usually restricted to the destal end. Flowers pentamerous; stamens 10; style hairy. Fruit usually small, circumalate, or 2-winged, sometimes with one or more horns, tubercules or irregular ridges, usually pubescent; wings always longer than broad.

Geographical range: Northern Australia (Map 8/5).

3 species.

The affinites of this section are with some species of section Oblongae.

14. Sect. Rhombocarpae Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 8 & 30 (1900).

Lectotype: Terminalia lucida Hoffsgg ex C. Martius, designated here as it is one of only two described species, the other T. tanibouca) having a name which has been applied to different taxa.

Syn.: Tanibouca Aublet, Hist. Pl. Guiane 1 : 448, t. 178 (1775).

Type: T. guianensis Aublet.

Sect. Bialatae Engler & Diels in Engler, op. cit. : 25 (1900), pro parte quoad Terminalia scutifera.

Small to large trees. Leaves spirally arranged or alternate, usually crowded at the ends of the branchlets; petiole short to medium, eglandular or biglandular; lamina chartaceous to coriaceous, medium or medium-large, oblong obovate or obovate or narrowly obovate or elliptic; apex often acuminate or acute; base cuneate; upper surface glabrous; lower surface pubescent or glabrous. Domatia absent. Venation eucamptodromous-brochidodromous or brochidodromous; secondary veins 5-8(10) pairs; tertiary veins percurrent or randomly reticulate, higher-order veins distinct. Inflorescence long; rachis up to 12 cm long. Flowers small to medium, pentamerous, hermaphrodite; stamens 10; style densely villous. Fruit medium, 2-winged, suborbicular or rhomboid; body large, rounded or elliptic-ovate, 1-2.5 cm wide; wing often narrow, 0.4-1.5 cm wide.

Geographical range: Central America, South America, Trinidad and Western Africa (Map 8/5).

2 species.

Section Rhombocarpae is closely related to section Oblongae but it also shows some similarities with sections Platycarpae and Terminalia.

Terminalia lucida is the only amphi-atlantic species in the genus and the only non-mangrove one in the family.

15. Sect. Chicharronia (A. Rich.) Alwan, comb. et stat. nov.

Based on Chicharronia A. Rich. in R. de la Sagra, Hist. Phys. Cuba, Bot. Pl. Vasc. : 529, t. 43 (1846).

Type: Chicharronia intermedia A. Rich. loc. cit. = T. chicharronia

Shrubs or trees. Leaves usually alternate or spirally arranged; petiole short to medium; lamina thickly chartacious to thickly coriaceous, small or medium, obovate, obovate oblong to narrowly obovate, or elliptic or oblong; apex usually obtuse to rounded sometimes acute or retuse; base cuneate or obtuse; margin often revolute; upper surface slightly pubescent, glabrescent or glabrous, usually verruculose; lower surface densely ferruginous-tomentose to completely glabrous. Domatia absent. Venation typical brochidodromous, usually prominently raised below; secondary veins 5-14 pairs; areolation usually well developed. Inflorescence axillary, medium to long, with rachis up to 15 cm long. Flowers medium or large, hermaphrodite pentamerous; stamens 10; style often hairy but occasionally glabrous. Fruits medium up to 4 cm wide, 2 winged, always wider than long, usually shortly stipitate, pubescent or glabrous.

Geographical range: Endemic to West Indies (Cuba, Haiti and Dominican Rep.) (Map 8/6).

2 species: T. chicharronia and T. eriostachya.

The affinities of this section are with section Oblongae.

16. Sect. Oblongae Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 8 & 30 (1900).

Lectotype: T. oblonga (Ruiz Lopez & Pavon) Steudel, designated here as it gives rise to the sectional name.

Syn. Sect. Bialatae Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 25 (1900), pro parte includ. type. Lectotype T. superba Engler & Diels in Engler, op. cit. : 26 (1900), designated here, one of only two species, the other T. scutifera being transferred by me to section Rhombocarpae.

Sect. IV of C.B.Clarke, Fl.Brit.Ind. 2 : 49 (1978).

Medium to large trees. Leaves alternate or spirally arranged; petiole short to long; lamina chartaceous to coriaceous, variable in size, oblong or elliptic or obovate or oblong obovate; apex rounded to acuminate; base cuneate; upper surface glabrous; lower surface pubescent or glabrous. Domatia absent. Ventation eucamptodromous-brochidodromous or brochidodromous; secondary veins 4-10 pairs; tertiaries usually randomly reticulate. Inflorescence axillary spike, long, with rachis to 24 cm long. Flowers small or medium, hermaphrodite or hermaphrodite and male,pentamerous; stamens 10; style hairy or glabrous. Fruit 2-winged, medium to large, variable in size and shape; body variable in shape and size, wings transversely and widely spread.

Geographical range: Central and South America, south-western Africa, Asia (from Burma throughout IndoChina and South-East Asia to New Guinea) and Australia (Map 8/6).

12 species.

The affinities of this section are with sections Chuncoa and Diptera.

17. Sect. Australes Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 31 (1900).

Type: Terminalia australis Cambess. (The only species mentioned under the section by Engler & Diels).

Shrubs or small trees. Leaves spirally arranged or alternate; petiole short, eglandular; lamina chartaceous, usually small, narrowly elliptic to elliptic or obovate-elliptic; apex usually acute, sometimes obtuse of shortly acuminate; upper surface verruculose, pilose or pubescent or glabrescent; lower surface densely to sparsely pubescent. Domatia absent. Venation brochidodromous or eucamptodromous-brochidodromous; secondary veins 4-9 pairs; tertiary veins randomly reticulate or weakly percurrent. Inflorescence capitate or subcapitate, with few flowers up to 12, borne in clusters of 2-6 or solitary; peduncle 1-5 cm long. Flowers pentamerous, hermaphrodite; stamens 10; style slightly hairy at base. Fruit small or medium, with 2 wings.

Geographical range: South America, southern Brazil, southern Paraguay, southern Bolivia, northern Argentina and Uruguay (Map 8/6).

4 species: T. australis, T. reitzii, T. triflora and T. uleana.

This section is very closeley related to section Diptera.

18. Sect. Diptera (Eichler) Engler & Diels in Engler, Mon. Afr. Pflanz. 4 : 8 & 30 (1900).

Based on subgenus Diptera Eichler in Martius, Fl. Bras. 14, 2 : 82 (1867), pro parte quoad type.

Lectotype: T. argentea C. Martius, designated here as it is a widespread and well-known species.

Small to large trees, leaves alternate or spirally arranged; petiole short to long, biglandular or sometimes eglandular; lamina chartaceous to subcoriaceous, medium or medium-large, ovate to oblong, or obovate; apex acute or acuminate or aristate; base often decurrent into the petiole; upper surface pubescent to glabrous; lower surfaces densely silvery, sericeous to nearly glabrous. Domatia absent. Venation eucamptodromous-brochidodromous or eucamptodromous or brochidodromous; secondary veins 5-14 pairs. Inflorescence capitate to subcapitate or slightly elongate, with rachis 1-5 cm long. Flowers pentamerous, small to medium; stamens 10; style hairy. Fruit large to very large, broader than long, highly legnified, with 2 large wings; wings always wider than body, transversely spread; body medium to large, variable in shape.

Geographical range: South America (Map 8/7).

5 species: T. argentea, T. phaeocarpa, T. januariensis, T. guyanensis and T. kuhlmanii.

The affinities of this section are with section Oblongae. It is distinct from section Oblongae by its capitate-subcapitate inflorescence.

19. Sect. Actinophyllae Eingler & Diesl in Engler, Mon. Afr. Pflanz. 4, 8 & 30 (1900).

Type: Terminalia actinophylla C. Martius (the only species mentioned by Engler & Diels under the section).

Shrubs or small to medium sized trees. Leaves spirally arranged, crowded; petiole very short, eglandular; lamina chartaceous to subcoriaceous, small to medium, obovate to narrowly obovate or elliptic, often pilose, occasionally sparsely pubescent. Domatia absent. Venation often eucamptodromous sometimes mixed craspidodromous or brochidodromous; secondary veins usually straight, raised and narrowly spaced (except T. actinophylla); tertiary veins often regularly percurrent. Inflorescence capitate to subcapitate or slightly elongate, andromonoecious; peduncle 2-3.5 cm long; rachis up to 2.5 cm long. Flowers small, pentamerous; stamens 10; style glabrous. Fruit very small to small, 0.4-1.0 (1.2) x 0.7-3 cm with 2-3 small wings; body small, not or slightly lignified.

Geographical range: South America (Brazil) (Map 8/5).

3 species: T. actinophylla, T. eichleriana and T. fagifolia.

Section Actinophyllae is closely related to section Diptera. It differs from section Diptera in having much smaller fruits.

20. Sect. Chuncoa (Pavon ex A. L. Juss.) C. B. Clarke, Fl. Br. Ind. 2 : 448 (1878).

Based on Chuncoa Pavon ex A. L. Juss., Gen. Pl. : 76 (1789). Type: - "Chunco du Margon" (Chuncoa amazonia = Terminalia amazonia) the only species from Peru to which the generic description applies.

Syn. Gimbernatea Ruiz Lopez & Pavon, Prod. : 138, t. 36 (1794).

Type G. obovata = T. amazonia.

Subgenus Chuncoa (Pavon ex A. L. Juss.) Eichler in C. Martius Fl. Bras. 14 : 82 (1867).

Clarke (1878) was obviously basing his section on the genus Chuncoa Pavon ex A. L. Juss., but the only three species he included in it were actually members of section Myriocarpae.

Small to large trees or sometimes shrubs. Leaves spirally arranged, crowded at the end of the branchlets; petiole short to medium; lamina chartaceous to subcoriaceous, small to medium, obovate to narrowly obovate or oblong obovate; apex acuminate or subacute to rounded or retuse; base cuneate or attentuate; upper surface verruculose, nearly glabrous; lower surface rufous tomentose to glabrescent. Domatia present, hairy or glabrous. Venation eucamptodromous; secondary veins 3-8 pairs, diverging at acute angle; tertiary veins percurrent, often perpendicular to the primary vein. Inflorescence terminal, long, with rachis to 15 cm long. Flowers small-medium, pentamerous, hermaphrodite; stamens 10; style glabrous. Fruit small, 5-winged, broader than long; wings very thin, three of them rudiemtary.

Geographical range: Central and South America (Map 8/2).

2 species: T. amazonia and T. glabrescens.

The affinities of this section are with section Oblongae.

21. Sect. Pachyphyllum Maguire & Exell, Mem. N. Y. Bot. Gard. 10 (1) : 92 (1958).

Type species: Terminalia virgata Maguire & Exell = T. guaiquinimae Maguire & Exell

Shrubs or small to medium-sized trees. Leaves spirally arranged; petiole very short, often winged, thick and flattened; lamina coriaceous to thickly coriaceous, medium, oblong to obovate or narrowly obovate; apex obtuse to rounded to retuse; base obtuse to slightly subcordate or broadly cuneate; upper surface tomentose to glabrous and shiny; lower surface densely silvery sericeous or greyish-villous-tomentose or pubescent to completely glabrous. Domatia absent. Venation weakly brochidodromous, not raised; primary vein flattened. Very narrow near the apex much wider near the petiole; secondaries fine-hair like or weak, usually not very conspicuous; intersecondary veins present; tertiary and higher-order venation not distinct from each other. Inflorescence axillary, very long to subcapitate. Flowers medium, male and hermaphrodite, tetra or pentamerous; stamens 10 or 8; style glabrous or hairy. Fruits small, with 5 or 4 equal wings, up to 15 x 12 mm, wings papyraceous.

Geographical range: South America, Southern and South-Eastern Venezuela and Western Guyana (Map 8/7).

4 species: *T. guaiquinimae*, *T. quintalata*, *T. yapacana* and *T. steyermarkii*. This section is closely related to section *Ramatuella*.

22. Sect. *Ramatuella* (Kunth) Alwan, comb. et stat nov.

Based on *Ramatuella* Kunth, Nov. Gen. & Sp. Pl. 7: 253 (1825). ("Ramatuela").

Type species: *R. argentea* Kunth = *T. ramatuella* Alwan.

Shrub or small tree. Leaves spirally arranged, usually crowded at the ends of the branchlets; petiole short or medium; lamina coriaceous, oblanceolate to obovate or oblong; apex retuse to rounded; base cuneate and slightly decurrent into the petiole; upper surface glabrous except sometimes sparesely puberulous on the primary vein; lower surface glabrous, puberulous, or densely silvery-sericeous. Domatia absent. Venation weakly brochidodromous; primary vein sometimes raised below; secondary veins fine or weak; intersecondary veins common; tertiary and higher order venation not distinct from each other. Inflorescence subcapitate to slightly elongate; peduncle 5-50 mm long, pubescent or puberulous; rachis 1-3(4-4) mm long, with male and hermaphrodite flowers, but the male flowers usually towards the base. Flowers tetramerous or pentamerous; stamens 8 or 10. Fruit 5-winged, actinomorphic, small, crowded into spherical capitula; wings narrow and coriaceous.

Geographical range: South America (Restricted to a small area on the borders of Venezuela with Colombia and Brasil) (Map 8/7).

3 species: T. argentea, T. virens and T. crispialata.

This section is closely related to section Pachyphyllum.

8.2.4. Sections excluded from Terminalia

Section Pteleopsoides Exelll

Exell (1968) based his section Pteleopsoides on a single species, Terminalia pteleopsoides Exell from Africa. The reason why Exell placed this species in Terminalia was mainly because of the lack of petals, the slightly zygomorphic upper receptacle and the "highly" sclerenchymatous pericarp of the fruit.

Vollesen (1981), after he had described a new species of Pteleopsis (P. apetala), which possesses no petals, transferred Terminalia pteleopsoides to the genus Pteleopsis, making the new combination Pteleopsis pteleopsoides (Exell) Vollesen.

I have examined all the specimens of Terminalia pteleopsoides at K (including istotypes), and consider that the new combination made by Vollesen (1981) was justified

I have also compared Pteleopsis pteleopsoides with other species of Pteleopsis available at K and found that it shares characters with both Terminalia and Pteleopsis. The leaves and inflorescences are more similar to Pteleopsis than to Terminalia, but the fruits are intermediate. Pteleopsis pteleopsoides and P. apetalata differ from all the other species of Pteleopsis in having no petals, this makes the two species a distinct group within the genus and suggests a separate section for them.

8.3. Bucida L., Syst. Nat. ed. 10, 2 : 1025 (1759), nom. cons.

Type species: Bucida buceras L.

Syn.: Buceras P. Browne, Civ. nat. Hist. Jamaica, t. 23 (1756) nom. nud., non Hall ex All. (1785) (= Trigonella of leguminosae).

The name Buceras is not valid because the author (Browne) did not use binomial nomenclature in his work.

Trees; branching sympodial; branches and branchlets often bearing spines. Leaves spirally arranged, usually crowded at the ends of the branchlets, petiolate; petiole moderate, eglandular or biglandular; lamina chartaceous to coriaceous, entire. Domatia absent. Venation usually brochidodromous. Inflorescence axillary spike. Flowers small, pentamerous; upper receptacle campanulate, with slightly developed lobes, persistent; petals absent; stamens 10, exserted; anthers versatile; style free, exserted; ovary completely inferior, unilocular with 2 pendulous ovules. Fruits leathery - fleshy drupe, wingless, usually with five obscure ridges, tapering into a neck, usually with persistent calyx until full maturity.

Geographical range: Central America, West Indies, Bahamas and Florida (Map 8/1).

3 species.

8.4. Buchenavia Eichler, Flora 49 : 164 (1866), nom. cons. prop.

Lectotype: B. capitata (Vahl) Eichler, designated by Alwan & Stace (in press).

Syn. Pamea Aublet, Hist. Pl. Guiane 2 : 946 t. 359 (1775).

Type : P. guianensis Aublet, the only species.

Hudsonia Robinson ex Lunan, Hort. Jamica 2: 310 (1814), non L. (1767). Type: H. arborea Robinson ex Lunan (= B. tetraphylla).

The name Buchenavia, which is antedated by the name Pamea Aublet, is recommended for conservation. (Alwan & Stace, in press). The genus Pamea was based on Pamea guianensis Aublet, the single species described under the genus. De Candolle (1828) treated the species as Terminalia pamea, but neither Aublet's figure nor the type specimen at BM (which consists of leaves only), is sufficient to place the plant in its correct genus. The acquisition of newly collected material from Brazil, possessing leaves, flowers and fruits, has undoubtedly shown that Pamea guianensis is a species of the genus Buchenavia but different from any species described in that genus.

Small to large-sized trees or shrubs, evergreen. Branching sympodial. Leaves spirally arranged, usually crowded at or near the ends of the branchlets, petiolate; petiole usually moderate, often biglandular; lamina chartaceous to coriaceous, entire. Domatia usually present. Venation brochidodromous or eucamptodromous or eucamptodromous - brochidodromous. Inflorescences axillary spike or capitate to subcapitate. Flowers small, pentamerous, usually hairy at the base of the lower receptacles, often glabrous on upper receptacle; lower receptacles always become narrower towards the apex and are joined to the upper receptacle by a pedicel-like apex; upper receptacel cupuliform, with scarcely developed lobes; petals basent; stamens 10, short, usually not exserted; anthers adnate to the filaments; disk intrastaminal, densely pilose; style free, very short, included; ovary completely inferior, unilocular, with 2 pendulous ovules. Fruits unwinged drupaceous with fleshy mesocarp.

<u>Geographical range</u>: South and Central America (from Southern Brasil to Costa Rica) and West Indies (Map 8/1).

21 species.

Table 8/1: Sections and approximate number of species of Terminalia in the world.

	Section	America incl. W. Indies	Africa including Madagascar	Asia, as far as Fiji and New Guinea	Australia	Total for World
1	Abbreviatae	0	10	0	0	10
2	Actonophyllae	3	0	0	0	3
3	Archipelagi	0	0	4	0	4
4	Australes	4	0	0	0	4
5	Catappa	0	12	28	16	55 *
6	Chicharronia	2	0	0	0	2
7	Chuncoa	2	0	0	0	2
8	Circumalatae	0	0	0	3	3
9	Diptera	5	0	0	0	5
10	Discocarpae	0	5	0	0	5
11	Fatrea	0	12	0	0	12
12	Myriocarpae	0	0	7	0	7
13	Myrobalanus	0	4	5	5	14
14	Oblongae	2	1	6	3	12
15	Pachyphyllum	4	0	0	0	5
16	Pentaptera	0	0	5	0	5
17	Platycarpae	0	13	0	0	13
18	Psidioides	0	6	0	0	6
19	Ramatuella	3	0	0	0	3
20	Rhombocarpae	2	1	0	0	2 *
21	Terminalia	3	1	26	2	29 *
22	Vicentia	1	0	0	0	1
		31	65	81	29	201 *

* These figures are less than the sums of the horizontal rows because one species (*T. complanata*) of section Catappa is common to Asia and Australia, one species (*T. lucida*) of section *Rhombocarpae* is common to America and Africa, and *T. catappa* of section *Terminalia* is common to America, Africa, Asia and Australia.

Map 8/1: Distribution of Terminalia (1), Buchenavia (2) and Bucida (3).

Map 8/2: Distribution of _Terminalia_ sections _Terminalia_ (1) and _Chuncoa_ (2)

Map 8/3: Distribution of <u>Terminalia</u> sections <u>Myrobalanus</u> (1), <u>Fatrea</u> (2) and <u>Psidioides</u> (3)

Map 8/4: Distribution of Terminalia sections Catappa (1), Archipelagi (2), Pentaptera (3), Abbreviatae (4) and Vicentia (5).

Map 8/5: Distribution of Terminalia sections Myriocarpae (1), Circumalatae (2), Discocarpae (3), Platycarpae (4), Rhombocarpae (5) and Actinophyllae (6).

Map 8/6: Distribution of _Terminalia_ sections _Oblonga_ (1), _Chicharronia_ (2) and _Australis_ (3).

Thesis

17.4.1984

CHAPTER 9

TAXONOMY AT THE SPECIFIC LEVEL IN THE NEW WORLD

9.1. Terminalia

9.1.1. Key to the American species of Terminalia

1 - Fruit unwinged, drupaceous, angled or sometimes ridged; leaves usually large, over 10 cm wide (except in T. arbuscula endemic to Jamaica); inflorescences always spicate with a few hermaphrodite flowers towards the base 2

1 - Fruit distinctly winged, but sometimes only narrowly so; leaves small or medium, usually less than 10 cm wide; inflorescences capitate - subcapitate, or spicate, or paniculate, andromonoecious or with only hermaphrodite flowers 4

2 - Leaf base subcordate . . . . 1. T. catappa

2 - Leaf base cuneate or attentuate 3

3 - Leaves usually large, 10-24 x 6-14 cm, obovate or broadly obovate or oblong-obovate, with 7-12 pairs of prominent secondary veins; domatia always present; style glabrous . . . . 2. T. latifolia

3 - Leaves medium, 5-13 x 2.5-5 (7) cm, elliptic - oblong, oblong or oblong-oblanceolate, with 5-7 pairs of secondary veins; domatia absent; style hairy at base . . . . 3. T. arbuscula

4 - Inflorescences paniculate; fruits with 3 or 4 equal wings . . . . 4. T. acuminata

4 - Inflorescences simply spicate or capitate; fruits with 2-5 equal or unequal wings 5

5 - Fruits usually 2-winged, sometimes 3-winged 6

5 - Fruits 4 or 5 (equal or unequal) winged 23

6 - Inflorescences distinctly elongate 7

6 - Inflorescences capitate - subcapitate or slightly elongate. . 12

7 - Fruits orbicular, suborbicular or rhomboidal; body suborbicular - orbicular, wider than the wing width 8

7 - Fruits transversely oblong; body elliptical, trigonal, ridged or slightly to strongly keeled, always narrower than the wing width. 9

8 - Fruit rhomboid, usually slightly wider than long, 2 x 1-1.5 cm, densely pubescent when young; wings up to 14 mm wide; leaves acute - subacuminate at apex, with moderately spaced secondary veins and small areoles; flowers densely pubescent . . . . 5. _T_. _lucida_

8 - Fruit usually suborbicular, slightly longer than broad, 2.5-4.5 x 2-4.2 cm, glabrous; wings less than 1 cm wide; leaves acuminate at apex, with widely spaced secondary veins and large areoles; flowers to densely pubescent . . . . 6. _T_. _dichotoma_

9 - Leaves coriaceous or thickly coriaceous, with obtuse or rounded apex and usually revolute margin; venation typically brochidodromous, often with small and orthogonally arranged areoles; fruit small, up to 2 x 4 cm (endemic to West Indies) 10

9 - Leaves chartaceous or sometimes subcoriaceous, with acuminate apex and flat margin; venation usually eucamptodromous - brochidodromous, usually with large and imperfect areoles; fruit medium to very large, 1.5-3 x 2-8 cm 11

10 - Inflorescences very long, up to 20 cm; flowers relatively large, up to 10 cm long, velutinous; style glabrous;leaves densely pubescent or tomentose . . . . 7. _T_. _eriostachya_

10 - Inflorescences medium, usually 3-7 cm long; flowers medium, usually 5-7 mm long, glabrous or pubescent; style hairy; leaves usually glabrous but sometimes densely pubescent. 8. _T_. _chicharronia_

11 - Fruit medium, usually 1.2-2 x 2-4 cm; body flattned or slightly ridged, easy to cut through; wings up to 2.5 cm long . . . . 9. _T_. _oblonga_

11 - Fruit large or very large, up to 8 cm wide; body sitinctly keeled and very hard to cut through; wings up to 4.3 cm long . . . . 10. T. valverdeae

12 - Inflorescences subcapitate or slightly elongate, with numerous flowers, if capitate then the fruits with 3 wings 13

12 - Inflorescences capitate or sometimes subcapitate, with few flowers (3-12); fruits always with 2 wings 20

13 - Fruit very large, 4-11 cm wide, 2 winged; leaves medium to large 14

13 - Fruit small or very small, up to 1 x 3 cm, 2 or 3-winged; leaves small to medium 18

14 - Leaves large, 8-27 x 5-14 cm, acute - rounded at apex (rarely acuminate), cuneate at base; venation eucamptodromous with prominent percurrent tertiary veins; rachis slightly elongate; petioles 2-5 cm; fruit glabrous . . . . 11. T. phaeocarpa

14 - Leaves medium, usually 2-12 cm but occasionally up to 18 cm long, usually acuminate or aristate at apex, decurrent at base; venation brochidodromous or eucamptodromous - brochidodromous; rachis usually very short; petiole 0.5-3 cm long fruit glabrous to densely tomentose 15

15 - Leaves usually ovate, aristate or long acuminate at apex, often silvery sericeous beneath; fruit usually densely tomentose, occasionally slightly pubescent or rarely glabrous . . . . 12. T. argentea

15 - Leaves usually obovate or oblong-ovate or oblanceolate, acuminate at apex, glabrous or slightly pubescent; fruit glabrous or slightly pubescent 16

16 - Fruit relatively small, up to 1.7 x 4.5 cm, pubescent; body slightly keeled or angled, easy to cut through; leaves nearly glabrous, with small and well developed areoles . . . . 13. T. kuhlmanii

16 - Fruit large, up to 4 x 11 cm, glabrous; body elliptical or

fusiform, hard to cut through; leaves sparsely to densely pubescent, with large, imperfect or incompletely closed areoles 17

17 - Fruit 2.5-4 x 5-10.5 cm; body elliptical and usually bulged, sometimes slightly keeled, 0.8-1.3 cm wide; wings 2-4.2 x 2.5-5 cm . . . . 14. _T. januariensis_

17 - Fruit 1.6-2.3 x 3.8-7.5; body fusiform or lanceolate, 0.4-0.7 cm wide; wings 1.4-2.5 x 1.7-3.5 cm . . . . 15. _T. guyanensis_

18 - Fruit 3-winged; inflorescences capitate . . . 16. _T. eichleriana_

18 - Fruit 2 winged; inflorescences subcapitate 19

19 - Fruit 0.8-1.2 x 1.5 - 3 cm; upper receptacle campanulate, with distinct lobes; leaves with moderate straight prominently raised secondary veins; areolation conspicuous and well developed . . . . 17. _T. fagifolia_

19 - Fruit 0.4 x 0.6 x 1.3-1.5 cm, with very small wings; upper receptacel cupuliform, with very short teeth; leaves with fine and curved secondary veins; areolation imperfect and not conspicuous . . . . 18. _T. actinophylla_

20 - Fruit longer than broad, with very narrow and stiff wings up to 4 mm wide; inflorescences with 6-12 flowers; leaves up to 2.5 cm wide . . . . 19. _T. australis_

20 - Fruit broader than long, with distinctly transversely spread wings; inflorescences usually with up to 6 flowers; leaves up to 5 cm wide 21

21 - Leaves elliptic or oblanceolate, up to 2 cm wide, acute or obtuse at apex; fruit 1-2.6 cm wide, rhomboid or elliptical . . . . 20. _T. triflora_

21 - Leaves obovate or obovate-oblong or obovate-elliptic, up to 5 cm wide, usually acuminate at apex; fruit 2.5-4.5 cm wide 22

22 - Wings transversely oblong (broader than long), downwardly curved;

body slightly bulged and keeled or ridged . . . .
. . . . 21. *T. uleana*

22 - Wings rounded or subrounded (usually slightly longer than broad), not curved; body flattened . . . . . 22. *T. reitzii*

23 - Fruit 5-winged, 3 wings rudimentary and the others distinctly and transversely spread; leaves chartaceous or subcoriaceous, with eucamptodromous venation; inflorescence always elongated 24

23 - Fruit with 4 or 5 equal wings; leaves coriaceous or thickly coriaceous, with weakly brochidodromous venation; inflorescence subcapitate or elongated 25

24 - Leaves usually obovate, usually abruptly acuminate at apex, nearly glabrous at maturity, with 3 - 5 pairs of secondary veins; fruit yellowish-cream . . . . 23. *T. amazonia*

24 - Leaves oblong obovate or narrowly obovate or oblanceolate, obtuse or retuse or rarely shortly acuminate at apex, with 5-8 pairs of secondary veins, usually densely rufous tomentose; fruit yellowish-brown or brownish . . . . . . 24. *T. glabrescens*

25 - Inflorescences slightly to distinctly elongate with hermaphrodite flowers usually towards the base; fruits loosely arranged along the long rachis 26

25 - Inflorescences usually subcapitate or slightly elongate with hermaphrodite flowers towards the apex; fruits crowded into spherical capitula 29

26 - Rachis 4-12 cm; flowers pentamerous; fruit 5-winged; leaf base cuneate 27

26 - Rachis up to 4 cm long; flowers 4-5-merous; fruit, 4-5-winged; leaf base subcordate, rounded or broadly cuneate 28

27 - Leaves 4-19 x 4-12 cm, obovate or oblong-obovate;fruit slightly longer than wide . . . . 25. *T. quintalata*

27 - Leaves smaller, up to 10 x 4.5 cm, narrowly obovate or oblanceolate;

fruit often slightly broader than long . . . . . . 26. T. yapacana

28 - Leaf base subcordate to obtuse; lamina sparsely to densely pubescent when young, nearly glabrous at maturity; rachis up to 2 cm long . . . . 27. T. guaiquinimae

28 - Leaf base broadly cuneate, decurrent into the petiole; lamina densely silvery sericeous beneath at maturity; rachis up to 4 cm long . . . . 28. T. steyermarkii

29 - Lower surface of leaves densely silvery-sericeous; fruit conspicuously beaked at apex and pseudostipitate at base; wings triangular, with pointed margins . . . . . . 29. T. ramatuella

29 - Lower surface of the leaves glabrous or sparsely pubescent except densely pubescent on the lower part of the midribs; fruit apiculate or sometimes shortly beaked at apex, usually without pseudostipe at base; wings more or less rounded in outline 30

30 - Leaves usually glabrous over the whole of both surfaces; fruits often slightly beaked or acuminate at apex; wings usually entire at margins . . . . 30. T. virens

30 - Leaves usually densely pubescent at the base of the midrib on the lower surface; fruits apiculate or truncate at the apex; wings usually crisped or undulated at margins . . . . . . 31. T. crispialata

9.1.2. The species of Terminalia

1. Terminalia catappa L., Syst. Nat. ed. 12, 2:674 (1767); Mant. 1 : 128 (1767). Type : L 1221.1 (LINN, holotype).

   Terminalia subcordata Humb. & Bonpl. ex Willd. in L., Sp. Pl. ed. 4, 4: 968 (1806).

Terminalia paraensis C. Martius, Flora 24. 2 Beibl. : 24 (1841).

Type: Prov. Paraensis, 1820, Martius (holotype, M; isotype M).

Terminalia intermedia Bertol. ex Sprengel, Syst. Veget. 2: 359 (1825).

Myrobalanus catappa (L.) Kuntze, Rev. Gen.: 237 (1891).

Buceras catappa (L.) A. Hitchc. ex Northrop, Mem. Torr. Bot. Club, 12 : 55 (1902).

Tree 5-18 m high. Leaves alternate or spirally arranged, usually crowded at the ends of the shoots; petioles often short and stout, 0.5-2.5 cm long, pubescent, usually biglandular; lamina chartaceous or thinly chartaceous, (8) 12-30 (35) x (5) 9-15(22) cm, usually typically obovate, sometimes broadly obovate; apex rounded or shortly acuminate; base usually subcordate, but sometimes rounded or subtruncate, or rarely cuneate; upper surface glabrous and shiny, usually verruculose; lower surface usually nearly glabrous but sometimes appressed. Pubescent or tomentose, especially when young. Domatia always present, particularly on secondary veins. Venation brochidodromous - eucamptodromous; primary veins stout to moderate, prominently raised beneath; secondary veins 8-11 pairs, distant, moderate, originating at moderately to widely acute angles; intersecondary veins present; tertiary veins usually irregularly percurrent, often alternate and oblique; quaternary veins sometimes conspicuous; areolation randomly reticulate, imperfect of incomplete. Inflorescences axillary spikes, up to 30 cm long, andromonoecious, with a few hermaphrodite flowers near the base; peduncle 3-5.5 cm long, glabrous or slightly pubescent; rachis 10-27 cm long, pubescent. Bracts 0.5-1 mm long, acuminate, early caducous. Flowers medium or large, male c. 4-5 x 4-5 mm; hermaphrodite 7-10 x 4-5 mm; lower receptaclè 3-7 mm long, pubescent to densely pubescent near the base, sparsely pubescent towards the calyx; upper receptacle 2 mm long, sparsely pubescent; calyx-lobes triangular, 1_1.5 mm long, nearly glabrous, disk villous; stamen 4 mm long; anther 0.4-0.5 mm long; style 3-3.5 mm long, glabrous. Fruit drupe-like, ovoid or ellipsoid,

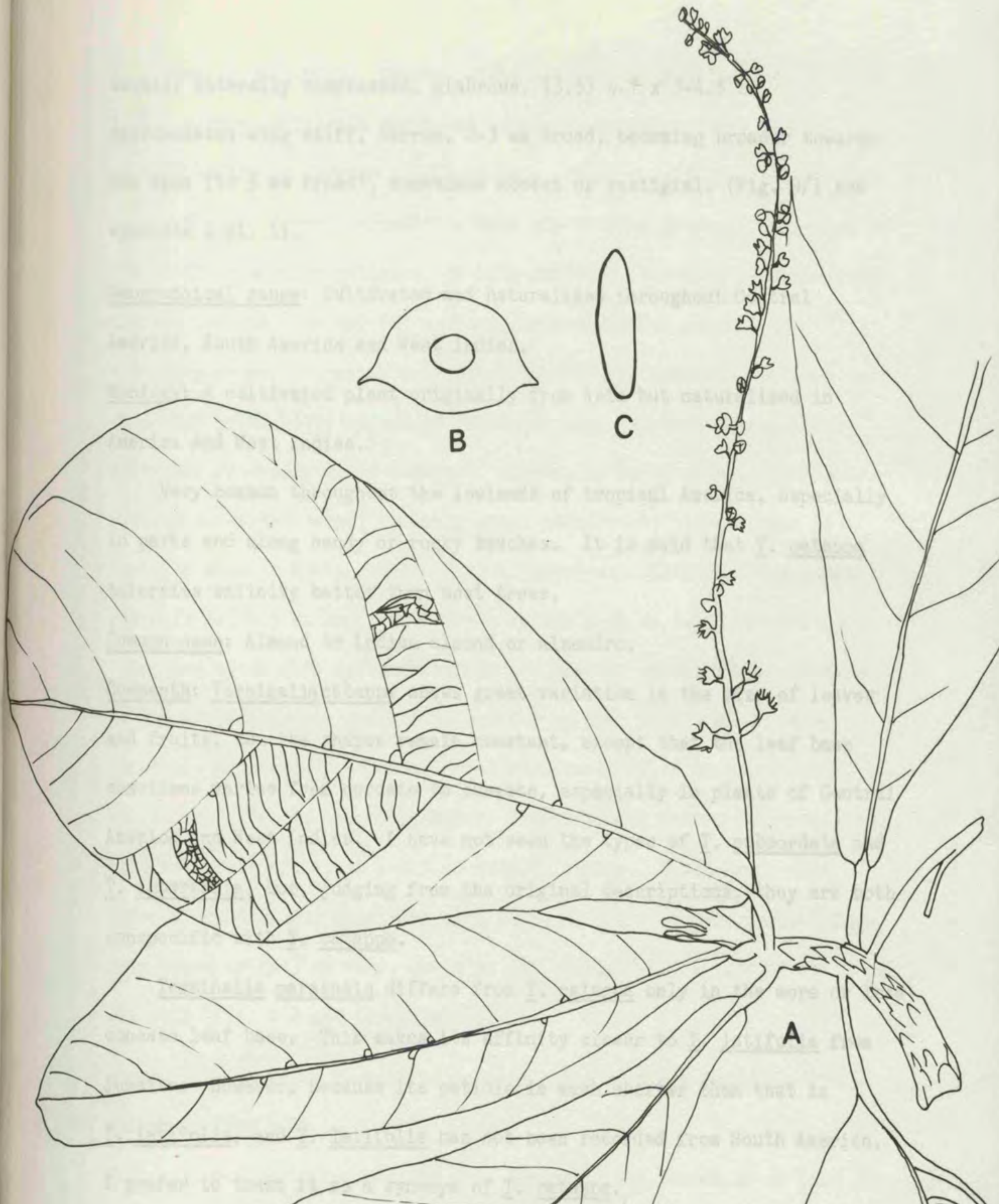


Fig. 9/1: Terminalia catappa. A. Branch with infl. and fr. B. section of fruit. C. Seed.

usually laterally compressed, glabrous, (3.5) 4-7 x 3-4.5 cm, circumalate; wing stiff, narrow, 2-3 mm broad, becoming broader towards the apex (to 5 mm broad), sometimes absent or vestigial. (Fig. 9/1 and appendix 4 pl. 1).

Geographical range: Cultivated and naturalized throughout Central America, South America and West Indies.

Ecology: A cultivated plant originally from Asia but naturalized in America and West Indies.

Very common throughout the lowlands of tropical America, especially in parks and along sandy or rocky beaches. It is said that *T. catappa* tolerates salinity better than most trees.

Common name: Almand or Indian almond or almendro.

Comments: *Terminalia catappa* shows great variation in the size of leaves and fruits, but the shapes remain constant, except that the leaf base sometimes varies from cordate to cuneate, especially in plants of Central America and West Indies. I have not seen the types of *T. subcordata* and *T. intermedia*, but, judging from the original descriptions, they are both conspecific with *T. catappa*.

Terminalia paraensis differs from *T. catappa* only in the more or less cuneate leaf base. This makes its affinity closer to *T. latifolia* from Jamaica. However, because its petiole is much shorter than that in *T. latifolia*, and *T. latifolia* has not been recorded from South America, I prefer to treat it as a synonym of *T. catappa*.

The specimen in the Linnean collection in London bears no indication of collector's name or the place of origin of the specimen. However, since this is the only species of *Terminalia* represented in the Linnean Herbarium, it is accepted as the type for the genus by Exell (1934).

2. *Terminalia latifolia* Sw., Prod. Veg. Ind. Occ. : 68 (1788). Type: Jamaica, Swartz (Lectotype S; Isolectotype S, BM).

Myrobalanus latifolia (Sw.) Kuntze, Rev. Gen: 237 (1891).

Tree to 30 m high. Leaves spirally arranged; petiole long, 1.8-4 cm long, appressed pubescent or glabrous, eglandular; lamina obovate or oblong-obovate or oblanceolate, 10-24 x 6-14 cm; apex rounded or shortly and broadly acuminate; base attentuate, gradually tapering to the petiole; usually pubescent on both surfaces, becoming glabrous later. Domatia present over all the surface particularly on primary and secondary veins. Venation eucamptodromous-brochidodromous, primary vein stout and prominently raised on lower surface, slightly pubescent or glabrous; secondary veins moderate, curved, up to 12 pairs, upper pairs usually brochidodromous; tertiary veins percurrent; higher order of venation usually distinct; areolation imperfect. Inflorescence long; peduncle 2.5-3.5 cm long, pubescent; rachis 6-10 cm long pubescent or tomentose often with a few hermaphrodite flowers at the base. Flowers (4)5-7 mm long; lower receptacle 2.5-4.5 mm long (1-1.5 mm in male flowers), appressed pubescent; upper receptacle 1-1.5 mm long, puberulous; calyx lobe 0.5-1 mm long triangular; disk villous; stamen 2-2.5 mm long; anthers 3 mm long; style 1-2.5 mm long, glabrous. Fruit drupe-like often without wings, sometimes with acute margins or very narrow wing-like edges up to 3 mm wide, ovoid or ellipsoid, 3-4.5 x 1.5-2.5 cm, glabrous (Fig. 9/2 and Appendix 4 pl. 1).

Geographical range: Endemic to Jamaica. One specimen found in Guatemala (Map 9/1).

Ecology: Medium to large-sized tree common in wet forest or at edge of forest, growing on limestone soil at 60-750 m altitude. Flowers February-May.

Common name: broadleaf.

Comments: Swartz's Prodromus (1788) says his plant is in Sloane's Natural History (Vol. 2) p. 130. This is correct, but there is no specimen in Sloane's Herbarium at BM. In Swartz's Obs. bot. (1791) (but not his Prodromus) he actually gives Sloane's name for the plant. The specimens

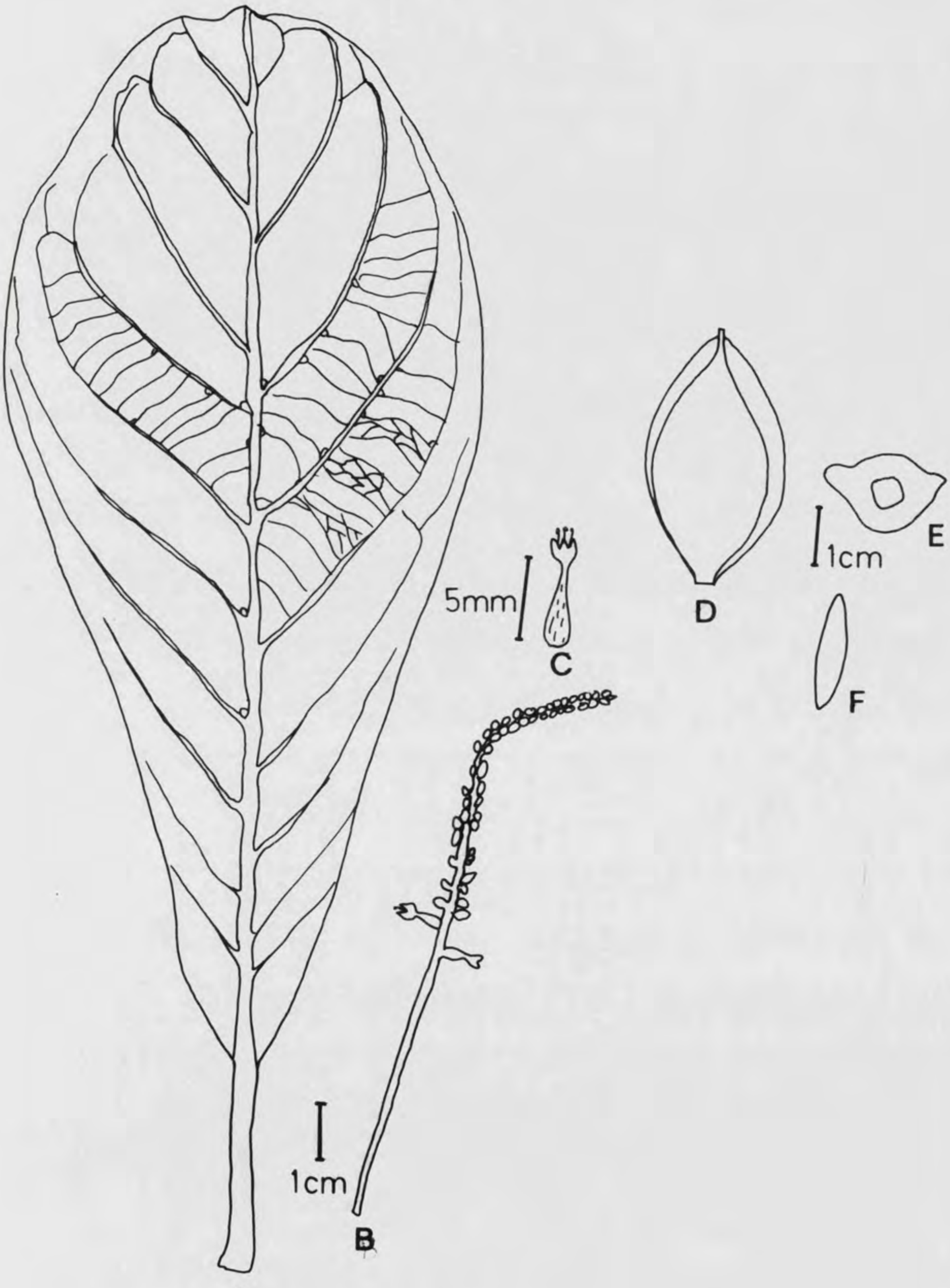


Fig. 9/2: Terminalia latifolia. A. leaf. B. inflorescence. C. flower. D. fruit. E. section of fruit. F. seed.

at BM & S collected by Swartz in Jamaica 1784-1786 can be considered the types.

Terminalia latifolia is very similar to T. catappa. The only difference between the two species is the shape of the leaf base, which is always cuneate and gradually tapering to the petiole in T. latifolia, whereas it is subcordate or subtruncate in T. catappa. The petiole is usually longer (2-4 cm) in T. latifolia than in T. catappa (0.5-2.5).

Terminalia catappa in the West Indies (Cuba) and Central America sometimes shows variation in the shape of the leaf base, varying from cordate to rounded to cuneate in the same plant. But usually there are some leaves with subcordate base and some with cuneate base; rarely are all leaves cuneate. One specimen from Guatemala (Tomas 317 at W) identified by Eichler as T. catappa? considered here as T. latifolia, has clearly all leaves with a cuneate base.

Although T. catappa is common in Jamaica, it is introduced there, and the native range of T. latifolia is extremely disjunct from that of its close relative T. catappa (S. E. Asia).

3. Terminalia arbuscula Sw., Prod. Veg. Ind. Occ.: 68 (1788). Type: Jamaica: Swartz (holotype, S; isotype BM, S)

Chuncoa arbuscula Griseb., Fl. Brit. W. Ind.: 275 (1860). Based on Terminalia arbuscula Sw.

Tree 7-30 m high. Leaves spirally arranged, usually crowded at the end of branches; petioles 1-4 cm long, moderate, usually glabrous, eglandular; lamina chartaceous or subcoriaceous when old, 5-13 x 2.5-5(7) cm elliptic-oblong or elleptic or oblong-oblanceolate; rounded-retuse or obtuse of shortly acuminate at apex; base broadly acute; upper surface puberulous when young, glabrescent or glabrous when mature, veruculose and usually shiny; lower surface pubescent or glabrous. Domatia lacking. Venation weakly brochidodromous; primary vein, moderate, straight prominently raised below; secondary veins 5-7 pairs, fine-moderate, angle of divergence widely acute (65°-80°), upper ones more obtuse than the lowers, often joined together in a series of conspicuous arches; intersecondary veins sometimes present, composite; tertiary veins random reticulate or sometimes weakly percurrent and irregularly and obliquely arranged; higher order venation distinct, reticulation very small, usually orthogonally orientated; freely ending veinlets sometimes present. Spike andromonoecious (some specimens annotated male and others female but these specimens either sterile or with only few hermaphrodite flowers), up to 8.5 cm long; peduncle 2-4 cm long, usually glabrous, pubescent when young; rachis up to 4.5 cm long, pubescent, becoming glabrous then. Lower receptacle 3-3.5 mm, puberulous; upper receptacle slightly pubescent or glabrous, 2-2.5 mm long inclusive of lobes, 3-4 mm across, infundibuliform, calyx lobe 1-1.5 mm long, ± glabrous, deltoid. Stamen 10; filament 3-3.5 mm long, anthers 0.3-0.4 mm diam. Disk densely villous. Style 1-2 mm long, hairy at base Fruit unknown. (Fig. 9/3 and Appendix 4 Pl. 1).

Geographical range: Endemic to Jamaica (Map 9/1).

Ecology: A shrub (Fawcett 1926 & Adams 1972) or medium-sized tree, (2)7-20 m high, D.B.H. 50-80 cm.Occurs at high altitude (900-2200ft) on wooded rocky limestone hillsides. Flowers May-July.

Common name: white olive or olive.

Comments: The Swartz specimen in BM agrees with that in S but has no flowers. There are two different branches mounted on the same sheet (which bears only the label "Jamaica Dr Swartz"); the upper one (A) is the Swartz specimen (therefore the isotype) but the other branch is not Terminalia.

Terminalia arbuscula is a distinct species, but without fruit it is difficult to put it in the right section. The flowers and the leaf textures are similar to T. latifolia. Some very mature ovaries show no

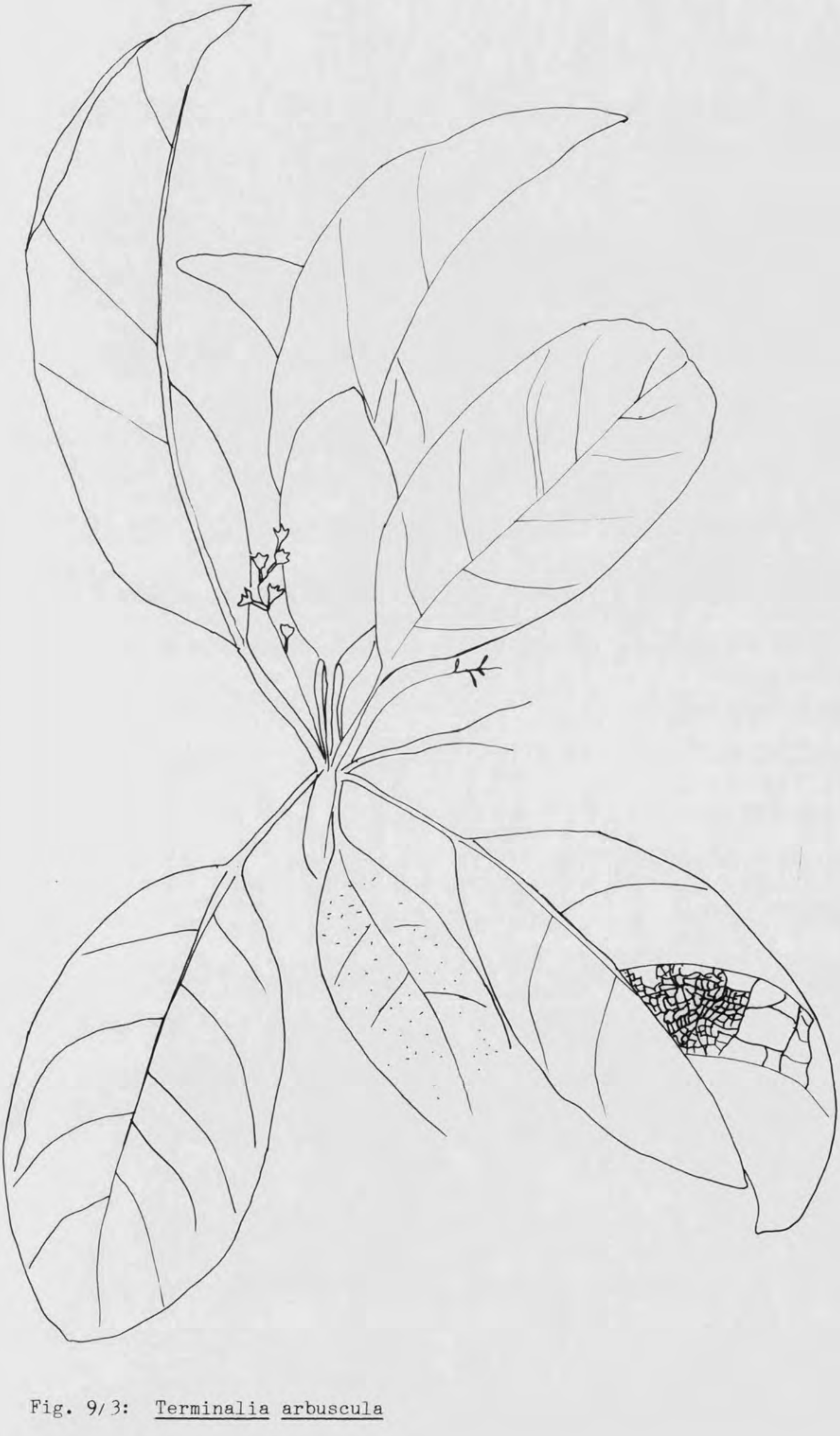


Fig. 9/3: Terminalia arbuscula

traces of wings. Therefore it may belong to section Terminalia.

4. Terminalia acuminata (Allemão) Eichler in Martius, Fl. Bras. 14, 2 : 92 (1867), based on Vicentia acuminata Allemao, Pl. Novas Brasil (1844) - cf. Bot. Zeit., 12 : 435 (1854).

Myrobalanus acuminata (Allemão) Kuntze, Rev. Gen: 237 (1891).

Type: Unknown (Figure 9/4).

Tree. Leaves alternate; petioles 1.5-4.5 cm long, moderate, pubescent, with 2 conspicuous glands near the top; lamina chartaceous or subcoriaceous, 5-12 x 2-5 cm, oblong or elliptic-oblong or elliptic ovate or ovate or sometimes slightly obovate; apex acuminate to long acuminate, acumin 10-20 mm long; base broadly cuneate or subacute; upper surface nearly glabrous; veruculose; lower surface almost pubescent, densely rufous-pubescent or sericeous on the midvein and secondary veins. Domatia present, visible with lens, usually hairy. Venation eucamptodromous; midvein moderate and straight; secondaries subopposite or alternate, in 7-10 pairs, diverging from the midvein at an angle of 45° to 60°, moderate, gradully curving apically toward the margin, often forking about midway; intersecondary veins very rarely present; tertiary veins percurrent, straight or sinuous, oblique and regularly orientated. Higher order venation forming a reticulum in which vein orders often cannot be distinguished; areolation imperfect; freely ending veinlets absent. Inflorescences of axillary panicles (4)5-9(10.5) cm long; peduncle 1.5-2.5 cm long, pubescent; rachis 3.5-5 cm long, densely pubescent. Bract very small 0.8-1 mm long, nearly filiform. Flowers small, all hermaphrodite, reddish-brown, sessile and numerous; lower receptacle (ovary) densley appressed pubescent, 0;1.5 mm long; upper receptacle sparsely pubescent, 1-1.5 mm long, cupuliform; calyx lobe very small 0.3-0.5 mm long, deltoid. Stamens 8; filaments 1.5-2 mm long; anthers 0.3-0.5 mm diam. Disk poorly developed, villous. Style

Fig. 9/4: Terminalia acuminata

glabrous, 1.5-1.8 mm long. Fruit broadly oblong or subrounded with usually three equal to subequal wings, 1-2 x 1.3-2 cm as a whole; body of fruit elliptic, 1.1.8 x 0.0-0.3 cm, glabrous; wing 1-2 x 0.5-1.1 cm, glabrous. (Fig. 9/4).

Geographical range: South-eastern Brazil (Rio de Janeiro) (Map 9/6).

Ecology: A medium sized tree growing at 500 m altitude. Flowers November-December.

Common name: Guarajuba

Comments: Allemáo herbarium should be in R or RFA but there is no specimen in R and I have not asked at RFA. Eichler (1867) cited a specimen from Rio Janeiro near Campo Grande collected by Allemáo and Sello but he did not mention the herbarium in which the specimen is deposited. I have not seen such a specimen in any of the herbaria mentioned in this work, but it is possible that the specimen was in B and destroyed, or is one of the next two.

In BR there are two specimens collected by Allemáo. One of them bears the following annotation of Allemáo, "Vicentia acuminata Freire Allemáo. Gharajuba Bras. an vere a Terminalia rift? Rio Jan. Legitet Freire Allemáo 1846"; the other specimen bears "Guarajuba" but no date and locality. The former specimen cannot be chosen as lectotype as it is dated after the original description.

Terminalia acuminata is a very distinct species and it is the only species in the section Vicentia. The species has similarity with some species of sections Myriocarpae and Pentaptera from Asia but in America its relationship is not clear, although its flowers have some similarities with those of T. actinophylla.

5. Terminalia lucida Hoffsegg ex C. Martius, Nov. Gen. et. Sp. 1 : 43 (1824).

Type: Pará, Siber, Hoffmannsegg (lectotype, BR; Isolectotype BM).

Terminalia firma C. Martius, loc. cit. Type: in editis ad Serra de Araracoára, in veg. fl. Japurá, Provinciae fl. Nigri, Brazil, Jan. (fl.), Martius (M, holotype & isotype).

Myrobalanus lucida (C. Martius) Kuntze, Rev. Gen. 237 (1891).

Terminalia hayesii Pittier, Contrib. U.S. Nat. Herb. 18: 239 (1917). Type: Panama, 1859-1860, S. Hayes (holotype, US no 202835).

Terminalia nyssaefolia Britton, Bull. Torr. Bot.Cl. 48: 333 (1922). Type: Coastal woods, Manzanilla, Trinidad, March 9, 1921 (fr), Britton 2177 (holotype, NY; isotypes, US, K (part)).

Terminalia eriantha Benth. in Hooker, Kew Jour. 2 : 240 (1850). Type: Caripi, (on the Rio Para according to original description) Brazil, Ang. 184 (fl), Spruce 166 (K. holotype).

Terminalia scutifera Planchon ex Lawson, Fl. Trop. Afr. 2: 417 (1971). Type: French Guinea, Heudelot 907 (K, isotype).

Myrobalanus scutifera (Planchon ex Lawson) Kuntze Rev. Gen. : 237 (1891).

Tree 6-20 m high. Leaves spirally arranged, crowded at the ends of the branchlets; petiole 0.7-2 cm long, moderate, pubescent or glabrous, eglandular; lamina coriaceous, 4.5-14 x 2-7.5 cm, oblong obovate, or obovate, or obovate elliptic to narrowly obovate; apex subacute to shortly acuminate or acute-obtuse; base attenuate or cuneate; upper surface glabrous, occasionally pubescent on veins; lower surface glabrous except sometimes on veins. Venation brochidodromous or eucamptodromous-brochidodromous; secondary veins 5-9 pairs, close, originating at moderately acute angle, slightly raised beneath; tertiaries often randomly reticulate; higher-order veins distinct, quaternary and quinternary veins usually conspicuous; areoles small, usually perfect. Inflorescence long; peduncle 1.5-2 cm long, pubescent; rachis 6-10 cm long, densely pubescent. Bracts small c. 1 mm long, sericeous. Flowers small, yellowish or greenish-white; lower receptacle 1.2-1.7 cm long, ovate, densely tomentose; upper receptacle 1.5 cm long, cupuliform, densely tomentose; calyx-lobes up to 1 mm long, pubescent outside, densely villous inside; disk villous; stamens 4-4.5 mm long, exserted; anther 0.4 mm long; style 4 mm long, villous. Fruit rhomboid or transversely elliptic, flattened, almost always broader than long, 1.7-2.6 x 2.5-3.8 cm, usually shortly stipitate, densely pubescent when young, pubescent to glabrescent when mature; body dorsally slightly raised, ventrally grooved, 2 x 1-1.5 cm; wings (6) 10-14 mm wide, thin, rounded to acute at margin, convex at base and apex. (Fig. 9/5 and Appendix 4 Pls. 1 & 2).

Geographical range: Brazil, French Guiana, Surinam, Guyana, Venezuela, Trinidad, Colombia, Panama, Nicaragua (Fide Frank Conkling Seymour 1980), Honduras, Guatemala. Also W. Africa: French and Portuguese Guinea and Sierre Leone. (Map 9/2).

Ecology: Small tree, sometimes with several trunks, 5-45 cm diam, growing on sandy soil along rivers or in flooded areas in forest or at edge of forest. Flowers February-May and August-January.

Common name: Fucadi (in Guyana).

Comments: Terminalia lucida was based on a Hoffmannseg specimen from Pará, Brazil. The type specimens of T. lucida (flowers and young leaves only) are similar to specimens of T. dichotoma except that the leaves of T. lucida are slightly smaller and less acuminate than those in T. dichotoma. However the most important organ by which T. lucida can be separated from T. dichotoma is the fruit, which was not known at the time of the original description.

Terminalia hayesii has been placed as a synonym to T. amazonia by Exell (1948), although Exell (1934) labelled the type specimen as T. lucda. However, the style of T. hayesii is densely villous whereas it is always glabrous in T. amazonia. Therefore it is more justified to treat it as a synonym of T. lucida. Terminalia nyssaefolia differs from T. lucida only in the slightly more obovate and acuminate leaves. However T. nyssaefolia comes within the range of variation of T. lucida.

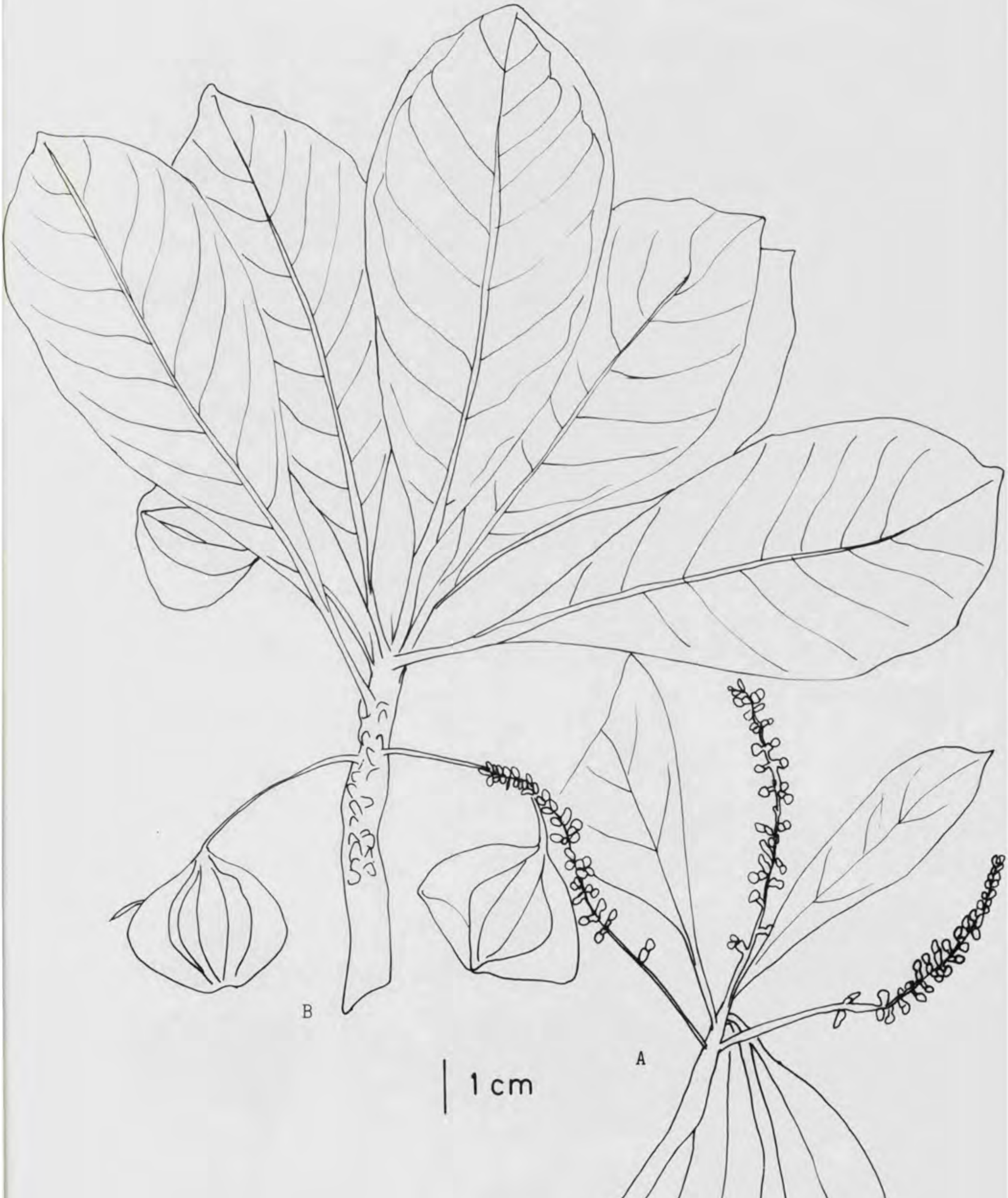


Fig. 9/5: Terminalia lucida

A. flowering branch

Terminalia scutifera was known as a West African species by previous workers (Engler & Diels 1900, Keay 1954, Griffiths 1959). But Griffiths 1959 stated that *T. scutifera* is extremely closely related to *T. nysaefolia* (treated in this work as a synonym of *T. lucida*), which occurs in Central America, northern South America and West Indies. The reason why she did not amalgamate them was because there was not enough material available at that time (Griffiths personal communication 1983). During this course of study I have examined a large number of specimens of *T. lucida* and *T. nyssaefolia*, and all the specimens of *T. scutifera* available at BM and K, and found them to be the same species.

Terminalia lucida shows consideration variation in the shape of the leaves, varying from obovate to oblong-obovate to elliptic to narrowly obovate. But the venation pattern always remains constant. The amount of indumentum of the fruits varies with age.

Terminalia lucida is very close to *T. dichotoma* but differs in the following characters: often more coriaceous and smaller leaves, with more conspicuous and closer reticulation; eglandular and shorter petiole to 2 cm long (in *T. di chotoma* to 4 cm long, often biglandular); tomentose inflorescence with more densely arranged flowers; shorter and densely tomentose ovary; shorter fruits, with wider and thinner wing. However, sometimes it is difficult to tell one species from another, particularly when no fruits are available.

6. *Terminalia dichotoma* G. Meyer, Prim. Fl. Esseq.: 177 (1818).

Type: In Silvis insulae Arowabish Essequebo, Meyer no. 113 (GOET, holotype).

Tanibouca guianensis Aublet, Hist., Pl. Guiane 1: 445, t. 178 (1775), not *Terminalia guyanensis* of Eichler in Martius, Fl. Bras. 14, 2 : 88 (1867). Type: Cayenne, 1775, Dr. Fusée Aublet (BM, lectotype).

├ Terminalia tanibouca Rich., Act. Soc. Hist. Nat. Par. 1: 109 (1792)
├ nom. illegt.

├ Terminalia tanibouca (Aublet) Smith, Rees. Cyclop. : 35 n. 11
├ (1817) nom. illegt.

├ Catappa guianensis Gaertner f., Fruct. sem. pl. 3: 207, t. 217,
├ (1807). Type: Cayenne, Desfontaines (not seen).

├ Myrobalanus guianensis (Aublet) Kuntze, Rev. Gen. 273 (1891).

Tree 10-60 m high. Leaves usually alternate, often crowded into pseudo-verticels; petiole medium or long, 1.5-4.5 cm long, moderate, often biglandular occasionally eglandular, glabrous or nearly so, pubescent when young; lamina subcoriaceous or coriaceous when very old, 9-22 x 4-10 cm, obovate or obovate oblong or oblanceolate; apex acuminate; base narrowly cuneate; upper surface glabrous, pubescent when young; lower surface densely pubescent when young, sparsely pubescent or glabrous when old. Venation eucamptodromous but sometimes eucamptodromous-brochidodromous; secondaries 5-8 (10) pairs, distant become closer near the margin, originating at acute to widely acute angle (45° to 80°); tertiaries percurrent; higher-order venation usually distinct; areoles usually large, imperfect or perfect. Inflorescence long; peduncle 2-3 cm long, usually glabrous; rachis 8-11 cm long, sericeous or glabrous. Bracts small, 0.5-1 mm long glabrous or slightly pubescent. Flowers medium-sized up to 6 mm long, not dense on the rachis; lower receptacle 2-3 mm long appressed rufous tomentose to nearly glabrous, gradually becomes narrower towards the apex; upper receptacle 2-2.5 x 4 mm, sparsely pubescent or glabrous; calyx-lobes 1-1.5 mm long, deltoid; disk villous; stamen 5-6 mm long, anther 0.5 mm long; style 5 mm long, densely hairy. Fruit suborbicular, often slightly longer than broad, occasionally triangular, rounded, retuse or apiculate at apx 2.5-4.5 x 2-4.2 cm, glabrous and shiny, with two narrow and stiff wings 4-6 (8) mm wide; body large 2-4.5 x 1.2-2.5 cm, round to elliptic, always wider than wing's width, exstipetate. (Fig. 9/6 and Appendix 4 Pl. 2).

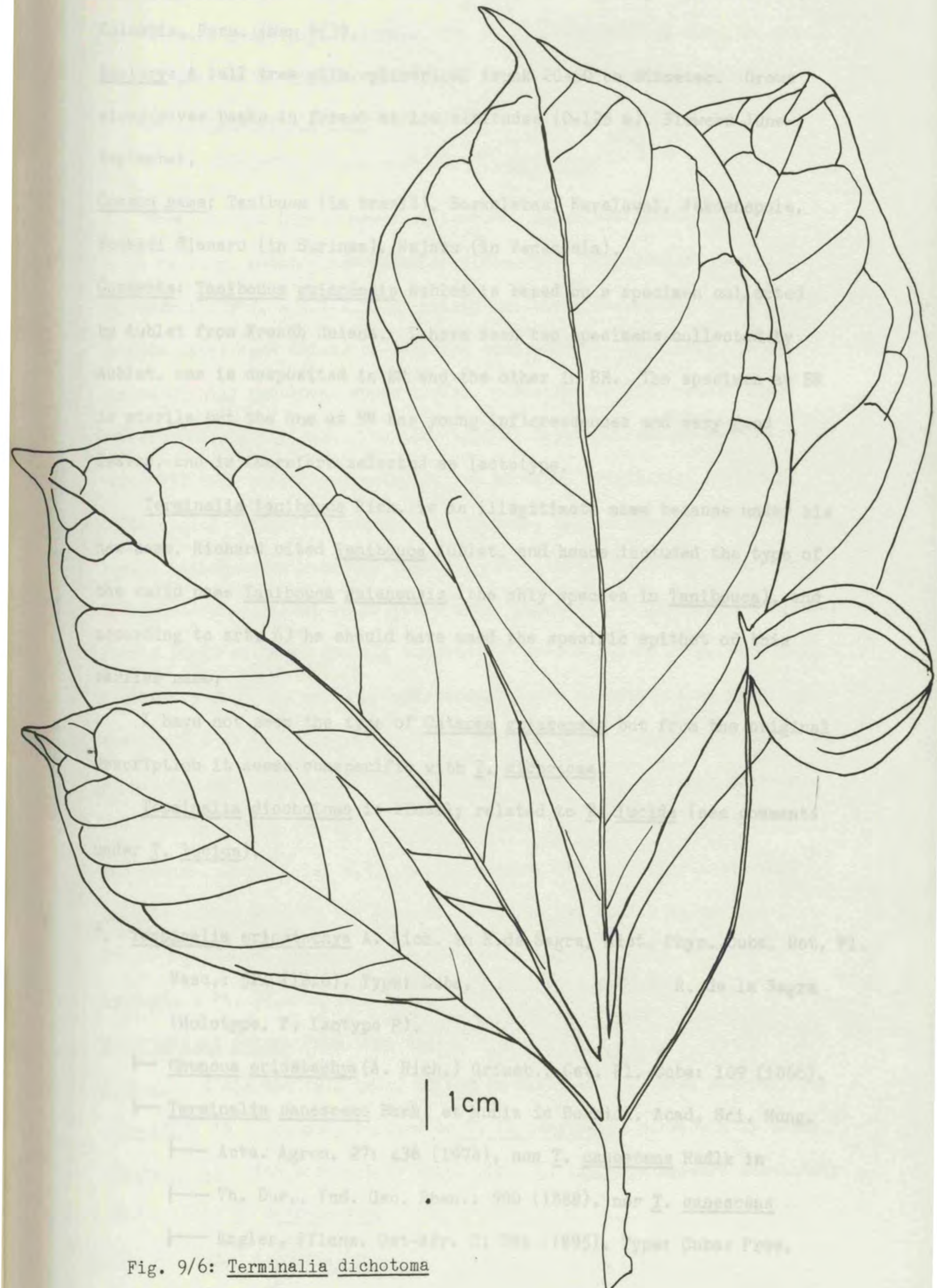


Fig. 9/6: Terminalia dichotoma

Geographical range: Brazil, French Guiana, Surinam, Guyana, Venezuela, Colombia, Peru. (Map 9/3).

Ecology: A tall tree with cylindrical trunk 20-50 cm diameter. Grows along river banks in forest at low altitudes (0-125 m). Flowers June-September.

Common name: Tanibuca (in Brazil), Boskalebas, Karalawai, Jakoenepole, Foekadi djamaro (in Surinam), Najaru (in Venezuela).

Comments: Tanibouca guianensis Aublet is based on a specimen collected by Aublet from French Guiana. I have seen two specimens collected by Aublet, one is desposited in BM and the other in BR. The specimen at BR is sterile but the one at BM has young inflorescences and very good leaves, and is therefore selected as lectotype.

Terminalia tanibouca Rich. is an illegitimate name because under his new name, Richard cited Tanibouca Aublet, and hence included the type of the valid name Tanibouca guianensis (the only species in Tanibouca), and according to art. 63 he should have used the specific epithet of this earlier name,

I have not seen the type of Catappa guianensis but from the original description it seems conspecific with T. dichotoma.

Terminalia diochotoma is closely related to T. lucida (see comments under T. lucida).

7. Terminalia eriostachya A. Rich. in R.de Sagra, Hist. Phys. Cuba, Bot. Pl. Vasc.: 524 (1846). Type: Cuba, R. de la Sagra (Holotype, P; Isotype P).

⊢ Chuncoa eriostachya (A. Rich.) Griseb., Cat. Pl. Cuba: 109 (1866).

⊢ Terminalia canescens Borh. et Muñiz in Borhidi, Acad. Sci. Hung. Acta. Agron. 27: 436 (1978), non T. canescens Radlk in Th. Dur., Ind. Gen. Phan.: 500 (1888), nor T. canescens Engler, Pflanz. Ost-Afr. C; 294 (1895). Type: Cuba; Prov.

Oriente; litus meridionalis Baracoae, vallis rivi Rio Tacre, prope pug. Cajobaba, 17. Mart. 1970, Borhidi 4374, O. Muniz et S. Vazquez (Holotype, SV, not seen; Isotype BP).

Terminalia bipleura Borh. et Muniz, Acta. Bot. Hung. 26: 262 (1980). A new name for T. canescens.

Tree to 20 m high. Leaves alternate, sometimes crowded; petiole 0.5-2 cm long, densely pubescent or glabescent, biglandular; lamina coriaceous 5.5-14 x 2.5-7.5 cm, oblong or oblong obovate or elliptic or oblanceolate; apex obtuse or rounded; base narrowly to widely acute; margin usually revolute; upper surface pubescent or glabresent; lower surface densely villous. Venation typical brochidodromous; secondary veins (7) 8-14 pairs, moderate, raised beneath, originating at widely acute angle; tertiaries randomly reticulate, raised beneath, conspicuous above; higher-order venation randomly reticulate; areolation imperfect. Inflorescence axillary spike, very long; peduncle 2-5 cm long, pubescent; rachis 10-15 cm long, densely tomentose. Bracts 1.5 mm long, very acute. Flowers large, 8-10 mm long, velutinous; lower receptacle 4 mm long; upper receptacle 3 mm long; calyx-lobes 2-3 mm long; disk densely villous; stamen 5-6 mm long; anther 0.5 mm diam.; style 4-4.5 mm long, glabrous. Fruit transversely oblong, 2-winged, medium, 1-1.5 x 2.5-4 cm; body small and narrow, thin, 1-1.5 x 0.4 cm, pubescent, shortly stipitate; wings usually curved towards the base, 0.7-1 x 1-2 cm, convex at apex, concave at base, subcoriaceous and finely nerved. (Fig. 9/7 and Appendix 4 Pl. 3).

Geographical range: Cuba (Map 9/1).

Ecology: A big and tall tree, to 120 cm diameter. Flowers February-May.

Comments: It is closely related to T. chicharronia, particularly subsp. chicharronia, with which it is sympatric. T. bipleura appears absolutely identical to T. eriostachya.

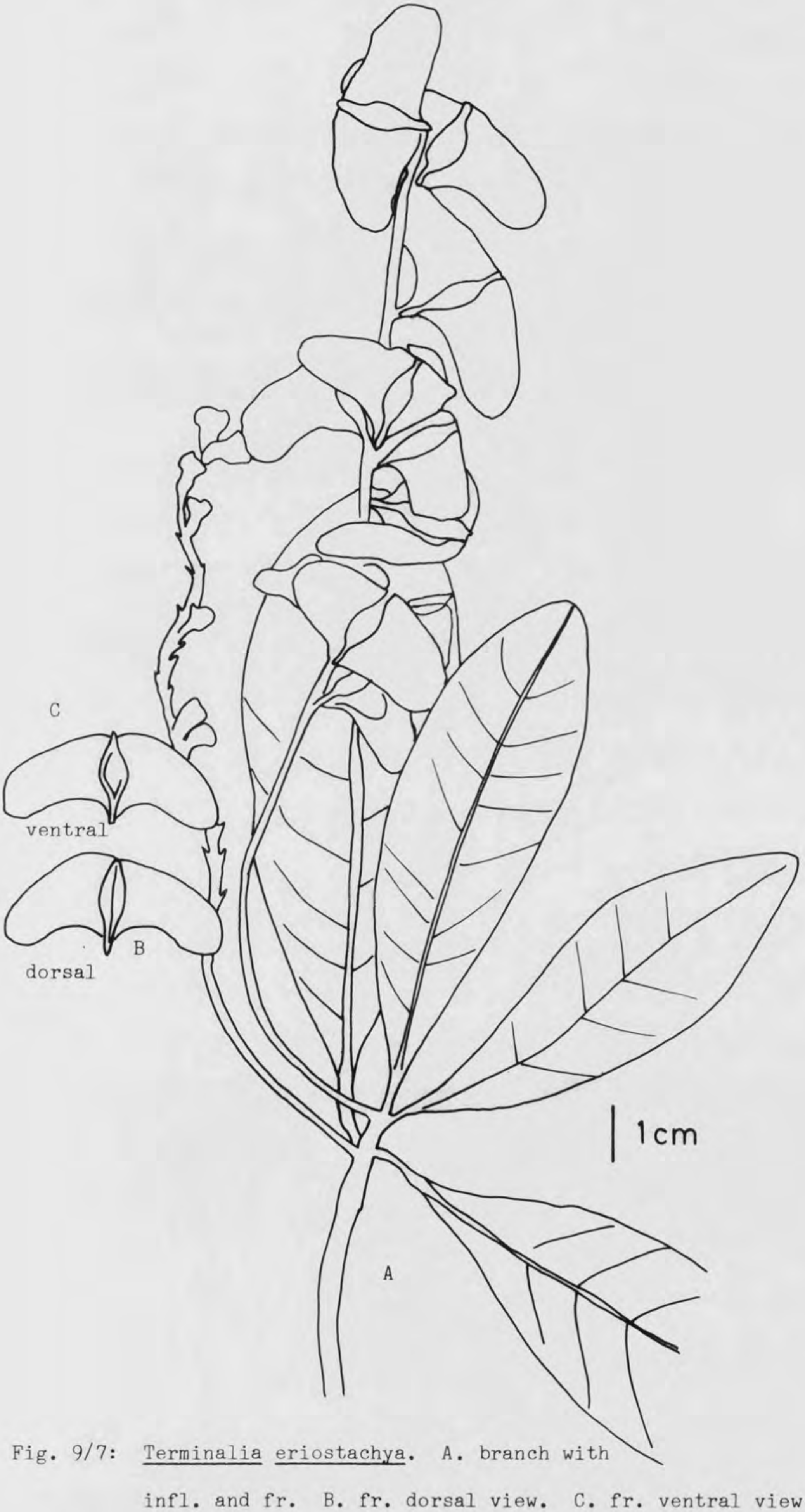


Fig. 9/7: Terminalia eriostachya. A. branch with infl. and fr. B. fr. dorsal view. C. fr. ventral view

8. *Terminalia chicharronia* Wright ex Sauvalle, Anal. Acad. Ci. Habana 5: 409 (1868) based on *Chicharronia intermedia* A. Rich. in R. de la Sagra, Hist. Phys. Cuba, Bot. Pl. Vasc: 529 t. 43 (1846). Type: Cuba, Guanab, 1829, Herbarium Richard no. 185 (lectotype, P; isolectotypes, F, G).

Chuncoa chicharronia (A. Rich.) Griseb., Cat. Pl. Cuba: 109 (1866) nom.: illegit.

Terminalia domingensis Urban, Sumb. Ant. 7: 524 (1913). Type: Rep. of Dominica, Azua in Arroyo Guayabal ad los Lagunos, 800 m. alt., 1912, Fuertes n. 1941 (holotype, B destroyed; isotypes, G, NY, P, S, U, W).

Terminalia intermedia (A. Rich.) Urban in Feddes Repert. 22: 367 (1926) nom. illegit., not *T. intermedia* Bert. ex Sprengel 1825 nor *T. intermedia* Span. 1836.

Terminalia orientensis Monach., Caribbean Forester 8: 79 (1947). Type: dry ridges east of Arroyo Blanco Valley, Oriente, Cuba. April 7, 1926, Grosby & Matthews 64 (holotype, NY).

Terminalia nipensis Alain, Contrib. Ocas. Mus. Hist. Nat. Col. de la Salle, Habana 12: 8 (1953). Type: Oriente, la Casimba, Sierra de Nipe, Mayori, July 1940, Leon & Alain 19237 (holotype, LS, not seen; isotype NY).

Terminalia maestrensis Bisse, Feddes Repert. 85: 606 (1974). Type: Cuba, Oriente, Sierra Maestra, Ocujal. en la Subida al Pico Turquino cerca de la Majagua, 1964, Bisse[1] et H. Lipppld[2] 14343 (holotype, HAJB not seen; isotype, JE).

Terminalia neglecta Bisse, Feddes Repert. 85: 607 (1974). Type: Cuba, Pinar del Rio, Bahia Honda, Loma Pelada de Cajalbana, 15 Sept. 1970, Bisse & H. Lippold 18254 (holotype, HAJB, not seen; isotype JE).

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1. Herbario, Jardin Botanico National, Universidad de la Habana, Habana, Cuba.
2. Herbarium Haussknecht, Sektion Biologie der Friedrich-Schiller-Universität DDR.

Terminalia aroldoi Bisse, op. cit.: 608 (1974). Type: Oriente, Baracoa, Mina Iberia, en las orillas del rio al pie de la loma, 1968, J. Bisse & E Köhler 6354 (holotype, HAJB, not seen; isotype, JE).

Terminalia pachystyla Borh., Acta Bot. Acad. Sci. Hung. 21: 224 (1976). Type: Prov. Oriente, Mayari, Sierra del Cristal, Los Mulos, 2-7 Apr. 1956, Alain 5368, Acuna & Figueras (holotype, SV*, not seen; isotype , A + GH).

Shrubs or small to medium-sized trees, 2-25 m high. Leaves alternate or spirally arranged, usually crowded at the ends of the branchlets; petiole 0.3-2(3) cm, densely pubescent to glabrous, eglandular or sometimes biglandular; lamina subcoriaceous to thickly coriaceous; 2-13 x 1.3-6.5 cm, obovate or obovate oblong or oblong or narrowly obovate; apex obtuse or rounded or retuse; base broadly acute or sometimes narrowly cuneate; margin often revolute; upper surface usually nearly glabrous; lower surface rufous tomentose of variously pubescent or glabrous. Venation typically brochidodromous; secondary veins 5-9(13) pairs, moderate, originating at widely acute angle but rather obtuse near the apex, usually prominently raised below, sometimes not raised; tertiary veins randomly or orthogonally reticulate or weakly percurrent, raised or not or sometimes not distinct from the higher-order venation; higher-order venation orthogonally reticulate or sometimes randomly reticulate, with usually perfect areolation. Inflorescence axillary, medium to long; peduncle 1.5-2.5(3.5) cm long, pubescent or glabrous; rachis 3.5-6 cm, densely to sparsely pubescent, rarely glabrous. Bracts 1.5-2(3) mm long, pubescent. Flowers medium. yellowish brown or yellow; lower receptace 2-5 mm long, tomentose to glabrous; calyx-lobes deltoid, 1-1.5 mm long pubescent or glabrous; disk piolose; stamen 3.5-5(7) mm long; anther 0.5 mm long; style 3-3.5 densely pilose to nearly glabrous, exserted. Fruit transversely oblong to rhomboid, or triangular, always broader than long, 1-2 x 1.4-4 cm;

body small and narrow, 0.4-0.8 cm wide, usually flattened but sometimes slightly keeled, usually shortly stipitate, pubescent; wings 0.8-2.2 x 0.7-1.8 cm, glabrous. (Fig. 9/8 and Appendix 4 Pl. 4).

Geographical range: Cuba, Haiti and Dominican Rep. (Map 9/1).

Ecology: A common tree usually growing at medium altitudes on mountains to 1000 m high. Flowers April and June-October.

Common name: Jucaro or Chicharron.

Comments: T. chicharronia is a very variable species showing considerable variation in the size and shape of the leaves, and in the amount of indumentum on the branchlets, leaves and inflorescence.

Terminalia chicharronia (Chicharronia intermedia) was based on Sagra 185 and 281. The specimens at G are the better ones, but there is no evidence that Richard saw them, but he did see those at P. In P there is one sheet with 3 shoots - 2 in flower and 1 in fruit. The label says "Herbarium Richard. No. 185, Combretum sp. no, Guanabo Marzo 1829, Coll R de la Sagra." The 2 flowering shoots are designated as the lectotype because in Geneva herbarium there is a note from Sagra saying that No 185 was sent first and was flowering, and no 281 was sent later (both March 1829) and was fruiting.

In G there are 3 sheets: one all 185 (isolectotype); one all 281 (lectoparatype) and one a mixture of 185 and 281.

Terminalia domingensis Urban is placed as a synonym of T. intermedia (A. Rich) Urban by Urban. His view is justified but the combination he made is illegitimate because there was an earlier homonym.

Terminalia orientensis differs from T. chicharronia in the glabrous leaves and not raised venation. This difference is also found in T. pachystyla, T. aroldi and T. nipensis. However they all come within the range of variation of T. chicharronia.

T. neglecta differs from T. chicharronia in having less pubescent leaves, and less raised venation.

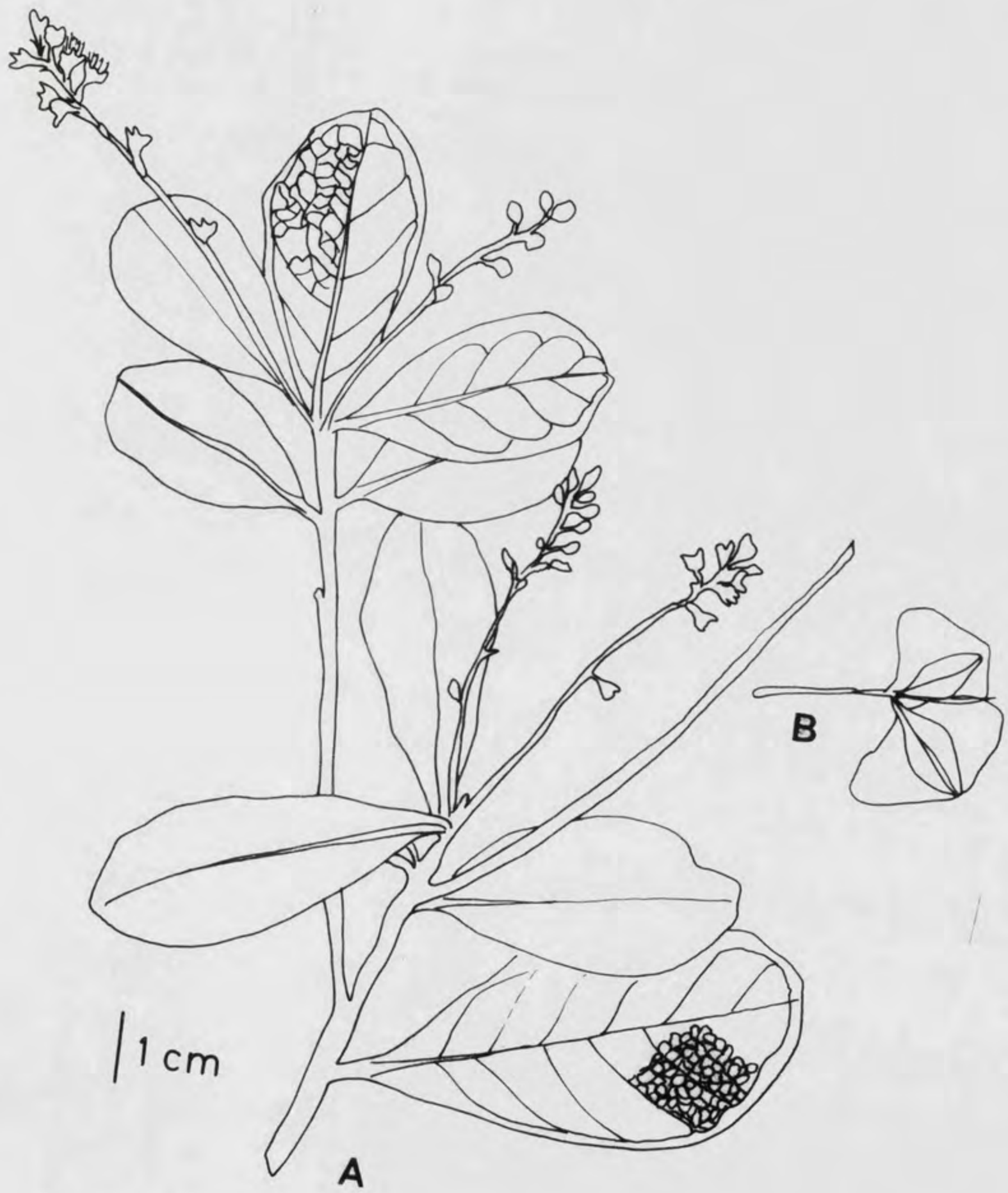


Fig. 9/8: Terminalia chicharronia

A. flowering branch. B. fruits.

T. maestrensis was based on a sterile specimen collected by Biss & Lippold. From the leaves it is clear that it comes well within the variation of *T. chicharronia*.

Four subspecies are recognized here, based on the degree of pubescence, the venation characters and the geographical distribution.

Key to the subspecies

1. Leaves often densely pubescent, or rufous tomentose. Venation strongly raised beneath . . . . (a) subsp. *chicharronia*

1. Leaves glabrous or glabrescent, or if pubescent then venation not prominently raised below 2

    2. Leaves, inflorescences and flowers pubescent. Tertiary and higher-order venation often orthogonally arranged; areolation well developed . . . . (b) subsp. *neglecta*

    2. Leaves, inflorescences and flowers glabrous or glabescent or slightly pubescent. Tertiary veins randomly reticulate or weakly percurrent 3

3. Tertiary veins weakly percurrent; areolation very conspicuous, closed and well developed . . . . (c) subsp. *domingensis*

3. Tertiary veins randomly reticulate; areolation not conspicuous, distant and imperfect or incomplete . . . . (d) subsp. *orientensis*

(a) subspecies *Chicharronia*

Synonyms: *Chicharronia intermedia* A. Rich.

Chuncoa chicharronia (A. Rich.) Griseb.

Terminalia intermedia (A. Rich.) Urban

Terminalia maestrensis Bisse

Small trees, 8-20 m high. Leaves usually crowded; petiole often short, densely pubescent; lamina thickly corieaceous with revolute margin, rufous tomentose beneath. Venation prominently raised beneath; tertiary veins and higher-order veins raised and conspicuous; areolation well developed and orientated. Inflorescence pubescent or densley pubescent. Flowers 6-7.5 mm long, densely hairy: style long, glabrous or hairy.

This subspecies is closely related to T. eriostachy and distributed in the same area in eastern Cuba.

(b) Subspecies neglecta (Bisse) Alwan, comb. nov. Based on Terminalia neglecta Bisse, Feddes Repert. 85: 607 (1974).

Shrub or small to large tree, 2-25 m high. Leaves alternate or spirally arranged, often crowded; petiole short, less than 1 cm long; lamina usually subscoriaceous, occasionally revolute, pubescent or glabrescent beneath. Venation not raised; tertiary veins and higher-order venation orthogonally reticulate; areolation well developed and orientated. Inflorescence pubescent. Flowers 4-6 mm long, pubescent to densley pubescent; style 3-6 mm long, hairy.

Common in western and central Cuba.

(c) Subspecies domingensis (Urban) Alwan, com. nov. Based on Terminalia domingensis Urban, Symb. Ant. 7: 524 (1913).

Small trees, 6-10 m high. Leaves crowded; petiole short-medium 0.5-1.7 cm, glabrous; lamina thickly coriaceous with revolute margin, usually narrowly obovate-oblong or oblong, pubescent to slightly pubescent on midrib and secondary veins glabrous elsewhere. Veins not raised except the primary vein; tertiary veins often weakly percurrent; areolation well developed. Inflorescence glabrous. Flowers glabrous, 5 mm long; style hairy, not exerted.

Common in Haiti and Dominican Republic.

(d) Subspecies orientensis (Monachino) Alwan, comb. nov. Based on Terminalia orientensis Monachon, Caribbean Forester 8: 79 (1974).

Synonyms: T. nipensis Alain

T. aroldoi Bisse

T. pachystyla Borhidi

Tree 8-25 m high. Leaves usually alternate, usually not crowded, petiole short or slightly long to 2.5 cm, glabrous or glabrescent; lamina thickly coriaceous or coriaceous, often with revolute margin, variable in shape, glabrous or glabrescent beneath. Veins not raised; tertiary veins randomly reticulate; areoles large and imperfect. Inflorescence glabrous or slightly pubrescent. Flowers relatively large to 10 mm long, glabrous or sparsely pubescent. Style long, hairy.

Common at high altitude in eastern Cuba.

9. Terminalia oblonga (Ruiz Lopez & Pavón) Steudel, Nom., ed. 2, 2: 668 (1841).

Gimbernatea oblonga Ruiz Lopez & Pavón, Fl. Peruv. Prodr.: 138 (1794). Type: in Pozuzo nemoribus, Peru (holotype, MA*; not seen photograph at F; isotype, F, part FI).

Chuncoa oblonga (Ruiz Lopez & Pavón) Pers., Syn. 1.486 (1805).

Chunco oblonga (Ruiz Lopez & Pavón) Por., Encyc. Meth., Suppl 2: 258 (1811).

Chuncoa diptera Dietr., Vollst. Lex. Gaertn. Machtr. 2: 244 (1816). Based on Gimbernatea oblonga.

Terminalia tarapotensis Van Heurck & Muell. Arg. in Van Heurck, Obs. Bot. 213 (1870). Type: Peruviae orientalis, prope Tarapoto, 1855-6, R. Spruce 4507, (Croton), (lectotype, G; isolectotypes, A + GH, BM, F, K, P, W).

Myrobalanus oblonga (Ruiz Lopez & Pavón) Kuntze, Rev. Gen. 237 (1891).

Terminalia chiriquensis Pittier, Contrib. U.S. Nat. Herb. 18:238 (1917). Type: Remedios and vicinity, eastern Chiriqui, altitude 0-100 meters, December 1911, and January 1912, Pittier 5467 (US, holotype).

* Herbarium, Jardin Botanico, Plaza de Murillo, Madrid, Spain.

Terminalia obidensis Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 147 (1925). Type: Matto do Cacaol Imperial, Obidos, Pará, 23. 6. 1912, Ducke Lectotype, RB 17676; isolectotypes, S, U, US; lectoparatype (Rio Ducoesdina, offl do Rio Branco de Obidos, Pará) RB 17675.

Terminalia bucidoides Standley & L. O. Williams, Ceiba. 3: 214 (1953). Type: Tree 60 ft. Trunk not strongly buttressed. Brown, flaking bark. Occasional. Forested hills near Golfito de Golfo Dulce, July 27, 1951, alt. 75 m., Allen 6282 (holotype, US; isotypes, F, US).

Terminalia mameluco Pickel, Arquiv. Bot. Estad. S. Paulo 3:200 (1958). Type: Pernambuco, Nazare da Mata. 13/1/1955 (fl.); 20/3/1956 (fr.). N.v. Mameluco. Arvore alta, na mata. J. C. de Moraes 1338 (holotype, SP 55579).

Tree to 50 m high. Leaves alternate or spirally arranged, or pseudo-whorled at the ends of the branchlets; petiole 0.5-2(5) cm long, pubescent or glabrous, usually eglandular occasionally biglandular; lamina thinly chartaceous to subcoriaceous, 6-20(15) x 4-7 (10) cm, oblong or elliptic or oblong-obovate or oblanceolate; apex usually acuminate or sometimes acute; base cuneate; upper surface, slightly pubescent when young, glabrous at maturity, verruculose; lower surface rufous-sericeous when young, glabrous when adult except sometimes slightly pubescent on major veins. Venation eucamptodromous - brochidodromous or sometimes brochidodromous; secondary veins 5-7 pairs, moderate, usually abruptly curved, widely spaced; intersecondary veins usually present; tertiary veins randomly reticulate or weakly percurrent, sometimes not inconspicuous; higher-order of venation distinct or not; areolation imperfect. Inflorescence axillary, usually one in each axil, long, with densely arranged flowers; peduncle 1-3 cm long, pubescent; rachis 10-14 cm long pubescent. Bracts 1-2 mm long, acuminate, pubescent at base. Flowers yellow; lower receptacle

1-2 mm long densely pubescent; upper receptace 1-1.5 mm long, cupuliform, pubescent; calyx-lobes c. 0.8 mm long, usually reflected; disk pilose; stamen 3.5-4.5 mm long; anther 0.5 mm long; style 3-4 mm long, densely hairy to above the middle. Fruit transversely oval, rhomboid or oblong, 1.2-2(3) x 2-4(5.5) cm, 2 winged, flattened; body fusiform, narrow,not bulged, 4 mm wide, often slightly ridged or keeled, sometimes with short stipe up to 3 mm long; wings coriaceous, yellowish, finely nerved, 1.2-2.5 x 0.8-2.5 cm, glabrous. (Fig. 9/9 and Appendix 4 Pls. 4 & 5).

Geographical range: Mexico, Guatemala, Nicaragua, El Salvador, Honduras, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Brazil and Bolivia. (Map 9/2).

Ecology: A large tree with a slender, tall trunk to 75 cm diameter, and with small to large buttresses reaching sometimes (in Venezuela) 5 m high; bark smooth or mottled. Very common tree in Central and South America, growing on limestone substrate at low altitudes. (0-500 m, occasionally 1200 m according to Standley & Williams 1967) in dense forest. Flowers August.

Common name: Guyaba de Montana or Guayabilla in Panama; Yacu Shapana in Peru; Volador in Mexico; Guayabillo and Salamo in Nivaragua; Guayabo in Honduras; Guayabo, wild guava or Volador in Guatemala, Guyung in Ecuador; Sura and Quiura in Costa Rica; Pelaom and Guabillo in Colombia; Guaybon in Venezuela.

Comments: Terminalia oblonga is a very distinct species, but it shows considerable variation in the texture, shape and size of the leaves, and in the length of petioles. It is closely related to T. amazonia.

Although the type material of Terminalia tarapotensis consists of flowering specimens, whereas that of T. oblonga has fully mature fruits, it is clear from the texture, venation and general shape of the leaves, and from the inflorescence that it is a flowering state of T. oblonga.

Fig. 9/9: Terminalia oblonga

The type material of T. obidensis consists of poor fruiting specimens. The fruits are only slightly smaller than those of T. oblonga. However, T. obidensis comes well within the range of variation of T. oblonga.

Terminalia bucidioides differs from T. oblonga in the more crowded leaves at the ends of the branchlets, slightly longer petiole and narrower leaves than in normal T. oblonga. However, T. bucidioides comes within the range of variation of T. oblonga.

Terminalia chiriquensis is placed as a synonym of T. oblonga by Standley & Williams (1962). I agree with this view.

10. Terminalia valverdeae A. Gentry, Phytologia 48 (3): 234 (1981). Type: Arbol de 30 m de altura. En easta especamin habia solo frutos. Cerro Azul, entrada por Casas Viejas, (200 m de altura) Cord. de Chongon Prov. Guayas, Ecuador, Aug 1978, F. M. Valverde 301 (holotype, MO; isotypes (according to the original description) ECU, SEL, not seen).

Large tree 30 m high. Leaves alternate, not crowded; petiole 1-2 cm long, slender, glabrous or sparsely pubescent, biglandular but not very conspicuous; lamina chartaceous, (5) 8-15 x 3-7 cm, obovate; apex acute to obtuse or subacuminate; base cuneate to obtuse; upper surface glabrous; lower surface sparsely puberulous near the base of the primary and secondary veins almost always glabrous elsewhere. Venation eucamptodromous; secondary veins 5-8 pairs, prominently raised below; tertiary veins irregularly and weakly percurrent, not raised beneath but conspicuous; quaternary veins conspicuous, areoles small, imperfect. Fruit large to very large, transversely oblong, 2-2.3 x 7-8 cm, 2-winged; body sharply keeled ventrally but flattened dorsally, 2-2.3 x 1-1.5 cm, distinctly triangular in section, very hard to cut, puberulous; wings very large, become shorter towards the centre of the fruit, 3.5-4.3 x 2.5-3.5 cm, coriaceous and finely nerved. (Fig. 9/10 and Appendix 4 pl. 6.

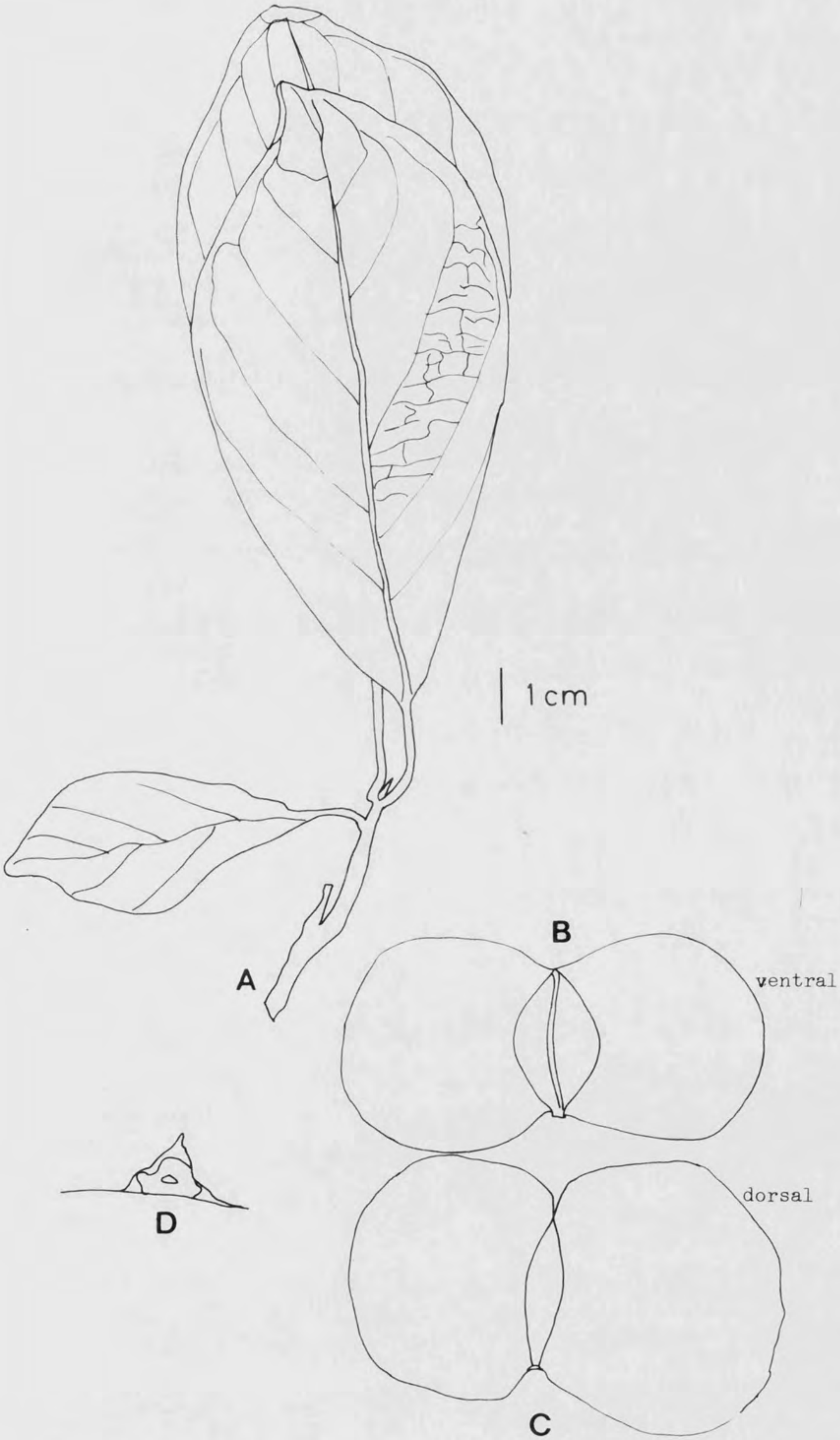


Fig. 9/10: Terminalia valverdeae. A. branch. B. fruit, ventral view. C. fr., dorsal view. D. section of fruit.

Geographical range: Ecuador. (Map 9/2)

Ecology: It is a mature forest canopy tree, growing at 200 m altitude. Fruit August.

Common name: Castano.

Comments: T. valverdeae seems to be closely related to T. oblonga. They are similar in general characters of the leaves and habit, but they differ in the size and shape of the fruits. Also T. valverdeae has some affinity with some extreme forms of T. guyanensis (Sect. Diptera). T. platyptera from Australia has fruits very similar to those of T. valverdeae, particularly with respect to the shape and size of the wings. Also, similar fruits are found in T. calamansanii from Malaysia and Indo-China.

11. Terminalia phaeocarpa Eichler in C. Martius, Fl. Bras. 14, 2: 89 t. 33 f. 10 (1867). Type: in silvis primaevis montosisque prope S. luzia. novemb. 34, Riedel 2521 (lectotype, LE; isolectotypes, A + GH, G, K, P).

Terminalia hylobates Eichler, Kjoeb. Vidensk. Keddel. 195 (1870). Type: Capto do Mato, Lagoa Sant, Minas Gerais, 4. IX. 64, Warming, s.n. (Lectotype, C; isolectotypes, C, F, P).

Myrobalanus phaeocarpa (Eichler) Kuntze, Rev. Gen. 237 (1891).

Small to medium sized tree 3.5-25 m tall. Leaves often alternate, occasionally spirally arranged; petiole usually long, 2-5 cm long, often glabrous, biglandular; lamina subcoriaceous-coriaceous, (8) 10-27 x (4) 5-14 cm, oblong to oblong ovate or elliptic or obovate to broadly obovate; apex broadly acute or acuminate or rounded; base usually alternate or sometimes acute; upper surface minutely and slightly pubescent; lower surface often minutely and densely pubescent. Venation usually eucamptodromous sometimes eucamptodromous - brochidodromous; primary vein moderate or stout, prominently raised beneath; secondary veins 9-14 pairs, curved or sometimes straight, prominently raised beneath, often thick and

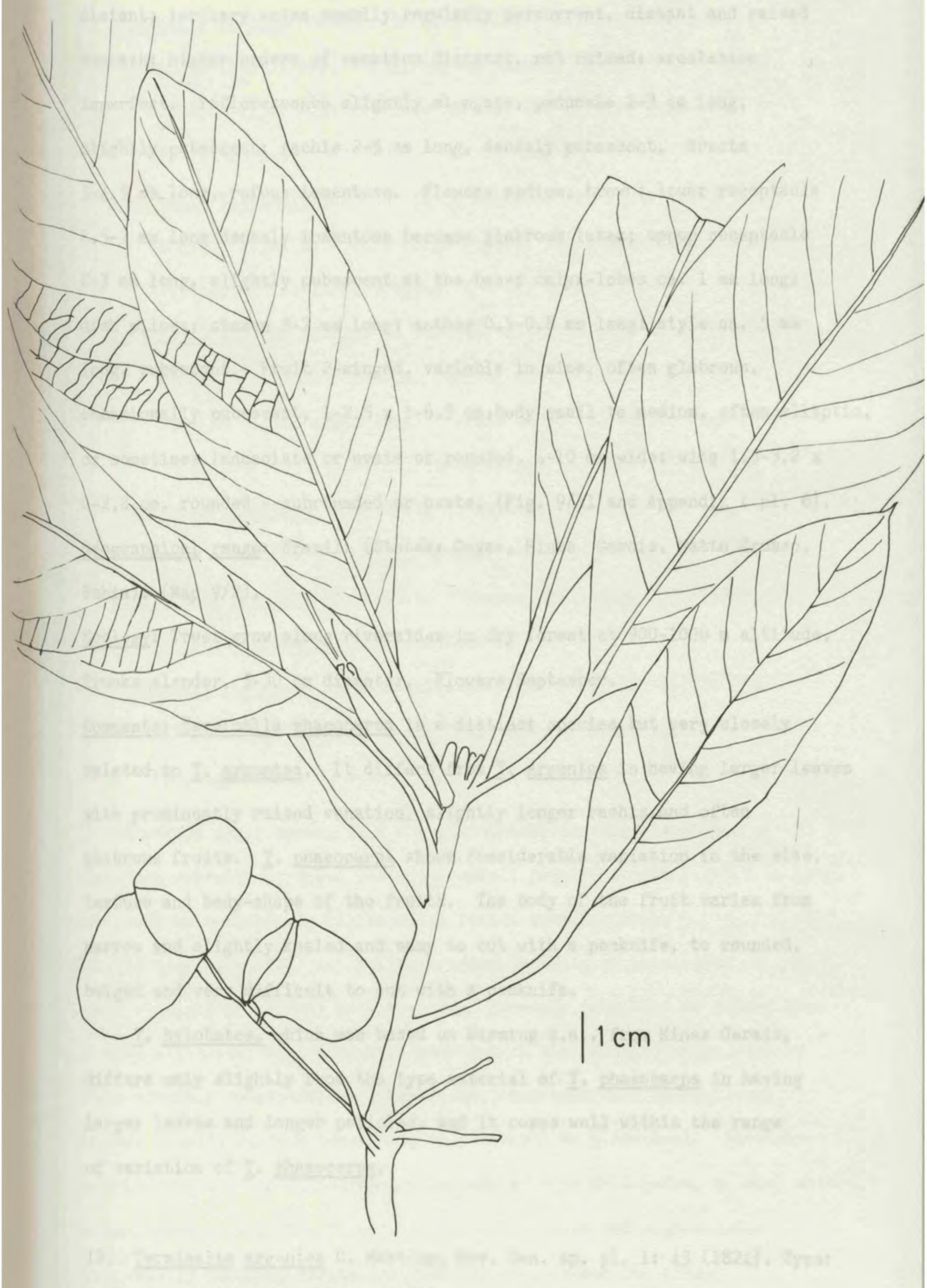


Fig. 9/11: <u>Terminalia</u> <u>phyaeocarpa</u>

distant; tertiary veins usually regularly percurrent, distant and raised beneath; higher orders of venation distinct, not raised; areolation imperfect. Inflorescence slightly elongate; peduncle 2-3 cm long, slightly pubescent; rachis 2-5 cm long, densely pubescent. Bracts 3-4.5 mm long, rufous tomentose. Flowers medium, brown; lower receptacle 2.5-3 mm long densely tomentose becomes glabrous later; upper receptacle 2-3 mm long, slightly pubescent at the base; calyx-lobes ca. 1 mm long; disk pilose; stamen 5-7 mm long; anther 0.5-0.8 mm long; style ca. 5 mm long, pubescent. Fruit 2-wingėd, variable in size, often glabrous, occasionally pubescent, 1-2.5 x 3-6.5 cm;body small to medium, often elliptic, or sometimes lanceolate or ovate or rounded, 4-10 mm wide; wing 1.5-3.2 x 0-2.8 cm, rounded - subrounded or ovate. (Fig. 9/11 and Appendix 4 pl. 6).

Geographical range: Brazil: (States: Goyaz, Minas Gerais, Matto Grosso, Bahia). (Map 9/2).

Ecology: Trees grow along riversides in dry forest at 900-1000 m altitude. Trunks slender, 5-30 cm diameter. Flowers September.

Comments: *Terminalia phaeocarpa* is a distinct species but very closely related to *T. argentea*. It differs from *T. argentea* in having larger leaves with prominently raised venation, slightly longer rachis and often glabrous fruits. *T. phaeocarpa* shows considerable variation in the size, texture and body-shape of the fruits. The body of the fruit varies from narrow and slightly keeled and easy to cut with a penknife, to rounded, bulged and very difficult to cut with a penknife.

T. hylobates, which was based on Warming s.n., from Minas Gerais, differs only slightly from the type material of *T. phaeocarpa* in having larger leaves and longer petioles, and it comes well within the range of variation of *T. phaeocarpa*.

12. *Terminalia argentea* C. Martius, Nov. Gen. sp. pl. 1: 43 (1824). Type: in montosis ad villa do Rio Contos, Provinciae Bahiensis, Martius 1714 (holotype, M; isotype, M).

Terminalia sericea Cambess. in A. St. Hil., Fl. Bras. Merid. 2: 243 (1829), nom. illeg. not of Buchell ex DC., Prod. 3: 13 (1828). Type: Brasil: Minas Geraes. St. Hilaire 1816-1821. (P, lectotype).

Terminalia biscutella Eichler in C. Martius, Fl. Bras. 14, 2: 88 (1867). Type: in siccis prope Cuyaba, Aug. 1827, Riedel 1095 (lectotype, LE; isolectotypes, A + GH, G, LE, P).

Terminalia modesta Eichler in Martius, Fl. Bras. 14, 2: 87 (1867), not of Tul., Ann. Sci. Nat. Ser. 4, 6: 102 (1856). Type: in silvis ripae fluvii Parana et ad fl. Pardo, Aug. 1826, Riedel 429 (lectotype, LE: isolectotype, A + GH)

Terminalia subsericea Eichler in C. Martius, op. cit: 127 (1867) nomen novum for T. modesta Eichler.

Myrobalanus argentea (C. Martius) Kuntze, Rev. Gen: 237 (1891).

Myrobalanus biscutella (Eichler) Kuntze, loc. cit.

Terminalia festinata S. Moore, Trans. Linn. Soc., Ser II, 4: 352 (1895). Type: Brazil, Santa Cruz, Spencer Moore 450 (holotype, BM).

Shrubs or small trees, 2-15 m high. Leaves usually alternate, sometimes spirally arranged but not crowded; petiole medium 1.2-3.7 cm long, pubescent or tomenntose, biglandular; lamina subcoriaceous, 6-12(15.5) x 2.5-5(6.5) cm, ovate to narrowly ovate of lanceolate or ovate - oblong or oblong; apex aristate, narrowly acuminate or acute; base usually attenuate, almost always decurrent on the petiole; upper surface often minutely pubescent, or glabrescent, sometimes very shiny; lower surface usually silvery tomentose, or pubescent or glabescent. Venation eucamptodromous - brochidodromous; secondary veins 6-10 pairs, curved, not raised beneath, moderate to widely spaced; tertiary and higher-order veins usually randomly reticulate; areoles conpsicuous but often imperfect or incompletely closed. Inflorescences crowded at the ends of new shoots, subcapitate to shortly elongate; peduncle 1-2.5 cm long, densely tomentose or pubescent; rachis 1-2.5 cm long, tomentose. Bracts 3-3.5 mm long, villous. Flowers small, yellowish-brown; lower receptacle 1-2 mm long, rufous tomentose or villous; upper receptacle 1-2 x 3 mm pubescent outside, villous inside; calyx-lobes very small 0.5-0.8 mm; disk pilose; stamen 3-3.5 mm long; anther 0.4-0.5 mm long; style 2.5-4 mm long, pilose at base. Fruit 2-winged, variable in size but usually medium-large, densely silvery pubescent or occasionally slightly pubescent or glabrous, 1.5-3 x 3-6(7) cm; body large, rounded, ovoid or ellipsoid or obovoid, 1-3 x 0.7-1.5 cm; wing 1.4-3 x 1.5-3 cm, rouned at margin, straight at apex and base. (Fig. 9/12 and Appendix 4 Pl. 7).

Geographical range: Brazil (Central, eastern and southern regions. States: Piaui, Bahia, Minas Gerdis, Goias, Mato Grosso, Para, Sao Paulo, Rio Grande do Sul), Paraguay and Bolivia. (Map 9/3).

Ecology: A small tree or shrub, with slender trunk 5-20 cm diameter, growing in gallery forest along rivers, on dry hills or at savanna margin, at 450-1000 m altitude. Flowers July to October in Brazil, May in Paraguay.

It is very common in Brazil, particularly in the states of Goiaz, Mato Grosso, Minas Gerais and Sao Paulo, but it is rare in Bolivia and Paraguay.

Common name: Cachaporra de gentio; Capitão do campo.

Comments: *Terminalia argentea* is a very variable species showing considerable range in the size and shape of the leaves and fruits, and in the amount of indumentum on the leaves, branchlets and fruits.

T. biscutella was based on Riedel 1095 from Mato Grosso. The fruits of this are nearly glabrous and 32-38 mm broad, with a rounded body of 9-11 mm diameter. They are slightly smaller and with a slightly more rounded body than in typical *T. argentea* (36-44(50) mm broad with body 8 mm wide). However, *T. biscutella* comes within the range of variation

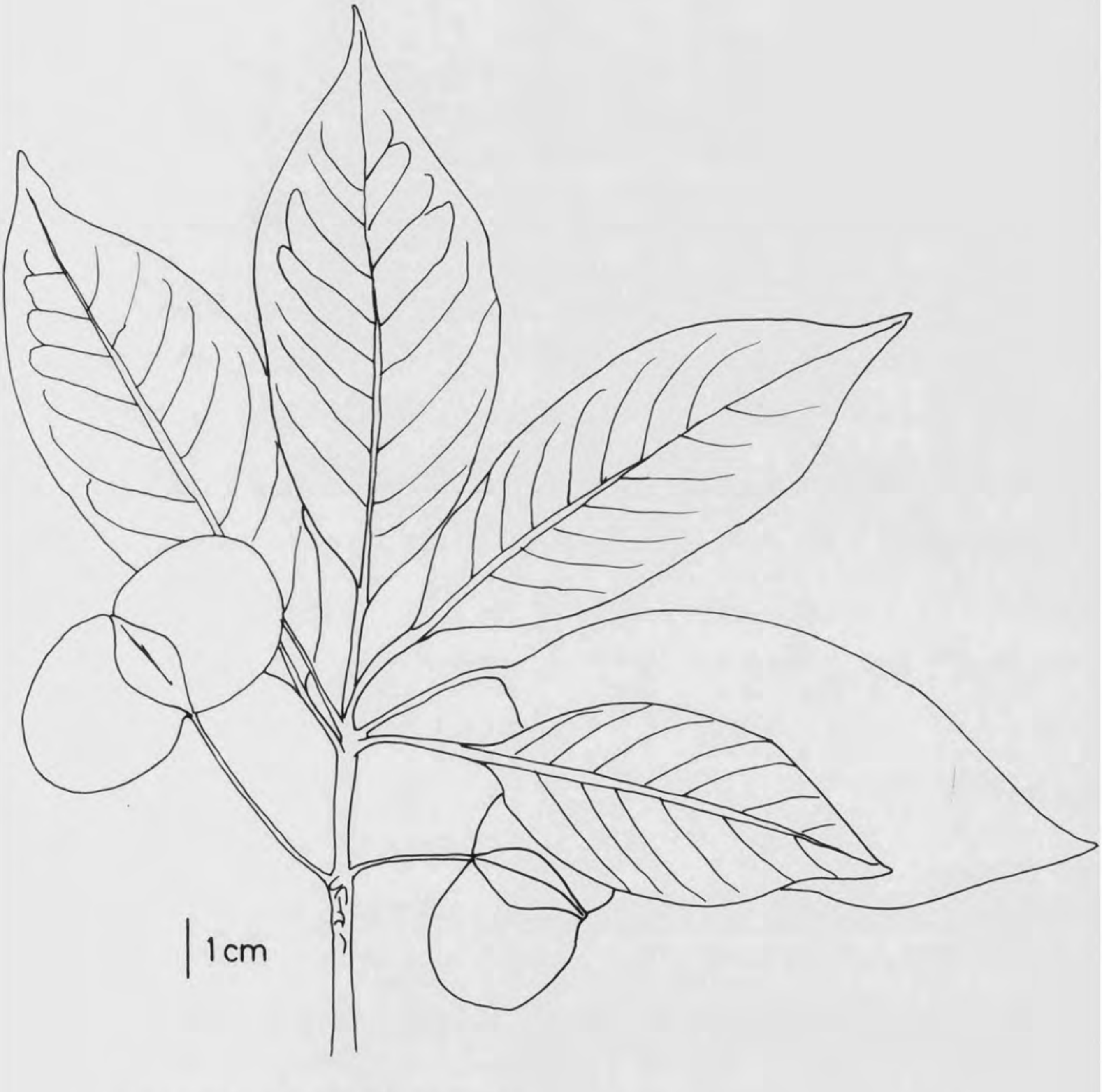


Fig. 9/12: Terminalia argentea

of *T. argentea*.

T. subsericea was based on Riedel 429 (fl. & fr.), 1956 (fr.) and Sello 5560 (fr) from Sao Paulo. *T. subsericea* differs from the type of *T. argentea* in having less indumentum on the leaves and fruits, but it comes within the range of the very variable *T. argentea*.

T. festinata was based on Moore 450 from Mato Grosso. The type has flowers, but the leaves are only just appearing. Although it is very difficult to identify species of *Terminalia* without fruits it is obvious from those flowers and young leaves that *T. festinata* is a synonym of *T. argentea*.

T. sericea has already been placed as a synonym of *T. argentea* by Eichler (1867) and this is obvious from the type specimen in P.

13. *Terminalia kuhlmannii* Alwan, sp. nov.

Arbor. Folia spiraliter ordinata ad ramulorum apices congesta; petiolus 1-2 cm longus, glabrous vel sparse pubescens, eglandulosus; lamina chartacea, 5-12 x 3-6 cm, obovata, apice subacuta vel acuminata, basi acuta, supra glabra, subtus ± glabra; venatio brochidodrma conspicua, nervis seconderiis subtus prominentibus 5-8 paribus, nervis tertiariis subtus reticulat is,venulis conspicuis vix prominentibus. Pedunculus (in fructus) 2-3.5 cm longus, pubescens; rachis (in fructus) 2-3.5 cm longa, dense pubescens. Fructus 2-alatus, transverali oblongus, 1.2-1.7 x 3.5-4.6 cm, dense pubescens, corpore 3-4 mm lati, alis oblongis, 1.4-2,1 cm lati.
Type: Brasil: Espirito Santo, Goytacazes, Rio Doce. n.v. "Pelada", arvore frequente no mato, da madelta a provei tavel, 16. 12. 1943, Kuhlmann 06688 (holotype, RB 62982; isotypes, NY, RB).

Tree. Leaves spirally arranged, crowded at the ends of the branchlets; petiole 1-2 cm long, glabrous or slightly pubescent, eglandular; lamina chartaceous, 5-12 x 3-6 cm, obovate; apex subacute or acuminate; base acute; upper surface glabrous, lower surface glabrous or nearly so. Domatia absent. Venation brochidodromous; secondary veins 5-8 pairs, moderate, intersecondary veins absent; tertiary veins randomly reticulate, conspicuous and slightly raised below; higher-orders of venation distinct; quaternary and quinternary veins conpspicuous. Peduncle (in fr.) 2-3.5 cm long, pubescent; rachis (in fr.) 2-3.5 cm, densely pubescent. Fruit 2-winged, transversely oblong, 1.2-1.7 x 3.5-4.6 cm, densely pubescent; body 3-4 mm wide, slightly keeled ventrally, flattened dorsally; wings oblong, 1.4-2,1 cm wide. (Fig. 9/13 and Appendix 4 Pl. 6).

Geographical range: Eastern Brazil.(Map 9/3).

Common name: Pelada.

Comments: This species seems to be most closely rleated to *Terminalia guyanensis*, which occurs in Venezuela and Guyana, but it differs from it in the pubescent and narrow fruits, wider leaves with more conspicuous venation, and longer inflorescence. In addition *T. kuhlmannii* occurs in an area which is very remote from the range of distribution of *T. guyanensis*.

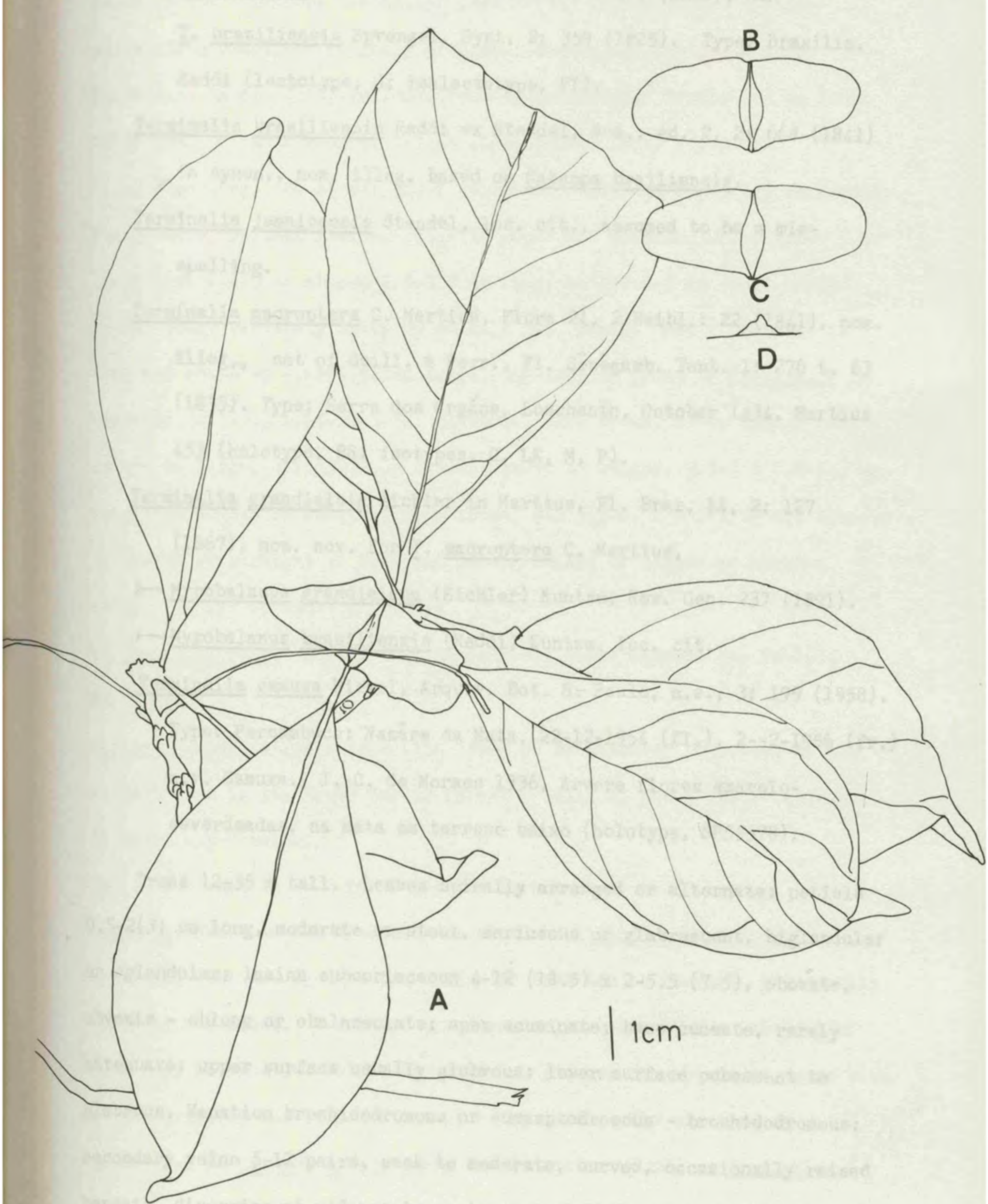


Fig. 9/13: Terminalia kuhlmannii A. fruiting branch.
B. fruit, ventral view. C. fruit, dorsal view.

14. Terminalia januariensis DC., Prod. 3: 11 (1828). Based on Catappa brazıliensis Raddi, Mem. Mod. (Fis) 18: 405 (1820), non T. braziliensis Sprengel, Syst. 2: 359 (1825). Type: Brasilia, Raddi (lectotype, G; isolectotype, FI).

Terminalia brasiliensis Raddi ex Steudel, Nom., ed. 2, 2: 668 (1841) in synon., nom. illeg. based on Catappa brailiensis.

Terminalia jamaicensis Steudel, loc. cit., assumed to be a mis-spelling.

Terminalia macroptera C. Martius, Flora 24, 2 Beibl.: 22 (1841), nom. illeg., not of Guill. & Perr., Fl. Sēnēgamb. Tent. 1: 276 t. 63 (1833). Type: Serra dos Orgáos, Luschanth, October 1834, Martius 453 (holotype, BR; isotypes, G, LE, M, P).

Terminalia grandialata Eichler in Martius, Fl. Bras. 14, 2: 127 (1867), nom. nov. for T. macroptera C. Martius.

⊢ Myrobalanus grandialata (Eichler) Kuntze, Rev. Gen. 237 (1891).

⊢ Myrobalanus brasiliensis (Raddi) Kuntze, loc. cit.

Terminalia camuxa Pickel, Arquiv. Bot. S. Paulo, n.s., 3: 199 (1958). Type: Pernambuco; Nazāre da Mata, 22-12-1954 (fl.), 2--2-1956 (fr.) n.v. Camuxa., J. C. de Moraes 1336, Arvore flores amarelo-esverdeadas, na mata em terreno baixo (holotype, SP55578).

Trees 12-35 m tall. Leaves spirally arranged or alternate; petiole 0.5-2(3) cm long, moderate or stout, sericeous or glabrescent, biglandular or eglandular; lamina subcoriaceous 4-12 (18.5) x 2-5.5 (7.5), obovate, obvoate - oblong or obalnceolate; apex acuminate; base cuneate, rarely attenuate; upper surface usually glabrous; lower surface pubescent to glabrous. Venation brochidodromous or eucamptodromous - brochidodromous; secondary veins 5-12 pairs, weak to moderate, curved, occasionally raised beneath, diverging at moderately acute angle but the upper and lower secondaries often more obtuse than the middles; intersecondary veins sometimes present; tertiary veins randomly reticulate or weakly percurrent, usually not conspicuous but sometimes raised below; higher-orders of venation not distinct; areolation imperfect. Inflorescence usually subcapitate sometimes slightly elongate; peduncle 1.5-3(5) cm long, pubescent; rachis 0.5-2 cm long, densely pubescent. Bracts 2-3 mm long, pubescent. Flowers medium, 5-7 mm long, brown; lower receptacle 2.5-3.5 mm long, tomentose; upper receptacle 2-2.5 mm long, 4-5 mm across, funnelshape, villous inside, slightly pubescent outside, calyx-lobes 1 mm long; disk villous; stamen 2.5-3.5 mm long; anther 0.5 mm long; style 3-4 mm long, variously hairy up to half its length. Fruit variable in size and shape of wings, often large (the largest fruit of Terminalia in America), 2.5-3.5(4)x5-10.5 cm, glabrous, dark brown, often shiny; body medium to large, ellipsoid or ovoid, keeled or bulged, 2.5-3 x 0.8-1.3 cm, very hard to cut in section; wing large, 2-3.3(4.2) x 2.5-4(5) cm, concave or convex or straight at apex and base, rounded or obtuse at margin. (Fig. 9/14 and Appendix 4 Pl. 8).

Geographical range: Brazil (Rio de Janeiro, Minas Gerais, Sao Paulo). Map 9/3).

Ecology: A medium-large tree with trunk 35 cm diameter, reported as the highest tree in the Minas Gerais forest growing at about 700 m altitude. Flowers July-October.

Uses: The wood is used for fence and furniture.

Comments: Raddi in his original description of Catappa braziliensis mentioned that the species was collected from Rio de Janeiro, principally Montagna Corcovado. I saw two specimens collected by Raddi but both of them bear no locality except "Brasilia". However the specimens agree with the description and illustration given by Raddi. The specimen in G identified as Catappa braziliensis and annotated by DC, as Terminalia januariensis DC, whereas the one in FI is labelled simply Terminalia and there is no evidence that De Candolle saw it. Therefore the former is designated here as lectotype.

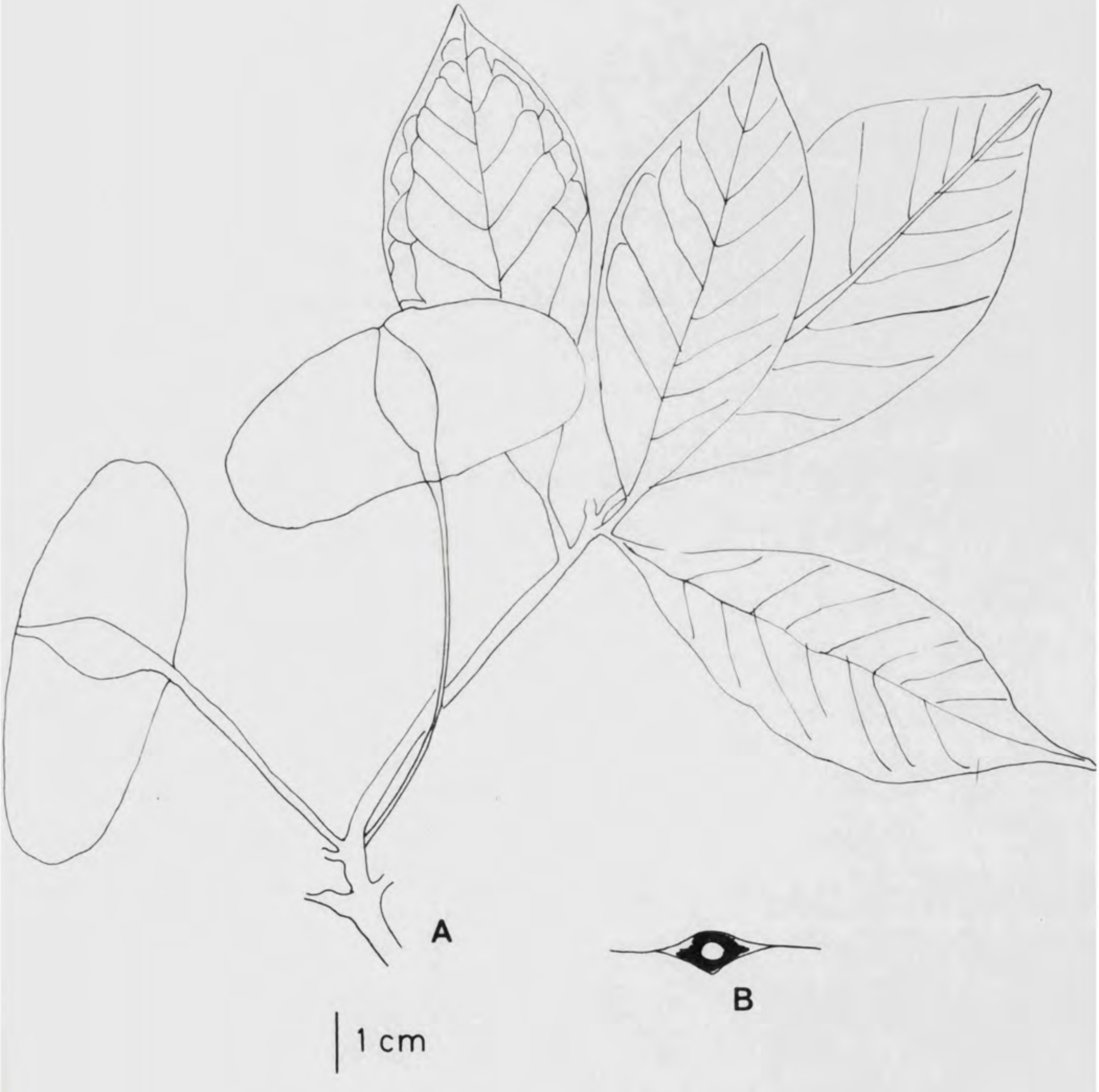


Fig. 9/14: T. januariensis

Terminalia macoptera Martius (= T.grandialata Eichler) was based on Martius 453 (fr.) from Rio de Janeiro. It is obvious from the type specimen that it is very similar to T. januariensis and comes within the range of its variation.

Terminalia camuxa which is known only from the type (Moraes 1336 from Pernambuco) has fruits (2-2.5 x 4-5.5 cm) only slightly smaller than in typical T. januariensis. However, it comes at the extreme end of the range of variation of T. januariensis which has fruit of 2.5-3.5 x 5-10.5 cm.

The leaves of T. januariensis show considerable variation in size, the largest being about 18.5 x 7.5 cm. The fruits also show considerable variation in size, and also in the shape and length of the wings.

15. Terminalia guyanensis Eichler in C. Martius Fl. Bras. 14, 2: 85 (1867).
Type: Guyana gallica, Poteau (holotype, B, destroyed; Photos, FI; isotype, U; paratypes, A + GH, K, P, no collector).
⊢ Myrobalanus eichleriana Kuntze, Rev. Gen. 237 (1891). Based on ⊢ T. guyanensis Eichler. (Plate 9/15 and Appendix 4 Pl. 3).

Tree 25-32 m tall. Leaves alternate or spirally arranged; petiole 1.2-3 cm long, moderate, usually glabrous, often biglandular, or sometimes eglandular; lamina chartaceous, sometimes thinly chartaceous, or subcoraceous, 4-11 x 2-4 (5.5) narrowly oblong or obovate or oblanceolate; apex long and narrowly acuminate; base cuneate or attenuate; upper surface glabrous and shiny; lower surface usually glabrous except on the midrib. Venation brochidodromous; secondary veins (5) 7-12 pairs, usually fine, curved, not raised, diverging at widely acute angles, upper ones often more obtuse or perpendicular to the midvein; tertiary veins randomly reticulate; higher-order veins not distinct, areoles conspicuous on both surfaces, imperfect and large. Inflorescence short capitate to subcapitate; peduncle 0.5-1.5 cm long, pubescent; rachis 0.8-1.5 cm long, densely pubescent. Bracts 1.5-2.5 mm long pilose. Flowers small, yellow; lower receptacle 1.5 mm long densely pubescent; upper receptacle c. 1 mm long, sparsely pubescent; calyx-lobes 1 mm long, sparsely pilose at apex and margins; disk pilose; stamen 3-3.5 mm long; anther 0.4-0.5 mm long; style 3-3.5 mm, pilose. Fruit medium to large, 1.6-2.3 x 3.8-6.7(7.5) cm, glabrous and usually shiny; body lanceolate, 0.4-0.7 cm wide, bulged from the middle on both surfaces; wing 1.4-2.5 x 1.7-3.5 cm, usually straight but sometimes convex or concave at apex and base, rounded at margin. (Fig. 9/15 and Appendix 4 Pl. 8).

Geographical range; French Guiana, Surinam,Guyana and Venezuela. (Map 9/3).

Ecology: A medium to large tree, with slender trunk to 45 cm diam., with buttresses to 1.5 m high; bark finely and shallowly fissured, brownish gray with yellow slash. Growing in rain forests at 600-900 m altitude. Flowers March.

Common name: Pato de danta amarillo.

Comments: *Terminalia guyanensis* is very close to *T. januariensis* but differs in the following characters: smaller fruits, with narrower body and wings; narrower and less pubescent leaves; shorter inflorescence, with smaller flowers. Until recently it was easy to separate *T. guyanensis* from *T. januariensis* by the fruit characters alone. However, three fruiting specimens (from Venezuela) recently became available which are very similar to *T. januariensis* in their fruits. The specimens are Steyermark 62174 from Monagas, Delgado 328 from Caracas, and Smith 5506 from Lara. The later has a very different fruit from that in *T. guyanensis*. It has a large and wide body 3-3.5 x 0-1.3 cm (even slightly larger than *T. januariensis*) and a long wing 3-4.1 cm long which is also longer than typical fruit of *T. januariensis*. But because the two species are geographically so well isolated, I prefer to leave them separate for the present time.

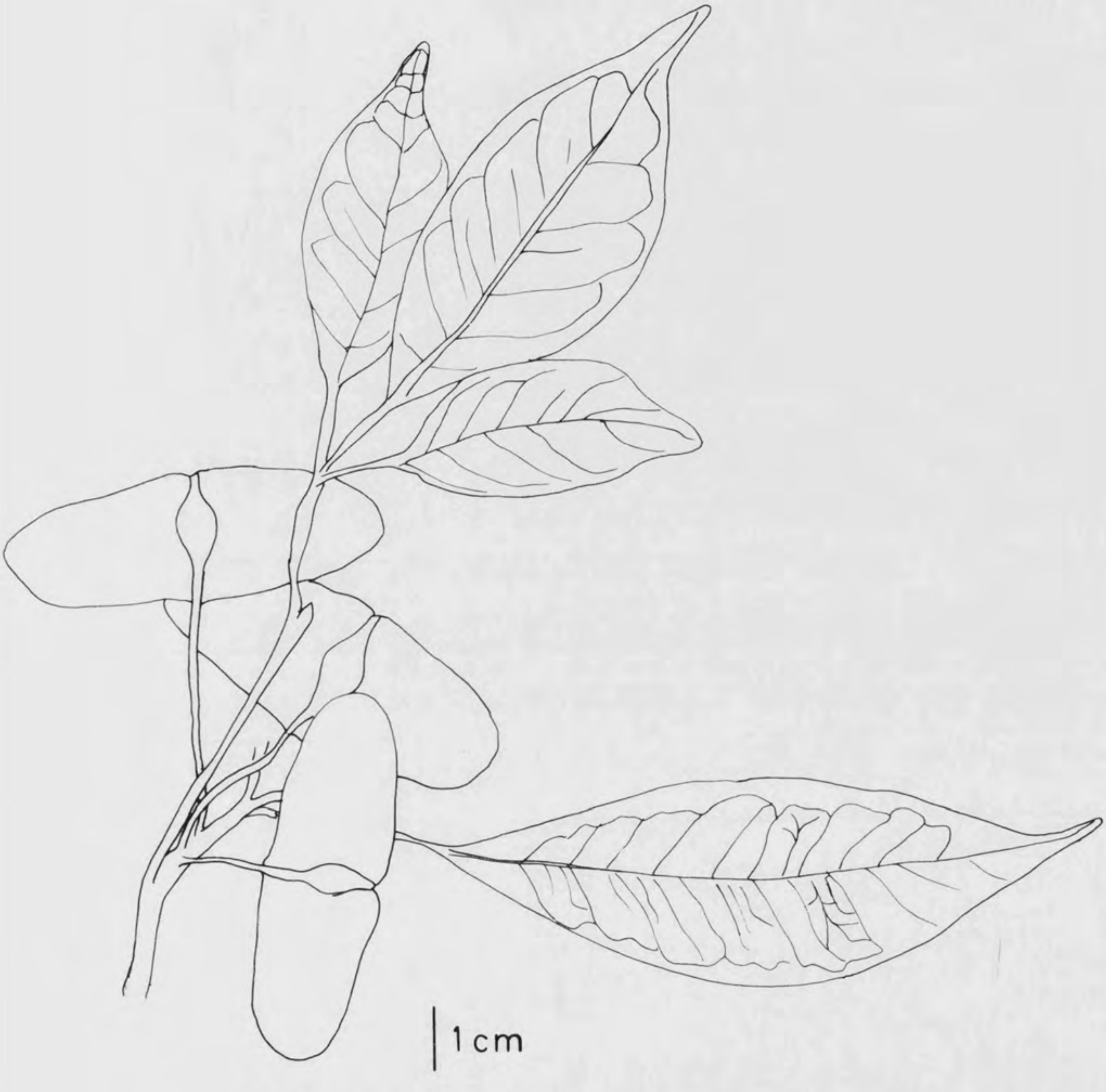


Fig. 9/15: T. guyanensis

16. Terminalia eichleriana Alwan, nom. nov.: pro Terminalia punctata Eichler in C. Martius, Fl. Bras. 14(2): 85 (1867), nom. illegit.; non Roth, Nov. Pl. Sp.: 381 (1821); nec Spruce ex Eichler (1867), nom. syn. = Buchenavia punctata Eichler. Type: in serra d'Acurua Prov. Bahiensis, Blanchet 2794 (BR, lectotype).

⊢ Myrobalanus punctata (Eichler) Kuntze, Rev. Gen.: 237 (1891).

Tree, 2-30 m high. Leaves spirally arranged, usually crowded at the ends of the branchlets; petiole0.3-0.7 cm long, tomentose or subvillous; lamina chartaceous, 2.5-6.5 x 1.5-4.5 cm elliptic or elliptic - narrowly obovate; apex acute or obtuse sometimes mucronate, rarely subacuminate; base broadly cuneate or subrounded; upper surface sparsely to densely pilose; lower surface densely pilose. Venation eucamptodromous; secondary veins 3-5(6) pairs, moderate or weak, nearly straight and parallel. Sometimes ending into the margin, narrowly spaced with narrowly acute angle of divergence (30^{o}-45^{o}); tertiary veins percurrent, slightly raised beneath; higher orders of venation distinct; areolation usually imperfect. Inflorescence capitate; peduncle 2.5-3.5 cm long, rather slender, tomentose; rachis very short 0.5 cm, tomentose. Bracts 4 mm long. Flowers 3-4.5 mm long; lower receptacle 2-2.5(3) mm long, appressed tomentose; upper receptacle 1 mm long, pubescent from outside, densely pilose from inside; calyx-lobes very short 0.3-0.5 mm long; disk pilose; stamens 3-5 mm long, exserted; style 3-5 mm, exserted. Fruit very small, subrounded or sometimes slightly longer than broad, 0.6-0.8 x 0.7-1.1 cm; body very small and thin and easy to cut in section, pubescent; wings usually 3, subequal or equal. 0.5-0.8 x 0.4-0.5 cm, a fourth small wing frequently present. (Fig. 9/16 and Appendix 4 Pl. 9).

Geographical range: Eastern Brazil (State of Bahia). (Map 9/4).

Ecology: A shrub or small tree 2-30 m high, growing on rocky soil on hillsides. Fruiting September to February.

Common name: "Camacary" or "Pau d'agua".

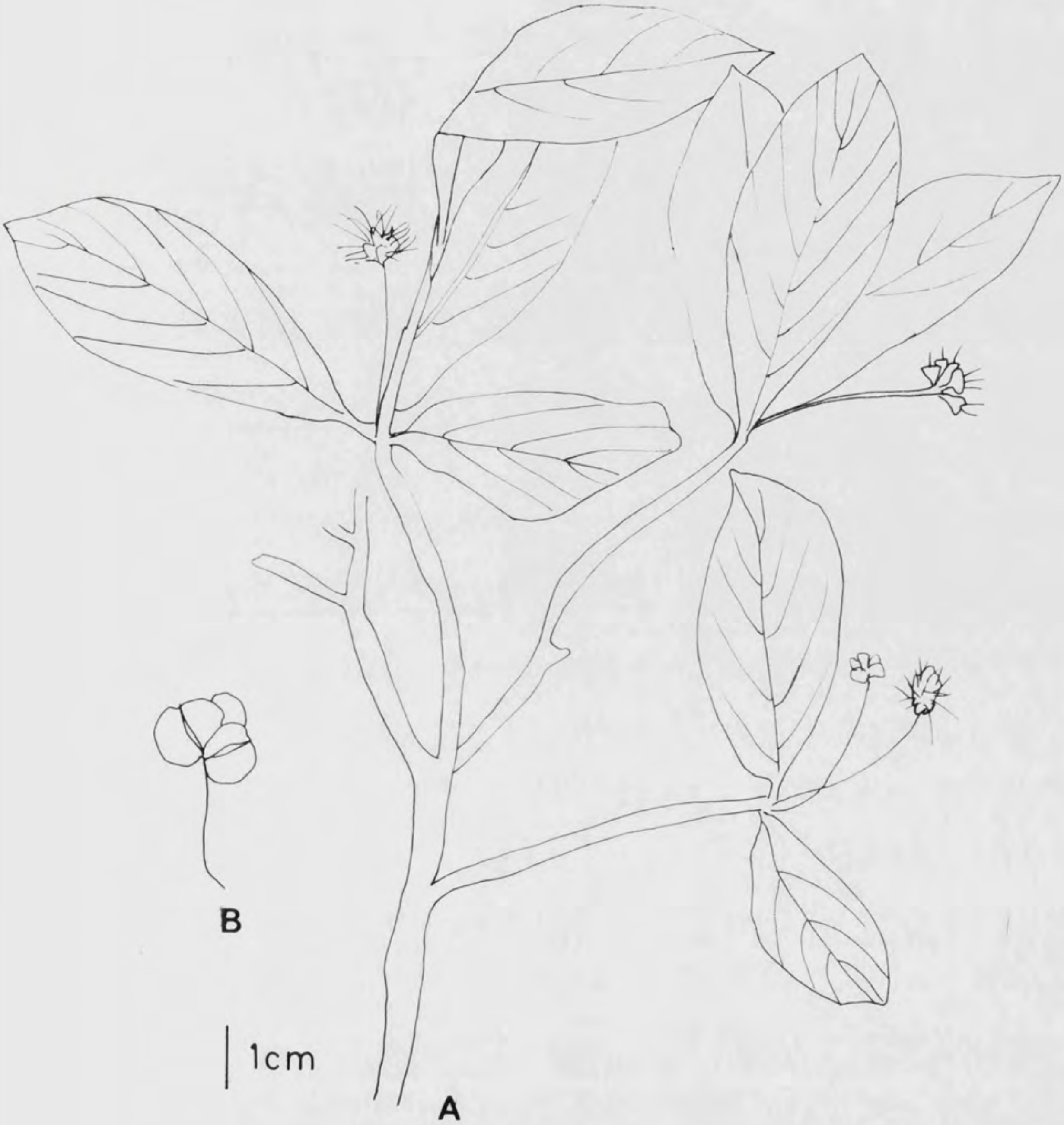


Fig. 9/16: T. eichleriana. A. flowering branch.
B. fruits.

Comments: Although the specimen Blanchet 2794 in BR has no fruits it is designated here as lectotype because its label bears exactly the same information as mentioned in the original description and it is annoted by Eichler. Eichler (1867) in his original description said fruit not known. But a duplicate (isolectoryptе) at G not annoted by Eichler (and evidently not seen by him) has fruits.

In the absence of fruits it is sometimes difficult to separate this species from T. fagifolia, to which is is closely related. Their leaves are similar in most respects, but in T. eichleriana they usually have fewer secondary veins (3-5) with a narrower angle of divergence. However this species can be easily distinguished from T. fagifolia by its small rounded fruits with three equal wings and often capitate inflorescence with rather slender penduncle, whereas in T. fagifolia the fruits always have two distinct lateral wings and the inflorescences are subcapitate to slightly elongate with moderate peduncles.

17. Terminalia fagifolia C. Martius, Nov. Gen. sp. Pl. 1: 42, 6. 27 (1824). Type: in Camps S. Philippi, Prov. Minaram, 1818, Martius s.n. (lectotype, M; isolectotype, M).

Terminalia lanceolata C. Martius, op cit.: 43 t. 29 (1824). Type: inter Malhada et Aitete, oppidulum Provinciae Bahiensis, Martius s.n. (holotype, M; 2 isotypes, M).

Terminalia fagifolia C. Martius var. angustifolia Eichler in C. Martius, Fl. Bras. 14, 2: 86 (1867). Type: Based on Terminalia lanceolata C. Martius.

Terminalia fagifolia C. Martius var. parvifolia Eichler in C. Martius, Fl. Bras. 14, 2: 86 (1867). Type: Du certam de Bahias d'Utinga dans le Certam du S. Francisco, 1839. Blanchet 2773 (lectotype, L.E; isolectotypes, BM, BP, BR, G, P, W).

Myrobalanus fagifolia (C. Martius) Kuntze, Rev. Gen. Pl.: 237 (1891).

Small to large trees, up to 30 m high. Leaves usually spirally arranged, occasionally alternate, crowded; petiole short, 1-4 mm long, densely pilose; lamina chartaceous or subcoriaceous, 3-12.5 x 1.5-4.5 cm, elliptic to elliptic oblong of oblanceolate or narrowly ovate; apex obtuse or acute-subacuminate, usually mucronate but sometimes shortly aristate; base cuneate, occasionally slightly decurrent into the petiole; upper surface slightly pubescent or pilose, not verruculose; lower surface densely to slightly pilose or pubescent to glabrescent. Venation eucamptodromous with tendency to mixed craspidodromous; midvein moderate; secondary veins 5-12 pairs of moderate thickness, straight and parallel, diverging at narrowly acute angle; intersecondary veins absent; tertiary veins regularly percurrent, oblique and opposite, usually originating from the secondaries at right angles; quaternary veins usually distinct from quinternary veins; areolation imperfect; freely ending veinlet usually present. Inflorescence up to 4.5 cm long, slightly elongate; peduncle c. 2 cm long, moderate, tomentose - sericeous; rachis 1.5-2 cm long, tomentose - sericeous or pilose. Bracts 2-2.5 mm long, pilose. Flowers 3-4 mm long; lower receptacle 1.5-2 mm long, densely pilose; upper receptacle 1.5-2 mm long, scarcely pilose; calyx-lobes 0.5-0.8 mm long; disk pilose; stamen 5-5.5 mm long; anther 0.5 mm long; style 5-6 mm long. Fruit 0.8-1.2 x 15.-3 cm, appressed tomentose; body ovoid or ellipsoid, thickly lignified, 0.6-1.2 x 0.4-0.5 cm; wings 2, 0.8-1.3 x 0.5-1.3 cm, opique, usually rounded at margins, straight at apex and base. (Fig. 17 and Appendix 4 Pl. 9).

Geographical range: Brazil (eastern and central parts) and Bolivia (Map 9/5).

Ecology: A small-medium sized tree rarely reaching 30 m high, usually with tall and slender trunk 10-60 cm diam., growing on sandstone rocks with scrub and dense lowwoodland on undisturbed summits at altitude 500-1250 m. Flowers September.

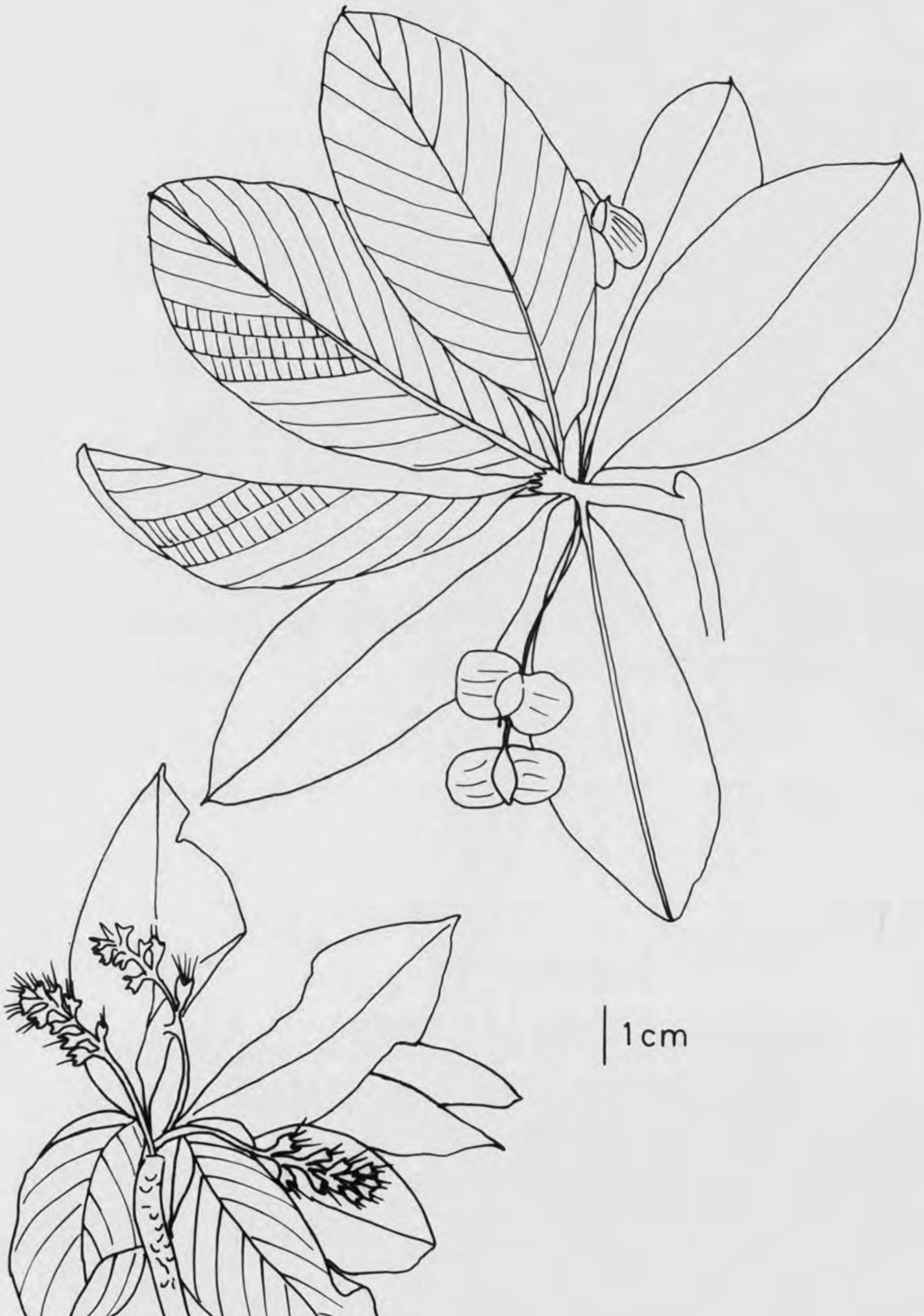


Fig. 9/17: T. fagifolia. A. flowering branch. B. fruiting branch.

Comments: The specimen of Martius in M is designated here as lectotype because it is the basis of the drawing in the original description.

Terminalia fagifolia is a very distinct species. It is closely related to T. eichleriana (for differences, see under T. eichleriana). The most important character by which to identify T. fagifolia from other species is the venation pattern, which is eucamptodromous or nearly mixed craspidodromous with 5-12 pairs of straight, raised, narrowly spaced secondary veins, originating at acute angles.

Terminalia fagifolia shows some variation in the size of th leaves, varying from small 2-3 x 1-2 cm to relatively large 10-12.5 x 4-4.5 cm. The amount of indumentum of the leaves varies with age, from place to place and from plant to plant from the same place. But the lower surface nearly always remains villous, particularly along the veins.

18. Terminalia actinophylla C. Martius, Flora 24, 2 Beibl.: 22 (1841).

Type: in Silvis Catingas in mediterraneae Prov. Bahiensis, Brazil, 1818 Martius s.n. (M, lectotype and isolectotype).

⊢ Chuncoa actinophylla (C. Martius) Griseb., Symb. fl. argent.: 133 (1879), based on T. actinophylla.

⊢ Myrobalanus actinophylla (C. Martius) Kuntze, Rev. Gen. 273 (1891), based on T. actinophylla.

Tree to 10 m high. Leaves spirally arranged, usually crowded; petiole very short, 2-5 mm long, moderate, usually eglandular, slightly pubescent or glabrous; lamina chartaceous or subcoriaceous, 2.5-10 x 1.4-4(6) cm, elliptic to narrowly obovate or obovate; apex subacute or obtuse to rounded; base cuneate; upper surface sparsely pubescent or glabrous and shiny, verruculose; lower surface usually rubiginous-pubescent, usually with tufts of hairs in the axil of the primary vein. Venation brochidodromous; secondary veins 5-7(9) pairs, weak with moderate angle of divergence (45^{o}-55^{o}), curved; intersecondary veins sometimes present; tertiary veins randomly reticulate or irregularly and weakly percurrent; higher orders of venation not very distinct; areolation imperfect. Inflorescence subcapitate; peduncle c. 2 cm long, minutely appressed rubiginous - tomentose; rachis 1.5-2 cm long minute appressed rubiginous - tomentose. Bracts very small, 0.5-0.8 mm long, appressed tomentellous. Flowers small, ca. 3 mm long; lower receptacel densely appressed rubiginous - pubescent or tomentose, 1-1.7 mm long; upper receptacle cupuliform, 1 x 2 mm, sparsely pubescent; calyx-lobes very short ca. 0.5 mm long; disk pilose; stamens short, 1 mm long, crimson; anther small, 0.2 mm long; style short, 1 mm long, glabrous. Fruit small, 0.4-0.6 x 1.3-1.5, transversely and narrowly oblong; body usually ovoid, 5 x 3 mm, slightly to densely pubescent, expanded laterally into 2 opaque pubescent or glabrous wings; wings 2, 5-6 x 6-7 mm, a third rudimentary wing occasionally present. Fig. 9/18 and Appendix 4 Pl. 9).

Geographical range: Eastern Brazil. (Map 9/4).

Ecology: A small to medium sized tree growing at medium or high altitudes. Flowers January.

Common name: "Cutinga de porco" or "Chapada".

Comments: Although Martius did not designate a type in his original description, in M there are three good specimens collected by Martius in 1818 and a poor specimen collected in 1819. The three specimens collected in 1818 are duplicates, but one of them is marked (as in the original description) "453 (1)". Therefore I have designated this as lectotype.

Terminalia actinophylla is a distinct species most closely resembling *T. fagifolia*, particularly with respect to the fruit shape.

The differences between the two species are as follows. The venation type in *T. actinophylla* is often brochidodromous or euchamptodromous - brochidodromous, whereas it is eucamptodromous or craspidodromous in

Fig. 9/18: T. actinophylla

T. fagifolia. The leaves in T. actinophylla are narrowly obovate or obovate with 5-7 pairs of curved and not raised secondary veins, while in T. fagifolia they are often elliptic with usually 7-12 pairs of straight and prominently raised secondary veins. The fruit of T. actinophylla is much smaller than that of T. fagifolia, and its wing width is about half of that in T. fagifolia.

19. Terminalia australis Cambess. in St. Hil., Fl. Bras. Mer. 2: 240 (1829). Type: Bord du ruisseau Toropaso, bords de l'Ibicui dans les missions, St. Hilaire 2591 (lectotype, P; isolectotype, P; lectoparatype, Ruisseau San Juan, St. Hilaire 2382, P)

⊢ Myrobalanus australis (Cambess.) Kuntze, Rev. Gen. 237 (1891).

Shrubs 2-5 m tall, leaves usually alternate, or spirally arranged and crowded at the end of shoots; petiole short 0.3-0 cm long, appressed pubescent or glabrous, eglandular; lamina thinly to thickly chartaceous, 3.5-6.5(10) x 0.8-2 cm, usually narrowly elliptic but sometimes elliptic or obancolate; apex acute or obtuse or mucronate rarely retuse; base cuneate to narrowly cuneate; upper surface appressed pubescent and verruculose; lower surface densely pubescent on veins but sparsely pubescent to glabrous elsewhere. Venation brochidodromous; secondary veins 4-7 pairs, fine, curved, not raised below; tertiary veins not conspicuous; higher-orders of venation not distinct; areolation imperfect or incomplete. Inflorescence capitate with 6-12 flowers; peduncle slender, 2-5.5 cm long, slightly pilose; rachis very short, 1-3 mm long. Bracts 2-3 mm long, pilose. Flowers up to 6 mm long, brownish-yellowish; lower receptacle 2-2.5 mm long, tubuliform, densely sericeous; upper receptacel 2-2.5 mm long, 4 mm across, infundibuliform, appressed pubescent; calyx-lobes 1 mm long, deltoid often reflected; disk 2-2.5 mm diam. pilose; stamen 3-4.5 mm long; anther 0.5 mm long; style 4-5.5 mm long, pubescent, exserted. Fruit small, 2-winged, always longer than broad, 1.5-2.8 x 0.8-2 cm,

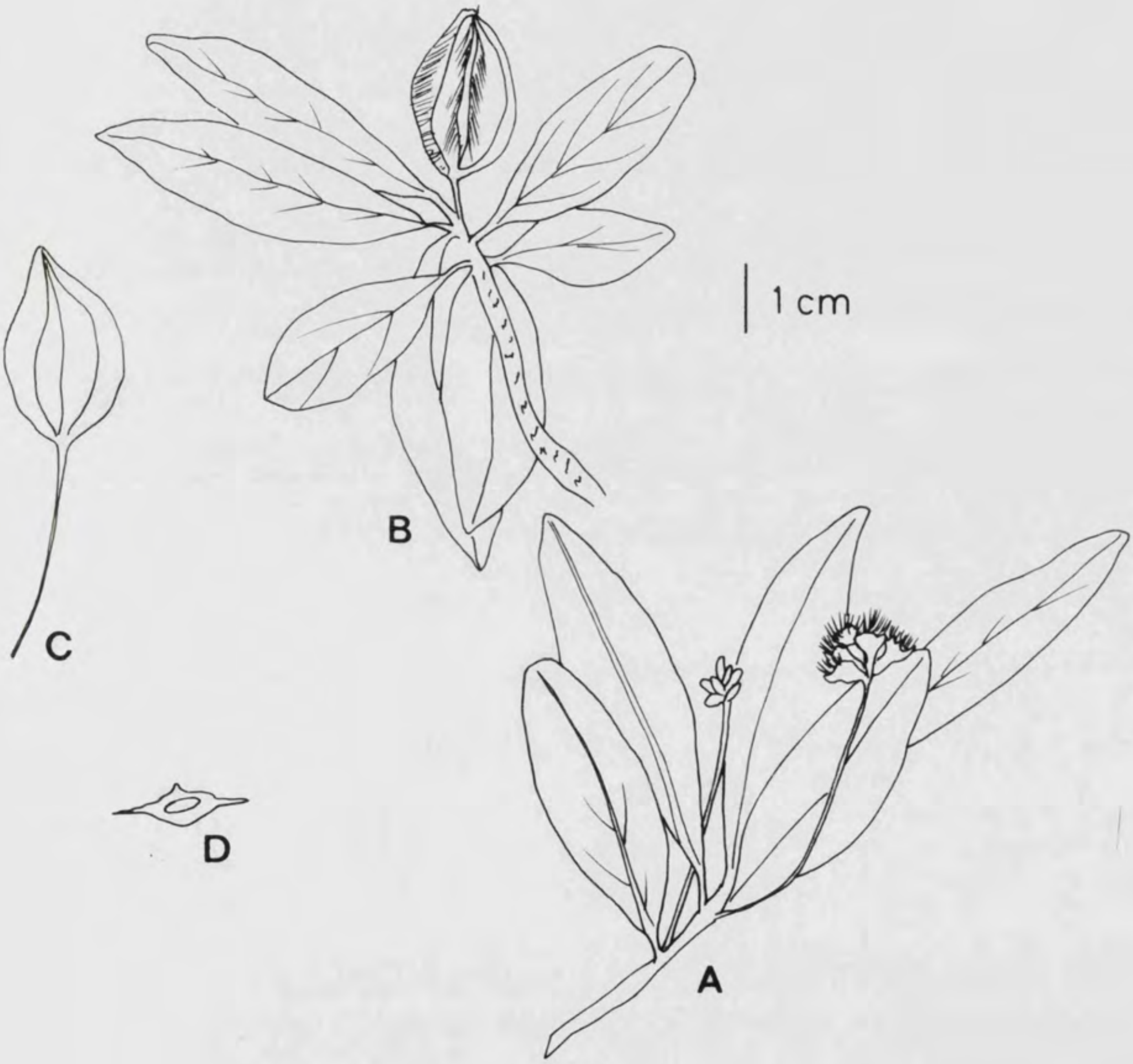


Fig. 9/19: T. australis. A. flowering shoot.

B. fruiting shoot. C fr. D. section of fruit.

pubescent or glabrous; body 0.6-1.1 cm wide; wing very narrow and stiff, up to 4 mm wide. (Fig. 9/19 and Appendix 4 Pl. 9).

Geographical range: Argentina, Uruguay, Brazil and Paraguay. (Map 9/4).

Ecology: Shrubs or small trees growing at 250-500 m altitude. Flowers September-November. Common in S. Brazil and N. E. Argentina, frequent in Uruguay and rare in Paraguay.

Common name: Sarandi in Brazil; Amarillo in Uruguay.

Comments: Terminalia australis was based on St. Hilaire 2382 & 2591 from Uruguay. In Paris those two specimens are mounted on three sheets, one bears the number 2382 with flowers and one bears the number 2591 with fruits, and the third is a mixture of both specimens having one branch in flower and one in fruit. The latter has the same number (1) and symbol (+) as in the original description. Although the first sheet (2382) is labelled as a type by Paris herbarium, I think the fruiting specimen on the mixed sheet is much better as lectotype because of the symbol of Cambessedes.

T. australis is closely related to T. triflora, although they were placed under different sections by Engler & Diels (1900) (see under T. triflora).

20. Terminalia triflora (Griseb.) Lillo, Contrib. Conc. Arb. Argent.: 20 (1910). Based on Chuncoa triflora Griseb., Abh. Königl. Gescll. Wiss. Gött. 14: 132 (1879). Type: Argentina, Oran, x 1873, Lorentz & Hieronymus (lectotype, GOET; isolectotypes, B (destroyed, photograph in F), BAF, BR, F, G, GOET, LE, P, PRC, S).

Myrobalanus balansae Kuntze, Rev. Gen. 3, 2: 87 (1898). Type: Paraguay "dans les bois" (Concepcion, according to the original description), 1877, Balansa 2233a (lectotype, P; isolectotypes, B (destroyed, Photo. in F), BM, G).

Terminalia balansae (Kuntze) A. Schum. in Just's Jahresber. 26, 7: 346 (1900).

Terminalia hassleriana Chodat, Bull. Berb. Boiss., sér.2, 3: 45 (1910), nom. illegit. Type: Cordillera de Altos, Aug. fr. Hassler 750a (lectotype, G; isolectotypes, NY, P).

Terminalia hassleriana Chodat var. bernardiensis Chodat loc. cit. In camp. near San Bernardino, Aug., Hassler 866 (holotype, G; isotypes K, P).

Terminalia balansae (Kuntze) Hassler, Feddes Repert. Nov. sp. 8: 45 (1910).

Terminalia balansae var. bernardinensis (Chodat) Hassler, loc. cit.

Terminalia paraguariensis Chodat, not published (written on various specimens of Hassler and Balansa in G & P).

Terminalia balansae var. glabrata Hassler, not published (written on Hassler 11830 (fl.) & 11830a (fr.) in G).

Shrubs or trees 4-20 m high. Leaves usually crowded at the end of branchlets or singly alternate; petiole short 1-9 mm long, slender, appressed pubescent or rarely glabrous, eglandular; lamina chartaceous, 2.5-4.5(7) x 1-2 cm, narrowly elliptic to broadly elliptic or oblanceolate; apex usually acute or sometimes obtuse or rounded; base narrowly cuneate to attenuate; upper surface appressed pubescent, usually verruculose; lower surface densely pubescent to nearly glabrous. Venation brochidodromous; secondary veins 4-7 pairs, fine, curved,not raised; tertiary and higher-order veins randomly reticulate, not conspicuous. Inflorescence capitate, with usually 3-5(6) flowers, often borne in clusters of 2-6 on short branchlets; peduncle short, 1-2 cm long, usually sericeous, occasionally nearly glabrous; rachis up to 6 mm, rather sericeous. Flowers up to 5.5 mm long, yellowish or brownish; lower receptacle 2-2.5 mm long, rhomboid to fusiform, sericeous; upper receptacle 1.5- 2 x 4 mm, cupuliform, appressed pubescent; calyx-lobes 1 mm long, deltoid, sometimes reflected; disk pilose, 1-1.4 mm diam; stamen 2-4 mm long, exserted, anther 0.5 mm; style 3-3.5(4) mm long, pubescent, exserted. Fruit transversely rhomboid or elliptic, or triangular, always broader than long, 0.6-1.7 x 1-2.6 cm, pubescent to glabrous; body small, elliptic 0.6-15. x 0.3-0.6 cm, usually flattened, sometimes with slightly raised ridges, thin, easy to cuty with penknife; wings transversely spread, 0.5-1.2 x 1 - 1.3 cm, thinly nerved, acute to rounded at margins. (Fig. 9/20 and Appendix 4 Pl. 10).

Geographical range: Argentina, Paraguay, Brasil, and Bolivia. (Map 9/5).

Ecology: Shrubs or small-medium-sized trees with trunks 15-30 cm diam. Growing in forest at medium to high altitudes (300-1700 m). Flowers August to October. Common in Argentina (in the north-eastern border between Brazil and Paraguay, and in the north-west in the Andes) and southern Paraguary; frequent in Brazil and rare in Bolivia.

Common name: Palo amarillo (in Argentina).

Comments: Chuncoa triflora was based on Lorentz 103, from Tucuman, Prope La Cruz, XII 1972, and Lorentz & Hieronymns 9, from Oran, near Oran, x 1873. The latter is designated here as lectotype because it is the better specimen in GOET.

Myrobalanus balansae comes within the range of the variation of Terminalia triflora, differing only in having slightly narrower leaves than usual.

Terminalia hassleriana was based on several specimens, including Balansa 2233a, the lectotype of M. balansae, so that the name T. hassleriana is illegitimate.

Terminalia triflora is very closely related to T. australis and the two are very difficult to distinguish without fruits. Their leaves are very similar in all features. The flowers are also similar in most features, except that the ovary is usually fusiform in T. triflora while it is often tubuliform in T. australis. Although the two species are distributed in the same geographical area, T. triflora can be easily separated from T. australis by the shape and texture of the fruits and wings which are always broader than long. Also the inflorescence in T. triflora is often shorter and with fewer flowers (up to 6).

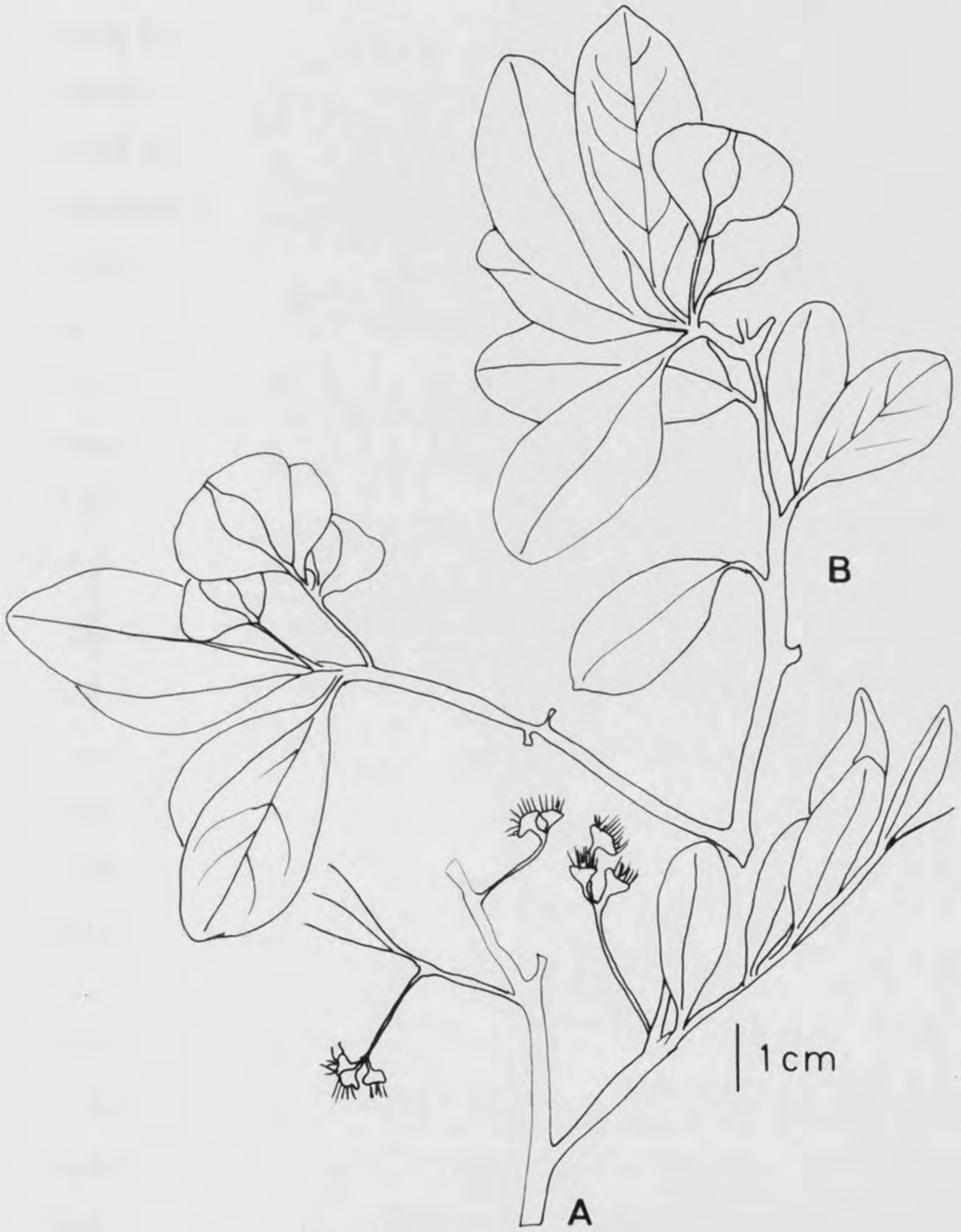


Fig. 9/20: T. triflora. A. flowering branch.
B. fruiting branch.

21. Terminalia uleana Engler ex Alwan, sp. nov.

Arbor? Folia alternata, non congesta; petiolus 1 cm longus, pubescens vel dense pubescens, eglandulosus; lamina subcoriacea, 5-12 x 2-5 cm, obovata vel anguste obovata, apice acuminata vel acuta, basi cuneata, supra pubescens vel glabrescens, subtus pubescens. Venatio eucamptodromo-brochidodroma; venae secondariae infra prominentes, 5-9 paribus; venae tertiariae fortuito reticulatae, conspicuae; areolae imperfectae. Flores ignoti. Fructus bialatus, transversali oblongus, 1.3-1.5 x (2.5) 3-4.5 cm, glaber; corpus ovato-ellipticum, 1.5 x 0.8 cm, protuberans vel parum cavinatum; alae latiores quam longae, 1.3-1.7 x 1.3-2 cm, deorsum curvatae. Type: Pr. St. Catharina, Baum um User des Capivary, Tubarão, Jan. 89, E. Ule 1004 (holotype, HBG; isotypes, B (destroyed, Photo F), P, US).

Leaves alternate, not crowded; petiole 1 cm long, pubescent to densely pubescent, eglandular; lamina subcoriaceous, 5-12 x 2-5 cm, obovate to narrowly obovate or obovate elliptic; apex acuminate or acute; base cuneate; upper surface pubescent to glabrescent; lower surface pubescent, densely tomentose in the axil of primary vein. Venation eucamptodromous brochidodromous; secondary veins 5-9 pairs, moderate, curved, widely spaced, raised beaneath, intersecondary veins common; tertiary veins randomly reticulate, conspicuous; quaternary veins conspicuous; areolation imperfect. Flowers unknown. Fruits large, 2-winged, 1.3-1.5 x (2.5) 3-4.5 cm, downwardly curved, glabrous; body obovate-elliptic, 1.5 x 0.8 cm, slightly bulged, and keeled from the middle on both surfaces; wings usually wider than long, 1.3-1.7 x 1.3-2 cm, often convex at apex and concave at base, obtuse at margin; a third rudimentary wing frequently present. (Plate 9/1.)

Geographical range: Brazil (Santa Catarina). (Map 9/5).

Comments: Engler wrote the name Uleana on the specimen at B (destroyed, photograph in F) but he did not publish it. It is also written on the

Specimen that it has affinity with Terminalia argentea. This species is closely related to T. triflora and T. reitzii. It has fruits similar to those in T. triflora and leaves somewhat similar to those in T. reitzii. However, it differs from T. triflora by having much wider leaves and fruits and from T. reitzii by having a different shape of fruit. The fruit of T. uleana has narrower wings which are always wider than long and often downwardly curved, while in T. reitzii the wings are always longer than wide and straight.

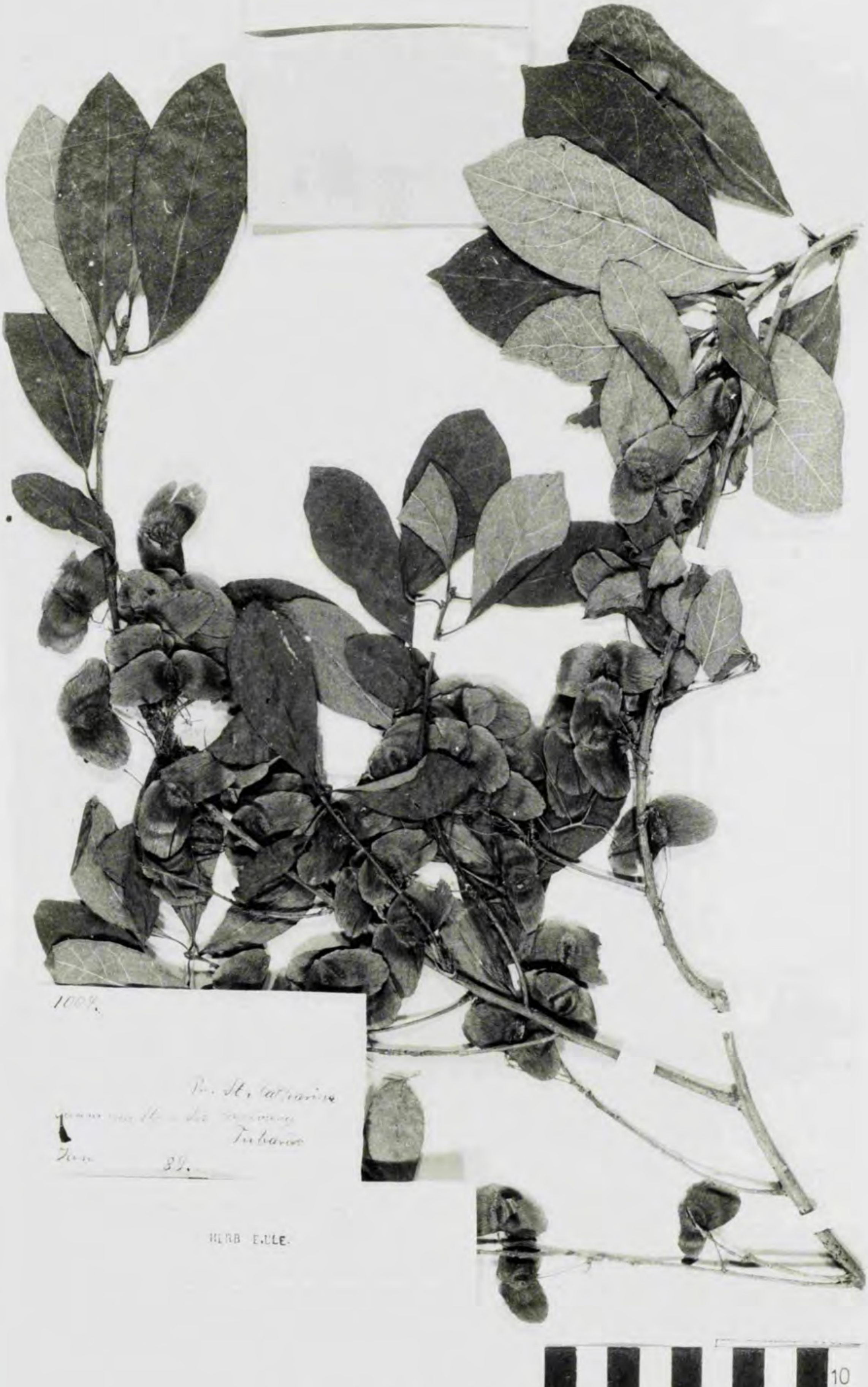


PLATE 2/1

Plate 9/1: <u>Terminalia</u> <u>uleana</u> (holotype, HBG)

22. Terminalia reitzii Exell, Sellowia 16: 191 (1964). Type: Brazil: Santa Catarina, Rio do Sul, Sevra do Matador, 21.11.1962 (fr.), Reiz & Klein 12194 (holotype, BM; isotypes, BM, NY).

Tree 12-15 m high. Leaves alternate or spirally arranged, not crowded; petiole 5-12 mm long, pubescent or glabrous; lamina thickly chartaceous, 3.5-10 x 1.5-7.5(4), elliptic or obovate-elliptic; apex acute - acuminate, base narrowly cuneate; upper surface verruculose, glabrous; lower surface pubescent on primary vein, sparsely pubescent or glabrescent elsewhere. Vendtion brochidodromous or eucamptodromous - brochidodromous; secondary veins 5-8 pairs slightly raised below; tertiary veins randomly reticulate, conspicuous; higher order veins distinct; areolation imperfect. Inflorescence short, subcapitate, with few flowers; peduncle short, 1-2 cm long, pubescent; rachis 4-10(15) mm long pubescent or sericeous. Flowers small, similar to T. triflora; lower receptacle 1.5-2 mm long, fusiform, densely sericeous; upper receptacle 2 x 3 mm, campanulate, pubescent, calyx-lobes 0.5-0.7 mm long deltoid; disk densely pilose; stamen 3-3.5 mm long; anther 0.4-0.5 mm long; style 4 mm long, hairy. Fruits 2-winged, transversely oblong, 1.3-2.5 x 2-4 cm, slightly pubescent; body small and thin, 1-2 x 0.3-0.7 cm; wings 1.5-2.5 x 0.8-1.7 cm, rounded at margins, straight at apex and base. (Fig. 9/21 and Appendix 4 Pl. 11).

Geographical range: Brazil (S. Catarina). (Map 9/5).

Comments: T. reitzii is very similar to T. triflora. However, it differs in having slightly larger leaves and larger fruits with longer wings.

23. Terminalia amazonia (J. Gmel.) Exell in Pulle, Fl. Surinam 3: 173 (1935). Based on Chuncoa amazonia J. Gmel. in L., Syst. Nat. ed. 13, 2: 702 (1791). Type: "Chunco du Margnon" from Peru (according to the original description of the genus), not seen.

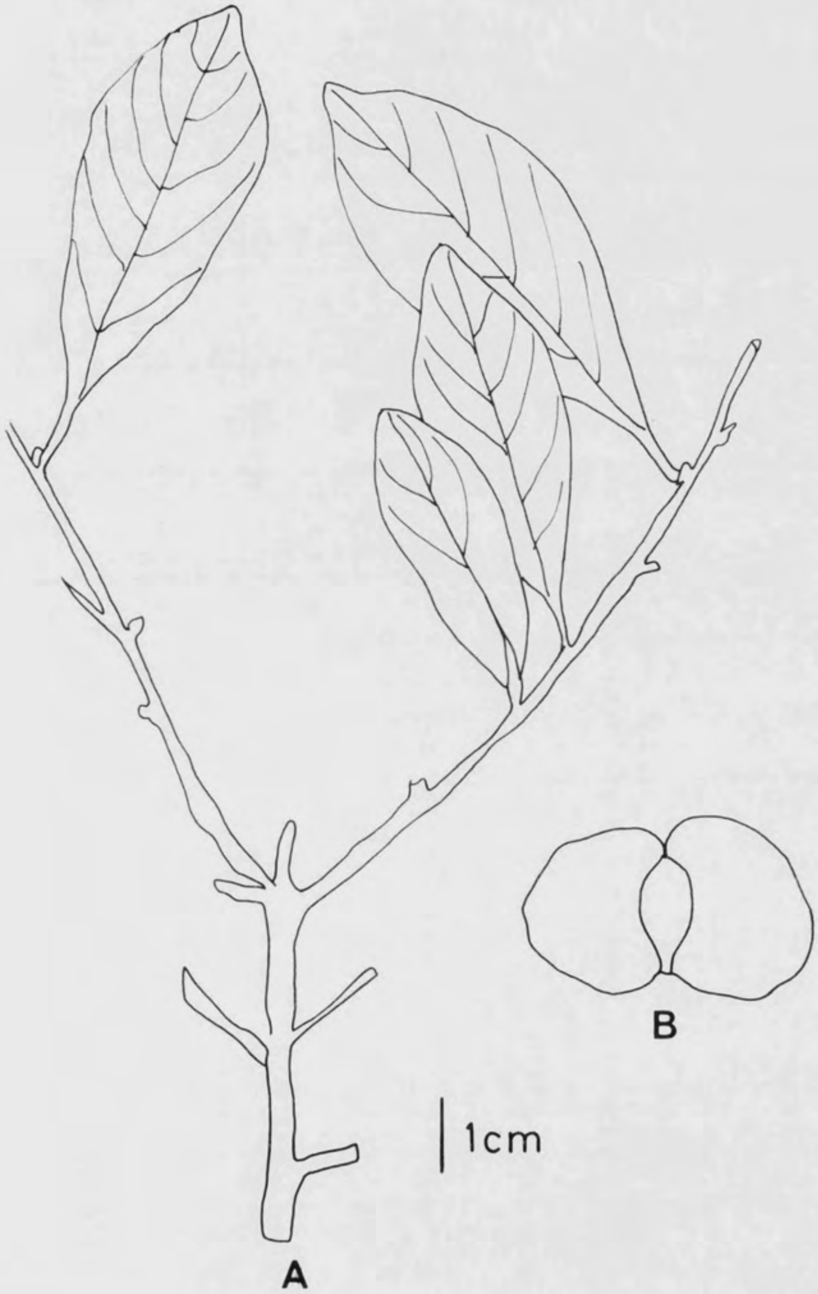


Fig. 9/21: T. reitzii. A branch. B. fruit.

<u>Gimbernatea</u> <u>obovata</u> Ruíz Lopez & Pavón, Fl. Peruv. Prodr:138 (1974).
Type: Peru, Ruíz & Pavón (holotype, MA, not seen; isotype, F, fragments).

<u>Chuncoa</u> <u>obovata</u> (Ruíz Lopez & Pavón) Pers., Syn. 1: 486 (1805).

<u>Chuncoa</u> <u>obovata</u> (Ruíz Lopez & Pavón) Poiret, Encyc. Meth., Suppl. 2: 258 (1811).

<u>Terminalia</u> <u>obovata</u> (Ruíz Lopez & Pavón) Steudel, Nomencl. Bot., ed. 2, 2: 668 (1841), not of Cambess. in St. Hil, Fl. Bras. Merid. 2: 241 (1829).

<u>Terminalia</u> <u>odontoptera</u> Van Heurck & Muell. Arg. in Van Heurck, Obs. Bot: 217 (1870). Type: Cayenne, Patris, Müller (G, holotype).

<u>Terminalia</u> <u>excelsa</u> Liebm. ex Hemsley, Biol. Centr. Amer. Bot. 1: 402 (1880), nomen nudum. Type: Marada, S. Mexico, Liebmann (K, holotype).

<u>Myrobalanus</u> <u>obovata</u> (Ruíz Lopez & Pavón) Kuntze, Rev. Gen. 273 (1891).

<u>Myrobalanus</u> <u>excelsa</u> (Liebm. ex Hemsley) Kuntze, Rev. Gen. 237 (1891).

<u>Bucida</u> <u>angustifolia</u> DC. Prodr. 3: 10 (1828). Type Guiana, Perrottet (G).

<u>Bucida</u> <u>buceras</u> var. <u>angustifolia</u> (DC.) Eichler in C. Martius, Fl. Bras. 14, 2 : 95 (1867).

Tree (4) 10-60 m high. Leaves spirally arranged in pseudo verticels at the ends of the branchlets; petiole short, 2-15 mm long, rufous pubescent or glabrescent, eglandular; lamina chartaceous or subcoriaceous, (2) 4-10 (15) x 2-5 (6.5) cm usually obovate occasionally obovate oblong or narrowly obovate; apex usually abruptly acuminate or sometimes obtuse - rectuse; base cuneate to narrowly cuneate; upper surface sparsely pubescent or glabrous; lower surface, appressed pubescent or appresssed pilose or nearly glabrous except on primary vein. Venation eucamptodromous; secondary veins 3-5 pairs, moderate, usually abruptly curved, moderately spaced; tertiary veins percurrent, often perpendicular to the primary vein;

higher-order veins occasionally distinct; areolation imperfect or incomplete. Inflorescence terminal, long, often in clusters of 3-8; peduncle 1-3 cm long, sericeous; rachis 4-15 cm long, sericeous. Bracts 1 mm long, deltoid, pilose. Flowers 2-4 mm long; lower receptacle 1-2 mm long, sericeous; upper receptacle c. 1 mm long, cupuliform, appressed pubescent, calyx-lobe 0.3-0.7 mm long, deltoid; disk pilose; stamen 2-3.5 mm long, anther 0.4 mm long; style 3 mm long. Fruit small, 5-7(10) x 8-18(22) mm, papyraceous, not lignified, broader than long; wings 5, of which 2 are larger than the others and transversely spread to 5-10 mm; the other three rudimentary up to 2 mm wide; body small and thin 5-6 x 2-3.5 mm, usually sparsely pubescent. (Plate 9/2).

Geographical range: From Mexico throughout Central America to Venezuela, Trinidad, Guiana, Brazil, Colombia, Equador, Peru and Bolivia. (Map 9/6).

Ecology: A medium to large sized tree sometimes reaching 70 m high, with cylindrical trunk (often inclined) up to 100 cm diam. and large buttresses up to 1.5 m high. Bark yellowish-brown or brown with yellor or pink slash, finely and shallowly fissured, peeling off in flakes. Growing in primary forest on sandy soil or on steep forested slope of crumbling metamorphic rocks or along rocky ridges of hills with low deciduous trees, or along streams, at altitude 50-1200 m. Flowers March to April. Very common in Central and South America.

Common name: In Venezuela Guire, Guacharaco, Mezela, Pardillo negro, Copito de Cerro, Pada de donta blanco; in Cayenne Approuague; in Peru Rifari negro; in Belize Nargusta; in Honduras Membrillo and Almendro.

Uses: The wood is said to be very hard and good quality and used for house construction and railroad ties. In Venezuela it is said that ash from burned bark is used as an alkali source to mix with Yopo (Adenothera pepegrina) to make a hallucinogen.

Comments: *T. amazonia* is a very distinct species. Its closest relationship is with *T. glabrescens* but it also has some similarities with *T. oblonga*.

Plate 9/2: Terminalia amazonia


10
cm
4062
Combretum
Rio Jarí, Monte Dourado, Planalto, monte alto, terra firme.
Árvore de 20-22m, flôr clara.
1.2.968

PLATE 9/2

24. Terminalia glabrescens C. Martius, Flora 20, 2 Beibl.: 124 (1837). Type: Serra da Broca Prov. Sebastianopol Brazil, July-Aug. 1833, Luschnath (holotype, BR; isotypes LE, M, P).

Chuncoa brasiliensis Cambess in A. St. Hil., Fl. Bras. Merid. 2: 244 (1829). Type: Fazenda do negro in Certáo, Brazil, Minas Gerais, St. Hilaire 1816-1821, Cat. B', N, 1951(lectotype, P; lectoparatype, P).

Terminalia brasiliensis (Cambess.) Eichler in C. Martius, Fl. Bras. 14, 2: 91 (1867), nom. illegit, not of Sprengel, Syst. 2: 359 (1825), nor of Raddi ex Steudel, Nom., ed. 2, 2: 668 (1841).

Chuncoa flavescens Presl, Epim. Bot. 215 (1849). Type: Brasilia, Luschnath (PRC, holotype).

Myrobalanus cambessedesii Kuntze, Rev. Gen. 237 (1891).

Myrobalanus glabrescens (C. Martius) Kuntze, loc. cit.

Terminalia excelsa Glaziou, Mem Soc. Bot. France 1,3: 203 (1908), nom. nud. non of Liemb. ex Hemsley, Biol. Centr. Amer. Bot. 1: 402 (1880). Type: Brasil, Minas, Biribiry, Glaziou 19145 (C).

Tree 3-30 m high. Leaves spirally arranged, crowded at the end of the branchlets; petiole 5-15 mm long, rufous tomentose, biglandular; lamina subcoriaceous to coriaceous, 3.5-16 x 1.5-7 cm, oblong obovate or narrowly obovate or oblanceolate or obovate; apex obtuse or retuse or shortly acuminate; base narrowly cuneate or attenuate; upper surface rubiginous tomentose or glabrescent on primary and secondary veins, sparsely pubescent to glabrous elsewhere; lower surface rufous tomentose to pubescent over the whole of the surface rather dense on primary and secondary veins but tomentum wearing off after fruit-fall. Venation eucamptodromous; secondary veins 5-8 pairs, moderate, gradually curved, moderately to narrowly spaced, often slightly raised beneath, usually densely rufous tomentose; tertiary veins percurrent, perpendicular to the midvein; higher-order veins usually distinct but not prominent; areolation imperfect. Inflorescence as in T. amazonia; peduncle 1-1.5 cm

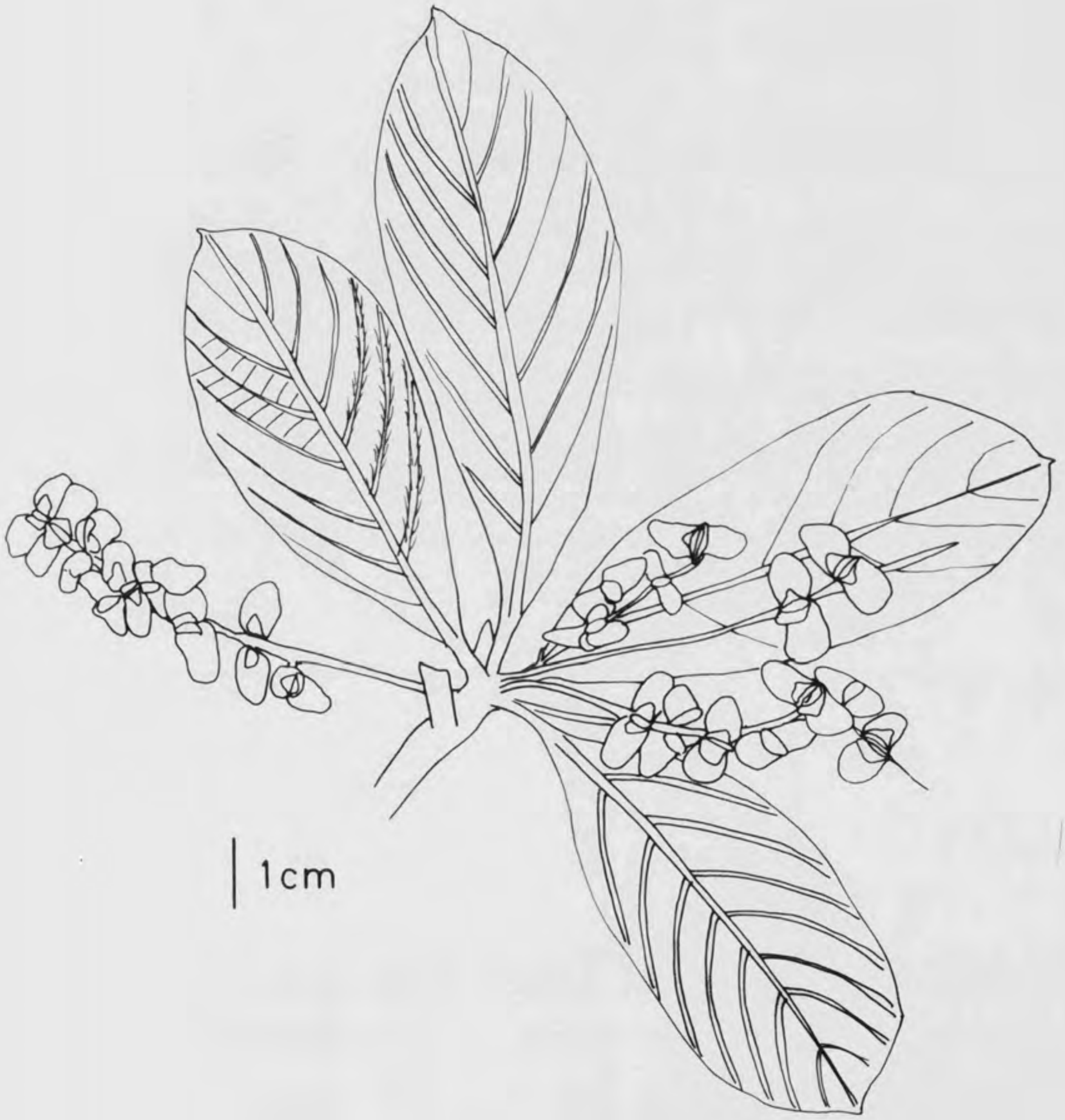


Fig. 9/22: T. glabrescens

long, rufous tomentose; rachis 4.5-10 cm long, rufous tementose. Flowers small, 2.5-3.5 mm long, brownish red, lower receptacle1.5-2 mm long, densely tomentose; upper receptacle 1-1.5 mm long, tomentose or pubescent; calyx-lobe c. 0.5 mm long, deltoid; disk pilose; stamen 3.5-5 mm long; anther 0.5 mm long; style 3-3.5 mm long, glabrous. Fruit as in T. amazonia, 4-6 x 10-22 mm, brown or yellowish-brown; lateral wings 4-7 x 5-9 mm, rudimentary wings 1-3 mm wide; body very small 2-3 mm wide, densely to sparsely pubescent. (Fig. 9/22 and Appendix 4 Pls. 11 & 12).

Geographical range: Brazil and Paraguay. (Map 9/6).

Ecology: Shrub or small to large tree with trunk 4-35 cm diam, growing in gallery forest or forest margins at (50) 700-1000 m altitude. Flowers June-August. Very common in Brazil, particularly eastern and central states; rare in Bolivia.

Common name: Miringiba da Mata, Maria Preta, Garrote.

Comments: Terminalia glabrescens is a variable species showing considerable range in the size and shape of the leaves and in the amount of indumentum on the leaves. It is very closely related to T. amazonia. The inflorescence, flowers and fruits are very similar in both species. But T. glabrescens differs in the shape and size of the leaves, number of secondary veins and amount of indumentum on the veins. However, it is sometimes hardly separable from T. amazonia in the areas of overlapping range (Pará, Maranhao, Piaui).

25. Terminalia quintalata Maguire, Bull. Torr. Bot. Club 25: 649 (1948).

Type: Potaro River Gorge, below Amatuk Portage, British Guiana, May 19, 1944, Maguire & Fanshawe 23551 (holotype, NY; isotypes, BM, BR, F, FDG, G, K, MO, P, U, US) (paratypes (Kaieteur Plateau 23459) A + GH, BM, K, P, U).

Tree 5-25 m high. Leaves spirally arranged, crowded at or near the ends of the shoots. Petioles short 3-15 mm long, often winged, glabrous

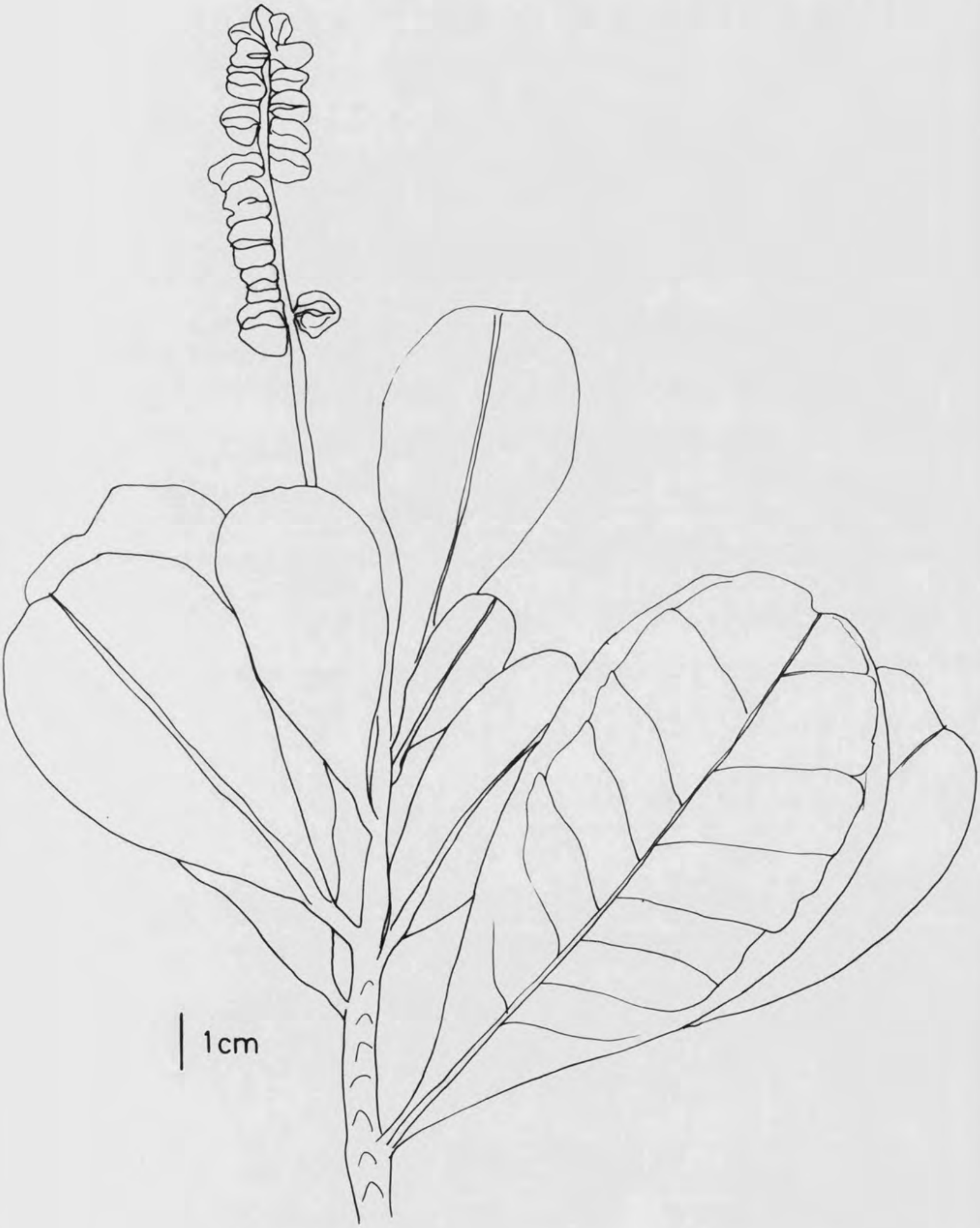


Fig. 9/23: T. quintalata

or pubescent; lamina thickly coriaceous, 4-18.5 x (2.5) 4-11.5 cm, oblong obovate, or narrowly obovate or obovate; apex rounded or obtuse or retuse; base decurrent to the petiole; upper surface glabrous and shiny; lower surface glabrous or slightly pubescent particularly on the primary vein. Venation weakly brochidodromous; secondary veins 7-15 pairs, fine or weak; tertiary veins, randomly reticulate, not conspicuous. Inflorescence axillary, long; peduncle 4-7.5 cm long, puberulent or glabrous; rachis 5-10 (12) cm long, slightly and minutely pubescent. Bracts up to 5 mm long. Flowers medium-large, to 10 mm long; lower receptacle 3-5 mm long, densely villous or glabrescent or glabrous; upper receptacle 1-2 mm long, usually glabrous; calyx-lobes 1-1.5 mm long; disk densely villous; stamen 3-5 mm long, exserted; style glabrous, 4-6 mm long. Fruit small, with five equal wings, (6) 8-12 (15) x 5-10 (12), usually slightly longer than broad; wings narrow, thin, 2-4(6) mm wide. (Fig. 9/23 and Appendix 4 Pl 12).

Geographical range: Guyana and Venezuela. (Map 9/7).

Ecology: Small to mediumsized tree with slender trunk 20-45 cm diameter, growing at 400-1450 m altitude. Flowers January-February, May and September-October.

Common name: Fukadi (in Guyana) and Vonta-Yek (in Venezuela).

Comments: T. quintala shows considerable variation in the size of the leaves and the amount of indumentum on the ovary.

26. Terminalia yapacana Maguire, Mem. N. Y. Bot. Gard. 8: 132 (1953).

Type: Tree 8 m high, fruit brownish-red, dominant savanna and marginal tree. Yapacana savanna III, Cerro Yapacana, Rio Orinoco, Amazonas, January 1, 1951, Maguire, Cowan & Wurdack 30590 (holotype, NY; isotypes BM, US, VEN).

Shrubs or bushy trees or small trees 0.5-12 m high. Leaves spirally arranged, crowded at the ends of the branchlets; petiole very short, 1.5 mm long, sometimes winged, usually glabrous; lamina coriaceous or thickly coriaceous, 3-10 x 1.5-4.5 cm, narrowly obovate, obalnceolate or oblong oblanceolate or obovate to elliptic-obovate; apex rounded or obtuse or retuse; base narrowly to broadly cuneate or decurrent to the petiole; upper surface glabrous; lower surface often glabrous but sometimes slightly puberulent on the midvein. Venation weakly brochidodromous; secondary veins fine or weak not conspicuous; tertiary veins hardly visible. Inflorescence axillary, often medium; peduncle to 5 cm long at flowering becomes longer at fruiting, glabrous or puberulent; rachis up to 5 cm long, pubescent or glabrescent. Bracts 3 mm long. Flowers medium, 4-5 mm long, white or yellowish-white; lower receptacle 2 mm long densely tomentose, upper receptacle 2 mm long, sparsely pubescent; calyx-lobes 0.7-1 mm long; disk villous; stamen 3-5 mm long; style glabrous 2-5 mm long. Fruit small, 3-8 x 2-9 mm, rounded or slightly broader than long but sometimes very slightly longer than broad, with 5 equal wings; wings, thin, small, 1-4 mm wide. Fig. 9/24 and Appendix 4 Pl. 12).

Geographical range: Venezuela. (Map 9/7).

Ecology: A shrub or small tree growing on the savannas about Cerro Yapacana on river banks in humid areas at 100-150 m altitude. Flowers February-March and June-August.

Comments: *Terminalia yapacana* is very similar to *T. quintalata* in general characters and habitat. It differs only in having smaller and narrower leaves, an often shorter rachis and slightly smaller fruit. Because *T. yapacanna* is often a shrub or bushy tree and restricted to an area on the western edge of the Guayana Highland, whereas *T. quintala* is usually a larger tree and occurs on the easternmost escarpment of the Guayana Highland, and because of the difference in the leaf anatomy of the two species, I prefer to maintain the two species spearate despite the occurrence of some intermediates.

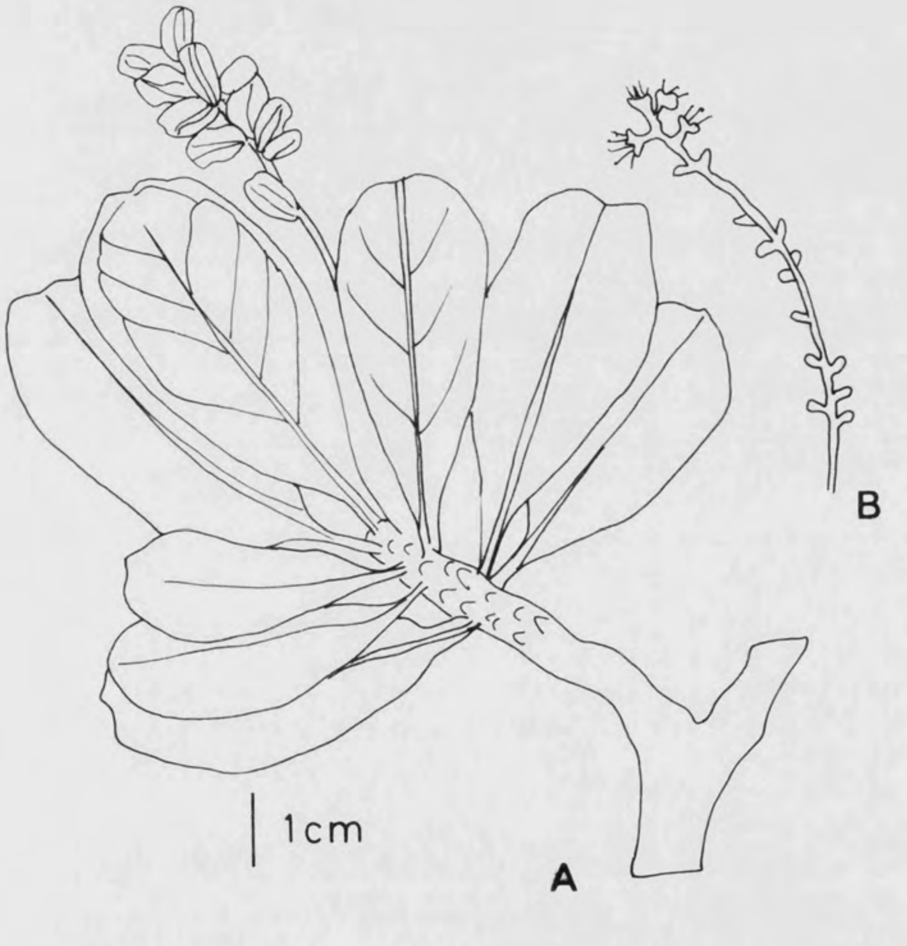


Fig. 9/24: T. yapacana.

A. fruiting shoot. B. inflorescence.

27. Terminalia guaiquinimae Maguire & Exell, Mem. N. Y. Bot. Gard. 10 (1): 93 (1958). Type: virgate slender tree 5-12 m high, ridges and rocky places below Southeast Escarpment, 1600-1700 m altitude, requent, Cerro Guaiquinima. Edo Bolivar, Venezuela, January 7, 1952, Maguire 33008 (holotype, NY; isotypes BM, VEN).

Terminalia virgata Maguire & Exell op. cit.: 92 (1958). Type: slender virgate flexuous tree 6-10 m high, leaves thickly coriaceous and brittle, ridge near Southeast escarpment at 1700 m altitude; Cerro Guaiquinima, Edo Bolivar, Venezuela, January 7, 1952, Maguire 33000 (holotype, NY; isotypes, BM, US, VEN).

Terminalia opacifolia Maguire & Exell op. cit.: 93 (1958). Type: spindly tree 5-15 m high, 5-8 cm diam., frequent, dense scrubbish (1-2 m high), savanna and ridges, at 1650 m altitude, North Valley, Cerro Guaiquinima, Edo Bolivar, Venezuela, Maguire 32951 (holotype, NY; isotypes, BM, S, US, VEN).

Tree 5-15 m high. Leaves spirally arranged or alternate; petiole very short 2-5 mm long, pilose or villous; lamina thickly coriaceous, 3.5-9.5 x 2.5-4(6), oblong or elliptic-obovate or elliptic-oblong; apex obtuse to rounded or retuse; base obtuse to rounded or slightly subcordate; margin often revolute; upper surface slightly pubescent on the primary vein, glabrous elsewhere at maturity; lower surface densely pubescent to glabrescent on the midrib (but rather tomentose or villous towards the base when young) sparsely pubescent or glabrous elsewhere when mature. Venation weakly brochidodromous, midvein flattened, not very conspicuous near the apex; secondary veins very weak, not visible; tertiary veins and higher-order venation often not visible but sometimes conspicuous on upper surface. Inflorescence axillary, subcapitate or slightly elongate; peduncle 3-6.5 cm long, pubescent or glabrous; rachis 0.5-1.5 cm, pubescent or glabrous. Bracts 3-6 mm long. Flowers 5-7 mm long, usually tetramerous; lower receptacle 1.5-3.3. mm long, villous glabrescent or glabrous; upper receptacle 2-3 mm long densely to sparsely pubescent or glabrous; calyx-lobes 4 or 5, deltoid, 0;0.5 mm long; disk villous; stamen 8, 3-5 mm long; style glabrous or nearly so, 3-5 mm long. Fruit immature small, with 4 or 5 equal and thin wings, aggregated at the ends of the peduncle. (Appendix 4 Pls. 12 & 13).

Geographical range: Venezuela. (Map 9/7).

Ecology: Small tree with slender flexuous virgate trunks, 5-8 cm diam., growing on rocky places at high altitude about 1600-1700 m. Flowers January.

Comments: *T. guaiquinima*, *T. virgata* and *T. opacifolia* were described at the same time and their type materials were collected from the same locality (Cerro Guaiquinima). The name *T. guaiquinimae* is maintained because it refers to the locality and its type specimen (holotype) consists of 2 shoots, one with flowers and one with young fruits.

T. virgata differs from *T. guaiquinimae* only in the denser indumentum on the branchlets and young leaves. *T. opacifolia* differs from *T. guaiquinimae* only on minor features of the flowers. I carefully examined all the type materials and found that *T. virgata* and *T. opacifolia* are conspecific with *T. guaiquinimae*.

One of the isotypes of *T. guaiquinimae* at VEN has branchlets and leaves with indumentum similar to that in *T. virgata*, whereas the other isotype has flowers similar to those in *T. virgata*.

Terminalia guaiquinimae, as in many other species of *Terminalia* (e.g. *T. quintalata* and *T. chicharronia*), shows variation in the amount of indumentum on the branchlets, leaves and flowers.

28. *Terminalia steyermarkii* Alwan, sp. nov.

Frutex 0.5-1 m altus, ramulis dense villosis. Folia spiraliter ordinata and ramulorum apices congesta; petiolus c. 5-10 mm longus, dense sericeus; lamina coriacea, obovata vel elliptico - obovata, 5-11 x 3-6.5 cm, apice retusa, basi cuneata-obtusa in petiolum decurrente, supra pubescens, subtus holosericeo-argentea. Inflorescentiae axillares, spicatae; pedunculus 4-5 cm longus, dense pubescens; rachis 4 cm longa, dense tomentosa. Flores 4 vel 5 meri; receptaculum inferum 3.5 mm longum, dense villosum; receptaculum superum 2 x 4 mm, dense pubescens; calycis lobi 5 vel 4, 1.5 mm longi; stamina 8 vel 10, exserta ad 4-5 mm; stylus 5-6 mm longus, pilosus. Fructus ignotus.

Type: Dwarf woody plant with branches spreading from near ground, only 0.5-1 m tall; flowers creamy-buff; leaves crowded at tip of branch, coriaceous, dull green above, gray-sericeous below, the apical youngest leaves buff-silvery sericeous; filaments greenish-white; ovary and calyx gray green; perianth pale green. Cumbre de cerro Guaiquinima, sector nororiental, entre las brazos nororiental del rio Carapo, en una meseta arenosa pedregosa y cuberta con vegetacion muy esparcida. lat. 5° 54' N., long. 63° 25' W. at 950 m altitude, Estado Bolivar, Venezuela, 30 de Mayo de 1978, Steyermark 117521, Paúl Berry, G. C. K. Y. Dunsterville (LTR, holotype; isotype, VEN,not seen).

Shrub 0.5-1 m high. Leaves spirally arranged, crowded at the ends of the branchlets; petiole short 5-10 mm long, silvery sericeous; lamina coriaceous, (3)5-11 x 3-6.5 cm, obovate or obovate-elliptic; apex obtuse to rounded or retuse; base broadly cuneate, usually decurrent to the petiole; upper surface densely to slightly pubescnet; lower surface silvery sericeous. Domatia absent. Venation weakly brochidodromous; secondary veins 7-9 pairs, weak; tertiary and higher-order veins not distinct from each other. Inflorescence axillary, slightly elongate; peduncle 4-5 cm long, densely pubescent; rachis 4 cm long, densely tomentose. Bracts 4 mm long. Flowers medium; lower receptacle 3.5 mm long, villous; upper receptace 2 x 4 mm, densely pubescent; calyx-lobes 4 or 5, 1.5 mm long; disk pilose, stamen 8 or 10, 4-5 mm long; style pilose up to the middle, 5-6 mm long. Fruit unknown. (Plate 9/3).

Plate 9/3: Terminalia steyermarkii (holotype, LTR)


10
cm
MINISTERIO DEL AMBIENTE Y LOS RECURSOS
NATURALES RENOVABLES
HERBARIO NACIONAL DE VENEZUELA
No. 117521
Terminalia steyermarkii sp. nov.
A. A. Alwan & C. A. Stace 1981
expedición patrocinada por OCCIDESA

PLATE 9/3

Geographical range; Venezuela (Map 9/7).

Comments: T. steyermarkii is closely related to T. guaiquinimae and T. ramatuella but it differs from the former in the very densely gray to silvery-sericeous leaves and in the shape and arrangement of the leaves; and from the latter in the shape and texture of the leaves and in its longer rachis. Its cuticular characters are intermediate between those of sections Pachyphyllum and Ramatuella.

29. Terminalia ramatuella Alwan, nom. nov.

Ramatuella argentea Kunth, Nov. Gen. & Sp. Pl. 7: 254, t. 656 (1825).

Type: Rio Atabapo, Humboldt & Bonpland (P, holotype, not seen).

Shrub or small tree 5-10 m high. Leaves spirally arranged, rarely alternate; petiole 5-16 mm long, appressed puberulous, usua lly eglandular; lamina coriaceous, 2-10 x 1-4 cm long, oblancolate to narrowly obovate; apex retuse to rounded, occasionally obtuse to very shortly abruptly acuminate; base narrowly cuneate and slightly decurrent into the petiole; upper surface nearly glabrous except slightly puberulous on the primary vein; lower surface densely silvery-sericeous; primary vein slightly raised below; secondaries and other veins not conspicuous. Inflorescence capitate - subcapitate; peduncle 2-3 cm long appressed puberulous; rachis very short, 2-8 mm long. Bracts 2 mm long. Flowers tetramerous; male and bisexual flowers borne on the same inflorescence or on different inflorescence; lower receptacle 3 mm long, densely pilose; upper receptacle 1-1.5 mm long pubescent; calyx-lobes 1 mm long, triangular; disk villous; stamen 3 mm long; anther 0.5 mm long; style 3 mm long, sparsely hairy at base. Fruit 4-5-winged, 8-12 x 8-13 mm, densely silvery sericeous, shortly (2-4 mm) beaked, pseudostipitate; pseudotype 2-3 m long, abruptly delimited from upper regions; wings -15 x 3-6 mm, with sharply or bluntly pointed margins, not undulate. (Fig. 9/25).

Fig. 9/25. T. ramatuella

Geographical range: Venezuela, Colombia and Brazil. (Map 9/5).

Ecology: Evergreen shrub or small tree of riverine forest, frequent in savannas on sandy soil at low altitudes (about 150 m). Flowers February-April and November.

Comments: This species differs from the other two species of section *Ramatuella* in its densely silvery-sericeous lower surface of the leaves. The epithet *argentea* is already taken up in *Terminalia*, so I have used the old generic name as the new specific epithet.

30. *Terminalia virens* (Spruce ex Eichler) Alwan, Comb., nov.

Ramatuella virens Spruce ex Eichler in Mart., Fl. Brasil, 14, 2: 100, t. 26, fig. 2 (1867). Type: Rio Guainia, above its confluence with Rio Casiquiare, Nov. 1854, Spruce 3758 (lectotype, W; isolectotypes, BM, GOET, K, LE).

Ramatuella latifolia Maguire, Mem. N.Y. Bot. Gard. 8: 131 (1953). Type: Venezuela, Amazonas, 15 km above San Fernando, Rio Atabapo, 125 m, small tree to 10 m high, post fruiting. Occasional on sandy banks of flood Caatinga, 17/10/1950, Maguire 29258 (holotype, NY; isotype VEN).

Ramatuella maguirei Exell & Stace, Bull. Brit. Mus. Nat. Hist. (Bot.) 3,1: 41 (1963). Type: Venezuela: Amazonas. Alto Rio Orinoco, Cano Yapacana from laguna to mouth, 125 m, tree 20 m high, occasional waterside, 17 March 1953, Maguire & Wurdack 34606 (holotype, BM, isotypes, S, VEN).

Shrub or small tree 2-20 m high. Leaves spirally arranged or alternate; petiole (1)4-30 mm long, sparsely puberulous, or glabrous, usually slightly winged and biglandular; lamina coriaceous or thickly coriaceous, 2-15 x 1-7 cm, oblanceolate to obovate or elliptic obovate or elliptic-oblong or oblong; apex retuse to rounded or obtuse or rarely very shortly acuminate; base cuneate, usually slightly decurrent into the petiole; upper surface glabrous and usually shiny; lower surface glabrous but sparsely puberulous on the primary vein; primary vein slightly raised below; secondary veins not very conspicuous; tertiary and higher-order veins often not conspicuous. Inflorescence capitate to subcapitate or slightly elongate, andromonecious sometimes with male and bisexual flowers on separate inflorescences, peduncle 1-4(5) cm long, pubescent to sparsely puberulous; rachis to 4.4 cm long. Bracts 4-5 mm long acuminate. Flowers tetramerous; lower receptacle 3-7 mm long, densely appressed pubescent or tomentose; upper receptac 2-3 mm long, sparsely pubescent; calyx-lobes 0.5-1.5 mm long; disk villous; stamen 8(10), 3-5 mm long; style 4-6 mm long very sparsely pilose at base. Fruit 4(5)-winged, 17-18 x 6-11, ovate or lanceolate in outline, usually beaked (up to 4 mm long), occasionally with short pseudostipe to 2 mm long; wings long and rather narrow, 8-15 x 2-6, with conspicuously but minutely sinuate margin. Fig. 9/26 and Appendix 4 Pl. 3).

Geographical range: Venezuela, Colombia and Brazil. (Map 9/6).

Ecology: As in *T. ramatuella.*

Comments: This species shows great variation in the shape and size of the leaves and fruits. *R. latifolia* and *R. maguirei* both come within the variation of *T. virens*.

31. *Terminalia crispialata* (Ducke) Alwan, comb. nov.

Ramatuella crispialata Ducke, Arch. Inst. Biol. Veg. Rio Janeiro 2: 65 (1935). Type: Caatinga ad Igarapē Juraxare aff. Rio Vaupēs, 2 Nov. 1932, Ducke 25024 (holotype MG, not seen; isotype K).

Ramatuella crispialata var. *obtusa* Maguire, Mem. N.Y. Bot. Gard. 8: 131 (1953). Type: Venezuela: cerro Yapacana, Rio Orinoco, tree to 7 mm high, fruit brown, occasional in Caatanga about Yapacana Savanana 1. 7 Jan. 1951, Maguire, Cawan & Wurdack 30796 (holotype, NY; isotype VEN).

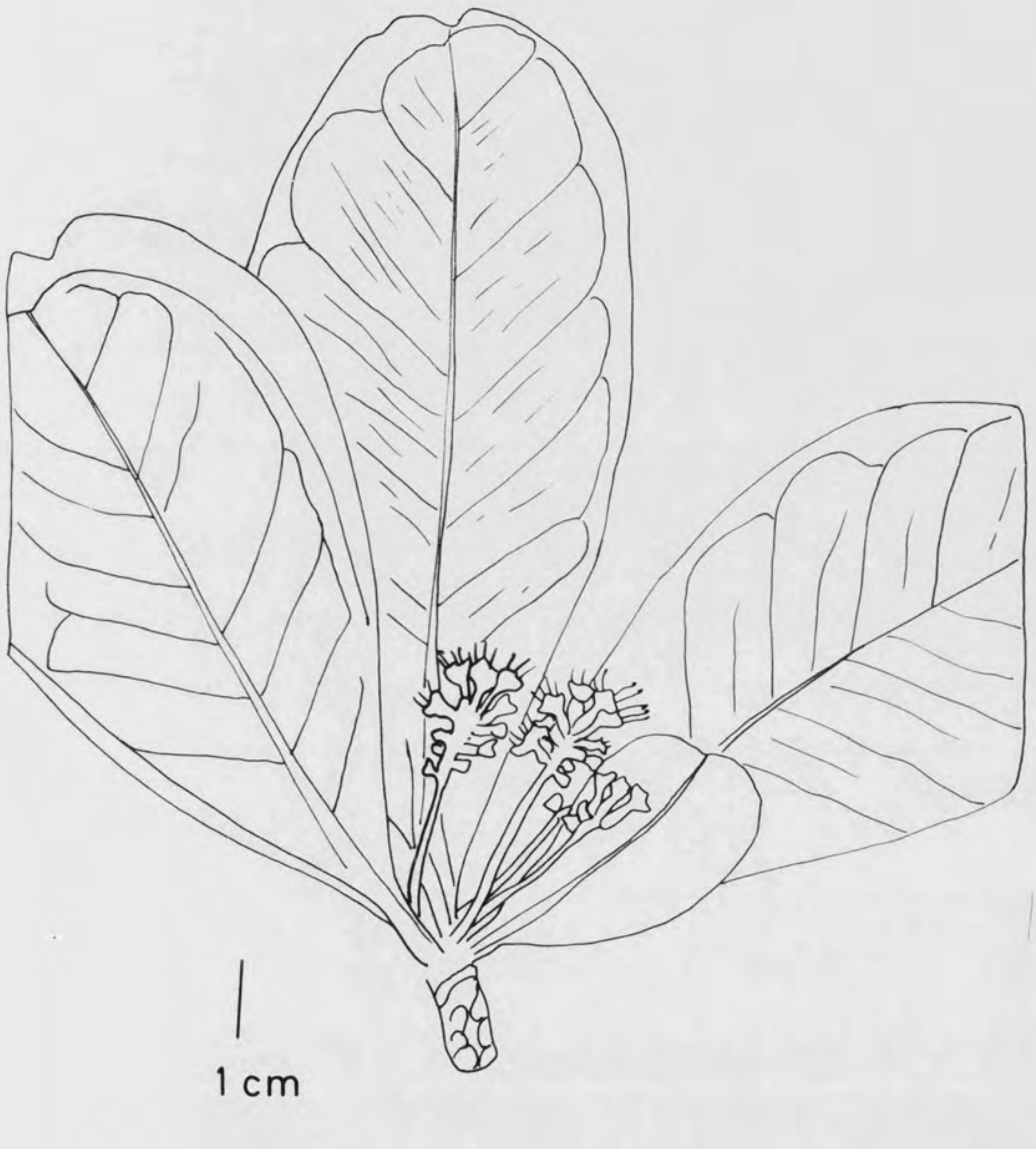


Fig. 9/26: T. virens

Ramatuella obtusa (Maguire) Exell & Stace, Bull. Brit. Mus. Nat. Hist. (Bot) 3, 1: 45 (1963). Based on Ramatuella crispialata var. obtusa Maguire.

Shrub or small tree 5-9 m high. Leaves spirally arranged or alternate, usually crowded near the ends of the branchlets; petiole (5)10-25 mm long, pubescent to puberulous or glabrous, inconspicuously biglandular, lamina coriaceous, 3-14 x 1.5-7.5, oblanceolate to narrowly obovate,oblong to elliptic or obovate; apex obtuse to rounded or retuse; base usually broadly cuneate sometimes obtuse, scarcely decurrent into the petiole; upper surface sparsely puberulous to glabrous; lower surface densely and minutely pubescent to glabrous, primary vein moderately raised below, secondary veins more or less conspicuous, 8-14 pairs; intersecondary veins common; tertiary veins ramified. Inflorescence subcapitate, often with only male flowers, or with male and bisexual flowers; peduncle 3-4 cm long, appressed puberulous; rachis 1-15. cm long, densely appressed puberulous. Bracts 1.5 mm long. Flowers tetramerous; lower receptacle 3-6 mm long, appressed tomentose, upper receptacle 2-4 mm long, appressed pubescent; calyx-lobes 1-1.5 mm long, obtuse; disk villous; stamen 8 or 10, 3-4 mm long; anther 0.5 mm long; style 3-4 mm long, slightly hairy at base. Fruit 4-winged circular to subcircular or ovate or oblong in outline, 10-20 x 8-18 mm, sometimes shortly beaked, with no pseudostipe, wing long and broad, 9-20 x 3-7 mm, with conspicuously crisped or undulate margin. (Fig. 9/27).

Geographical range: Venezuela, Brazil and Colombia. (Map 9/7).

Ecology: As in T. ramatuella.

Comments: T. crispialata shows considerable variation in the shape and size of the leaves and fruits and the amount of indumentum on the leaves. It is closely related to T. virens. However, it differs in having often wider leaves with more and conspicuous secondary veins and with rather dense indumentum at the base of the midrib on the lower surface, and larger fruits with longer and wider and usually wavy wings.

Fig. 9/ 27: T. crispialata

9.1.3. Imperfectly known species of Terminalia

1. Terminalia adamantium Cambess. in A. St. Hil., Fl. Bras. Mer. 2:241 (1830). Type: Brazil, Province de Minas Gerais. Voyage d'Auguste de Saint-Hilaire, 1816a;1821. Catal. B. No. 2065 (P, holotype).

Myrobalanus adamantium (Cambess.) Kuntze, Rev. Gen. : 237 (1891).

Leaves alternate; petiole 0.6-1 cm long, pubescent, eglandular; lamina chartaceous, 3-4.5 x 1.5-2 cm, oblong of oblong-elliptic, rounded-obtuse or muconate at apex, cuneate at base; upper surface sparsely pubescent or glabrous; lower surface pubescent on primary and secondary veins, glabrous to sparsely puberulus elsewhere. Domatia absent; venation brochidodromous; secondary veins 5-6 pairs, not raised. Inflorescences short, 2 cm long; rachis very short, 4 mm long, tomentose, with 3-5 flowers. Flowers yellowish-brown, perfect; lower receptacle 1.25-1.75 mm long, densely tomentose; upper receptacle 1.5-2 x 3 mm, pubescent, funnelform; calyx-lobes 5, deltoid, 0.8 mm long, reflected, villous inside; disk villous; stamen 10, 3-3.5 mm long exserted; style villous, 3-3.5 mm long. Fruit unknown. (Appendix 4 Pl. 13).

Ecology: Flowers September.

Comments: This "species" is known only by the type specimen. The type consists of only a few young and broken leaves and few flowers and this makes a comparison with known species very difficult. The short inflorescence with few (original description says numerous) flowers and the leaves with obtuse-rounded-mucronate apex are similar to those in T. triflora. But T. triflora has not been seen from Minas Gerais but it has been seen from São Paulo.

2. Terminalia riedelii Eichler in C. Martius, Fl. Bras. 14, 2: 92 (1867). Type: Arbor 40-50 ped. foliis obovato oblongis accutes basi

acuminates glaberri; floret terminalets congestis; in ambrosis slvati, Rio Janeiro, Aug. 1832, Riedel 1162 (lectotype, LE; isolectotypes, BM, FI, G, K, LE, NY, P, W).

Buchenavia fluminensis Glaziou, Mēm. Soc. Bot. France 1(3): 203 (1908), nom. nud. Type: Brasil, Rio Janeiro, Cororado, 12 spet., Glaziou 6142 (C, P), 6172 (K).

Tree 12-16 m high. Leaves alternate, often crowded near the ends of the branchlets; petiole 0.2-1 cm long, pubescent or glabrous, eglandular; lamina chartaceous, 2-4.5 x 1.1.8 cm, elliptic-obovate or oblanceolate, acuminate at apex, attenuate at base; upper surface glabrous; lower surface glabrous except pubescent on major veins. Domatia absent. Venation brochidodromous; secondary veins 4-7 pairs, fine; tertiary veins randomly reticulate. Inflorescence very short, peduncle 1-5 mm long, pubescent, rachis very short 1-1.5 mm long pubescent, with few flowers (4-5); bra cts 2.5-3 mm long, pubescent. Flowers hermaphrodite; lower receptacle 1-2 mm long slightly pubescent; upper receptacle 1.5 mm long; calyx-lobes 5, 0.8 mm long pubescent; disk nearly glabrous or slightly pubescent; stamen 10, 3.5-4 mm long; style 3.5-4 mm long sparsely pubescent. Fruits unknown. (Appendix 4 Pl. 14).

Comments: This species is known only by the type specimens. Most of the type materials consist only of young flowers but some of them have a few young leaves as well. Without fruit or at least mature leaves it is impossible to determine the species of Terminalia. The small leaves and very short inflorescences make this "specimen" close to T. triflora (sect. Australes). Buchenavia fluminensis Glaziou was based on Glaziou 6142 from R. Janeiro. I have examined the three specimens in C and the two specimens in P. The specimens consist only of very few young leaves, and flowers, which are borne on a very short inflorescence. The specimens are undoubtedly a Terminalia species. The general appearance, inflorescence and flowers are very similar to those of T.riedelii.

3. Terminalia rotundifolia Glaziou, Mém. Soc. Bot. France 1(3): 203 (1908). Type: Brasil, Minas, Biribiry, Glaziou 19 146 (C).

The specimen consists of sterile material (most leaves are young) but it differs from all other species in the New World in having broadly elliptic to rounded leaves with rounded base and apex (Appendix 4 Pl. 14). Its affinity is not clear; it could be mislabelled (see under T. microphylla).

4. Terminalia Sp. No. 1. Close to T. januariensis, but differing in the smaller fruits with thinner body and wings; the fruits are 1.7-2.5 x 3-4 cm. Fasenda do Ibiturana, Figueira, Rio doce, Minas, Brasil, 3/9/1930 Kuhlman, 296 (RB 441 2 sheets). Possibly a distinct species.

5. Terminalia Sp. No. 2. Venation typically eucamptodromous with very conspicuous percurrent tertiary veins. The venation is similar to that in T. amazonia but the leaves are much larger and narrowly oblong-obovate with a long acuminate apex. The fruits are similar to those of T. guyanensis. The label says fruits are not from the same plant as the leaves. However, whether the fruits belong to the same tree or not, the leaves are very different from those of both T. amazonia and T. guyanensis, and they also differ from those of T. oblonga. N.v. "Yumbingue", Estacion Experimental El Padmi, 52 km NE de Zamoru, Zamoru, Lat. 30 43' S., Long. 78 W., alt. 900 m. 12 Sept. 1975, Little, Ortega, Samaniego Vivar 317 (COL). If the leaves and fruits do represent the same species, it is probably a new one.

6. Terminalia Sp. No. 3.

Tree 8-20 m high; new shoots densely pubescent. Leaves more or less alternate, not very crowded at the ends of the shoots; petiole 0.5-1 cm long, densely and minutely pubescent or puberulus, eglandular; lamina chartaceous-subcoriaceous 3.5-9 x 2-5, ovate or oblong or obovate, acute-obtuse or shortly acuminate at apex, obtuse at base; upper surface densely pubescent to pubescent; lower surface densely villous or tomentose. Domatia absent. Venation eucamptodromous, secondary veins 8-10 pairs, prominently raised below; tertiary veins percurrent, very conspicuous and obliquely arranged; quaternary veins orthogonally arranged and conspicuous; quinternary veins also conspicuous but not raised. Inflorescence axillary, spike; peduncle 1-1.5 cm long, densely pubescent; rachis 3-4 cm long, tomentose to densely pubescent. Bracts 2-3 mm long tomentose-villous. Flowers 4 mm long; lower receptacle 1.5 mm long tomentose; upper receptacle 1.5 x 2-3 mm, funnelform, villous inside, pubescent outside; calyx-lobes 1.5 mm long, triangular; disk densely villous; stamen 10, 3-4 mm long; style villous, 3-4 mm long. Fruit unknown.

Specimens seen:

Ecuador: Prov. EL ORO: Junction of Rios Ambocas and Luis (10 mk due South of Portovelo) 2200-2500 fit. elev., Oct. 6, 1944, W. H. Camp. No. E-588 (NY, BM). Ecuador: Westlish Gūayaquil, Būschwald, 20 m, 6.11.1933. fls, Schimpff 395 (G). Peru: Dept. Tumbes, Tumbes, "Guarapo", Arbol, Tree number T-25, fls October 1970, Rafael Lao M., s.n. (F, G).

Comments: This species differs from all other species of *Terminalia* in America in its leaves (particularly the venation) and flowers. The basic venation type has some similarity with that in *T. amazonia* but details of the tertiaries and the higher-order venation are very different. The flowers also differ from those of *T. amazonia* in having triangular calyx lobes and a hairy style.

It seems that this species has no close similarity to any of the neotropical species of *Terminalia*, but without seeing the fruits it is impossible to make a definite judgement. It seems unlikely that it has been introduced.

9.1.4. Non-American species of Terminalia

Terminalia microphylla Eichler, Vidensk. Meddel. Kjoeb: 193 (1870).

Type: Ata da Boa Vista, via Macaco, Rio Janeiro, Brasil, 13/8/1868, Glaziou 2910 (lectotype, BR; isolectotypes BR, C, P). Other specimens (not cited by Eichler): Rio Janeiro, 8 Nov. 1873, Glaziou 6834 (C, K, P). (Appendix 4 Pl. 14).

All the above specimens were examined and labelled by me as T. microphylla, but after I had examined the type of T. fatraea (Poir). DC. from Madagascar I discovered that T. microphylla is without any doubt conspecific with the latter. I presume that, like so much of Glaziou's material, the above specimens were wrongly labelled.

As well as the above, several Asian and African species of Terminalia are cultivated in America, but T. catappa appears to be the only one naturalized.

9.1.5. Species excluded from Terminalia

Terminalia angustifolia Sauvalle, Fl. Cuba: 38 (1868) = Bucida buceras.

T. brasiliensis Sprengel, Syst. Veget. 2: 359 (1825) = Gouania blanchetiana Mig.

T. buceras (L.) Wright in Sauvalle, Fl. Cuba: 38 (1868) = Bucida buceras.

T. capitata Sauvalle, Fl. Cuba: 38 (1868) = Buchenavia tetraphylla.

T. debilis Glaziou, Bull. Soc. Bot. France, 1907, Mém 3: 203 (1908) nom. nud. Bras., Glaziou 10242 = not Combretaceae.

T. discolor Sprengel, Neue Entd. 2: 111 (1821) = Cupania sp. (fide Eichler) 1867).

T. erecta Bailly, Hist. Pl. 6: 266, 275 fig 240 (1877) = Conocarpus erecta.

T. hiliariana Steudel, Nom. ed. 2, 2: 668 (1841) = Buchenavia tetraphylla.

T. macrophylla Spruce ex Eichler in C. Martius, Fl. Bras. 14, 2: 98 (1867) = Buchenavia macrophylla.

T. macrostemon Sprengel, Syst. Veget. 2: 358 (1825) = Myrcia micrantha (fide Eichler 1867).

T. molineti Maza in Maza & Roig, Biol. Secr. Agric. Comerc. Trab. Cuba 22 : 75 (1914) = Bucida molineti.

T. nitidissima Rich., Act. Soc. Hist. Nat. Par. 1: 109 (1792) = Buchenavia nitidissima.

T. obovata Cambess., in A. St. Hill., Fl. Bras. Mer. 2 : 241 (1829) = Buchenavia tetraphylla.

T. octandra Sprengel ex Eichler in C. Martius, Fl. Bras. 14, 2: 93 (1867) nom. nud. = Cupania sp. (fide Eichler 1867).

T. pamaea Steudel, Nom. ed. 2, 2 : 668 (1841) = Buchenavia guianensis.

T. pamea DC., Prodr. 3 : 13 (1828) = Buchenavia guianensis.

T. punctata Spruce ex Eichler in C. Martius, Fl. Bras. 14, 2: 98, in syn. (1867) = Buchenavia oxycarpa.

T. spinosa Northrop, Mem. Torr. Bot. Club. 12: 54 t 13 (1902) = Bucida molineti.

T. suaveolens Spruce ex Eichler in C. Martius, Fl. Bras. 14, 2 : 97, in syn. (1867) = Buchenavia suaveolens.

T. tomentosa C. Martius ex Eichler in C. Martius, Fl. Bras. 14, 2 : 97, in syn. (1867) = Buchenavia tomentosa.

T. trifoliata Sprengel, Syst. veget. 2 : 358 (1825) = Mauria sp. (fide Eichler 1867).

T. vasivae Spruce ex Eichler in C. Martius, Fl. Bras. 14, 2 : 97 = Buchenavia suaveolens.

T. villosa Sprengel Neue Entd. 2: 111 (1821) = probably not Terminalia (fide Eichler 1867).

9.2. Bucida

9.2.1. Key to the species of *Bucida*

1 - Branches and branchlets bearing spines; lamina 0.5-2(3.5) x 0.3-0.7 cm; inflorescences capitate or sub-capitate, usually glabrous; flowers few (5-13), nearly glabrous; fruits often without persistent calyx . . . . 1. *B. molineti*

1 - Branches and branchlets usually without spines; lamina larger (3-25 x 2-11 cm); inflorescences elongate, usually densely pubescent; flowers numerous, always pubescent; fruits with persistent calyx . . . 2

 2 - Lamina 3-10.5 x 2-6.7 cm, with up to 8 pairs of secondary veins; rachis 2.5-5 cm long . . . . 2. *B. buceras*

 2 - Lamina 10-25 x 6-11 cm, with 8-16 pairs of secondary veins; rachis 5-13 cm long . . . . 3. *B. macrostachya*

9.2.2. The species of *Bucida*

1. *Bucida molineti* (M. Gomez) Alwan, comb. nov. Based on *Terminalia molineti* M. Gomez in M. Gomez & Roig, Fl. Cuba (Biol. Ser. Aric. Comerc. Trab. No 22) : 76 (1914), nom nov. for *Bucida angustifolia* A. Rich.

Bucida angustifolia A. Rich., Fl. Cuba: 521 (1846), not of DC. (1828). Type?

Terminalia spinosa Northrop, Mem. Torr. Bot. Club 12: 54 t. 13 (190), nom. illegit., not of Engler, Pflanzenw. Ost. Afr. C, 294 (1895). Type: Andros Island (Bahama), Fresh Creek, June 1890, John & Northrop 502 (F, holotype).

Bucida spinosa (Northrop) Jennings, Annals Carnegie Museum 11: 201 (1917).

Bucida ophiticola Bisse, Feddes Repert. 85 (9-10): 605 (1974). Type: Cuba, Prov. Matanzas, Canasi, Lomas de Galindo, sep. 1969, Bisse, Lippold & Berasain 18373 (holotye, HAJB, not seen; isotype JE).

Shrub or small tree; branches and branchlets always armed with pointed spines. Petiole very short, stout, 1-2 mm long, glabrous, sometimes bgilandular. Lamina coriaceous, small, 0.5-2 (3.5) x 0.3 - 0.7 (1) cm, obovate, or narrowly to very narrowly obovate, rounded to obtuse or retuse at the apex, cuneate to narrowly cuneate at the base, usually (strongly to slightly) inrolled at the margins, almost always glabrous on both surfaces except sometimes very sparsely puberulous on the primary vein below. Secondary veins often inconspicuous, diverging at narrowly acute angles; intersecondary veins common; tertiary veins ramified or inconspicuous; higher-order venation and areolation invisible. Inflorescence capitate or subcaptiate, with 5-13 flowers; peduncle 1.5-3 cm long, usually glabrous but sometimes sparsely pubescent; rachis 1-15(18) mm, almost always glabrous. Flowers 3-5 mm long; lower receptacle 2.5-3.5 mm long usually glabrous but sometimes sparsely pubescent round the ovary; upper receptacle 1.3-1.8 x 3 mm, glabrous, with very small teeth. Fruit ovoid, obsucrely ridged, 5-7 x 3-4 mm, abruptly or gradually narrowed into an acumen (1-2 mm long) at the apex, rounded at the base, usually glabrous but sometimes sparsely and minutely pubescent; acumen more or less pointed, curved or straight, usually without persistent calyx. (Plate 9/4).

Geographical range: Belize, Cuba and Bahamas. (Map 9/8).

Ecology: Marshy savanna, and scrub at low level and on hills.

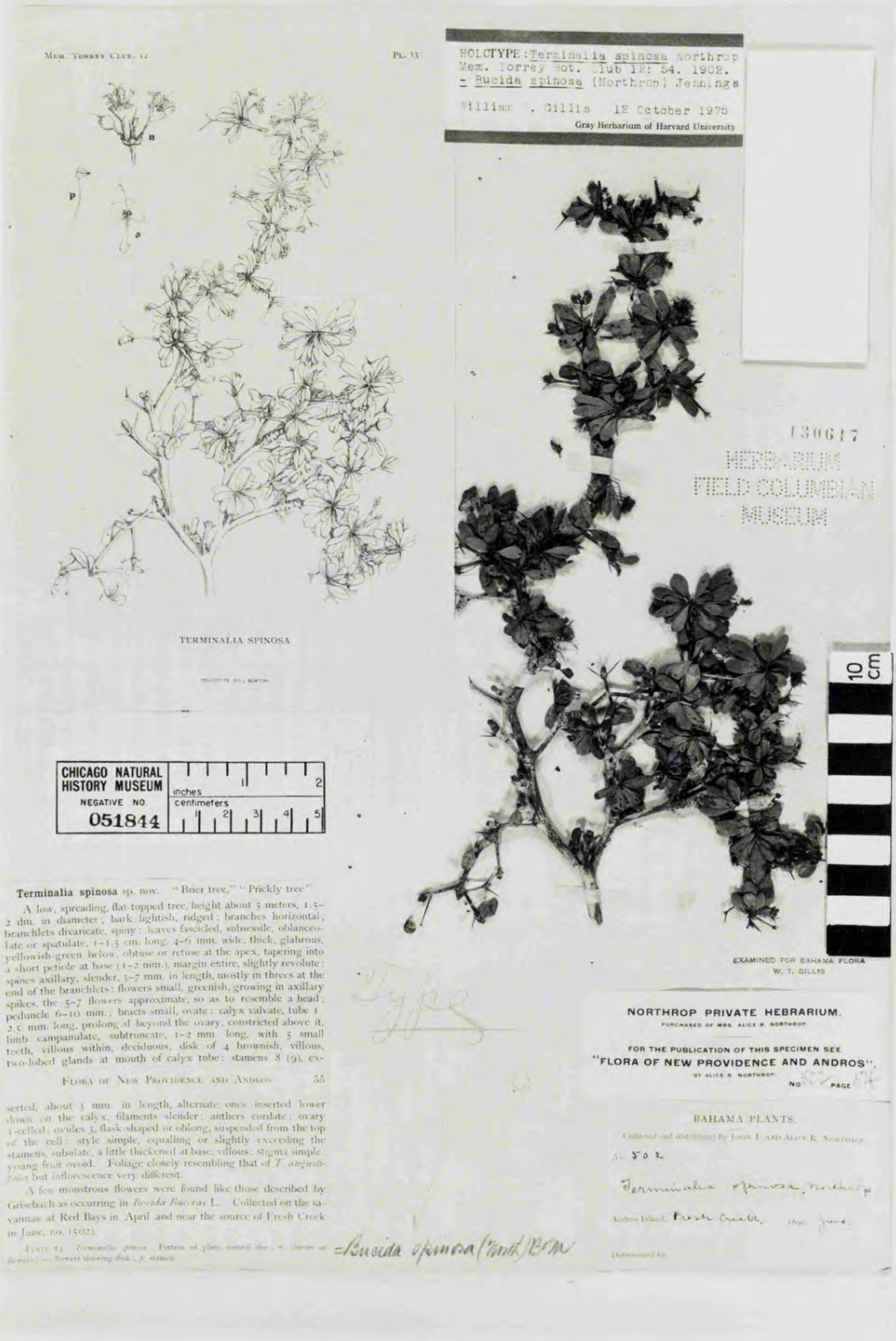
Common name: Jucaro espinosa.

Comments: *B. molineti* is a distinct species which differs from the other two species in having much smaller leaves and a much shorter rachis with fewer, usually glabrous flowers. However the leaves of this species sometimes are similar to those in some forms of *B. buceras*.

This species has been known in the literature as *Bucida spinosa* but the name *B. spinosa* is illegitimate because it is based on the illegitimate name *T. spinosa* Northrop. *Terminalia molineti* is a nom. nov. for *Bucida*

Plate 9/4: Holotype of <u>Terminalia</u> <u>spinosa</u> Northrop (F)

(= <u>Bucida</u> <u>molineti</u> (Gomez) Alwan)



Mem. Torrey Club, 12
Pl. 13
TERMINALIA SPINOSA
HOLOTYPE: Terminalia spinosa Northrop
Mem. Torrey Bot. Club 12: 54. 1902.
= Bucida spinosa (Northrop) Jennings
William T. Gillis 12 October 1975
Gray Herbarium of Harvard University
130617
HERBARIUM
FIELD COLUMBIAN
MUSEUM
10 cm
CHICAGO NATURAL HISTORY MUSEUM
NEGATIVE NO.
051844
inches
centimeters
Terminalia spinosa sp. nov. "Brier tree," "Prickly tree"
A low, spreading, flat-topped tree, height about 5 meters, 1.5–2 dm. in diameter, bark lightish, ridged; branches horizontal, branchlets divaricate, spiny; leaves fascicled, subsessile, oblanceolate or spatulate, 1–1.5 cm. long, 4–6 mm. wide, thick, glabrous, yellowish-green below, obtuse or retuse at the apex, tapering into a short petiole at base (1–2 mm.), margin entire, slightly revolute; spines axillary, slender, 3–7 mm. in length, mostly in threes at the end of the branchlets; flowers small, greenish, growing in axillary spikes, the 5–7 flowers approximate, so as to resemble a head; peduncle 6–10 mm.; bracts small, ovate; calyx valvate, tube 1 2.5 mm. long, prolonged beyond the ovary, constricted above it, limb campanulate, subtruncate, 1–2 mm. long, with 5 small teeth, villous within, deciduous, disk of 4 brownish, villous, two-lobed glands at mouth of calyx tube; stamens 8 (9), ex-
Flora of New Providence and Andros 55
serted, about 3 mm. in length, alternate ones inserted lower down on the calyx, filaments slender; anthers cordate; ovary 1-celled, ovules 3, flask-shaped or oblong, suspended from the top of the cell; style simple, equalling or slightly exceeding the stamens, subulate, a little thickened at base, villous; stigma simple; young fruit ovoid. Foliage closely resembling that of T. angustifolia but inflorescence very different.
A few monstrous flowers were found like those described by Grisebach as occurring in Bucida Buceras L. Collected on the savannas at Red Bays in April and near the source of Fresh Creek in June, no. (502).
Type
= Bucida spinosa (Northr.) Britton
EXAMINED FOR BAHAMA FLORA
W. T. GILLIS
NORTHROP PRIVATE HEBRARIUM.
PURCHASED OF MRS. ALICE R. NORTHROP.
FOR THE PUBLICATION OF THIS SPECIMEN SEE
"FLORA OF NEW PROVIDENCE AND ANDROS".
BY ALICE R. NORTHROP.
NO PAGE
BAHAMA PLANTS.
No. 502
Terminalia spinosa, Northrop
Andros Island. Fresh Creek, June.
Determined by

PLATE 9/4

angustifolia Rich, non DC. (type not seen) which is said to be spiny (Jūcaro espinoso), so a comb. nov. Bucida molineti (M. Gomez) Alwan is the correct name.

2. Bucida buceras L., Syst. Nat. ed. 10, 2 : 1205 (1759).

Buceras bucida Grantz, Inst. 1 : 133 (1766).

Terminalia buceras (L.) Wright in Sauvalle, Fl. Cuba: 38 (1868).

Myrobalanus buceras (L.) Kuntze, Rev. Gen.: 237 (1891).

Bucida wigginsiana Miranda, An. Inst. Biol. Mexico 26: 83 (1955).

Type: Mexico Las Tejas, unos 12 km al oeste de Tehuantepec, Oax. dominante en selva baja decidua, 30 Mar. 1955, Miranda 8178 (not seen).

Bucida subinermis Bisse, Feddes Repert. 85 (9=10); 605 (1974).

Type: Cuba, Prov. Oriente, manigua costera en el Sochucho, playa de Puerto Padre, 19-20 Mayo 1957, López Figueras 2904 (holotype, HAJB, not seen) (paratypes: Bisse & Rojas 1532, JE; Bisse & Rojas 1901, JE).

?Terminalia angustifolia Sauvalle, Fl. Cuba: 38 (1868). Type?

Tree up to 35 m tall and 130 cm diameter; branches sometimes armed with relatively long and stout spines 1-4 cm long. Petiole 0.5-1 cm long, slender, often biglandular, rufous pubescent at flowering time almost glabrous in fruit. Lamina subcoriaceous, obovate to suborbicular or elliptic to narrowly obovate, (2) 3-10.5 x 1-6.7 cm, rounded to obtuse or retuse or subacute at the apex, cuneate or broadly cuneate at the base, usually flattened at the margins, glabrous above, glabrous or sparsely to very sparsely pubescent except pubescent to sparsely pubescent on the primary veins below. Secondary veins fine, often conspicuous usually 4-8 pairs, diverging at moderately acute angles; intersecondary veins common; tertiary veins ramified or sometimes randomly reticulate; higher order venation and areolation inconspicuous. Inflorescence elongate spike with

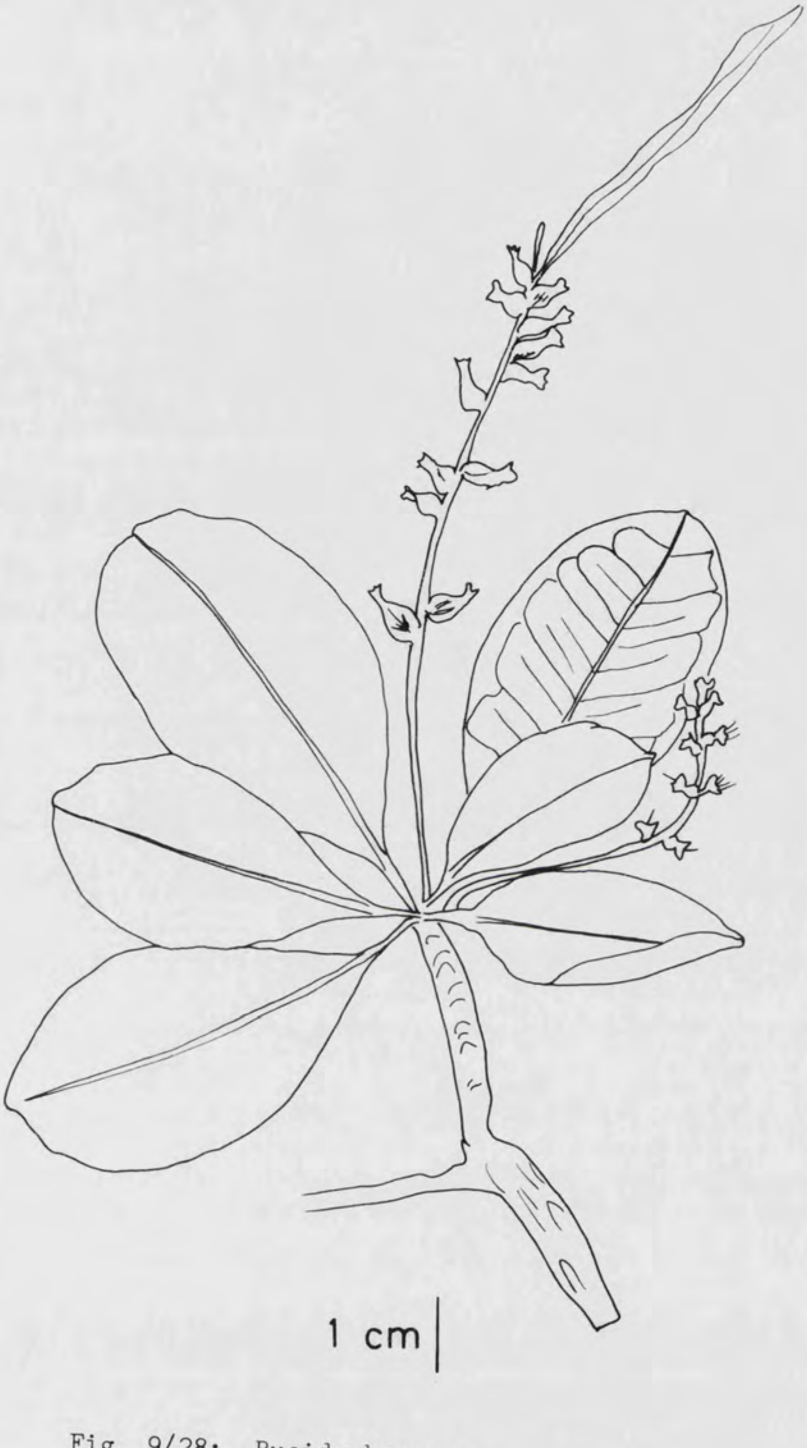


Fig. 9/28: Bucida buceras

numerous flowers; peduncle 2-5.5 cm long, rufous tomentellous; rachis 2.5-5 cm long (up to 7 cm in fruit), densely rufous tomentellous. Flowers 3-4 x 2-3 mm, densely pubescent; stamen 3-4 mm long; style 2.5-3.5 mm long, hairy. Fruit ovoid more or less ridged or angled, 0.4-0.7 x 0.2-0.3 cm, narrowed into a short neck and crowned with persistent calyx at the apex, rounded at the base, densely pubescent. (Fig. 9/28).

Geographical range: Central America, West Indies from Cuba to Trinidad, Bahamas and southern Florida. (Map 9/8). Eichler's record from the Guianas probably refers to De Candolle s Bucida angustifolia DC, the type of which (G) is Terminalia amazonia.

Ecology: Medium or large tree growing on hillsides up to 1000 m in wet forest, or near the sea at edge of mangroves or along rivers, in swamps and by lagoons.

Common name: "Black olive" in Jamaica; "Bullet tree" and "Bully tree" in British Honduras.

Uses: The timber is hard, close grained and yellowish or darkish brown. It is said to be of good quality and used locally for many purposes such as house posts, piling and constructions.

Comments: Bucida buceras is the most variable species in the genus. The leaves are very variable in size and shape. The amount of indumentum on the upper receptacle varies considerably. The inflorescences show considerable variation in rachis length.

I have not seen the type of Bucida wigginsiana, but judging from the description and the illustration given in the original description it comes well within the range of variation of B. buceras. Bucida subinermis differs from typical B. buceras in having narrower leaves and a glabrous peduncle and rachis. However, it comes within the variation of B. buceras.

3. Bucida macrostachya Standley, Field Mus. Nat. His. Chicago, Bot. Ser, 4: 240 (1929). Type: Guatemala, El Rancho, December 28, 1907,

W. A. Kellerman 7744 (F, 224629, holotype).

Bucida megaphylla Exell, Jour. Bot. 68 : 244 (1930). Type: Mexico, Chacalapa Estate, Liebman 3401 (holotype, C, not seen; isotype BM).

Tree to 20 m tall; branchlets usually spineless and thickened at the tip. Leaves crowded at the tips of the branchlets; petiole 1-4.5 cm long, moderate, densely pubescent, becoming glabrous when old, eglandular or biglandular near the apex; lamina subcoriaceous, (5) 10-25 x (4) 6-11 cm, elliptic or obovate-elliptic to oblong-elliptic, obtuse to rounded or subacute or sometimes apiculate at the apex, broadly cuneate at the base, sparsely pubescent to almost glabrous except pubescent on the primary vein above, almost glabrous except sparsely pubescent on the primary and secondary veins below. Secondary veins (8) 12 - 16 (20), fine but conspicuous; tertiary veins randomly reticulate or ramified; higher order venation not distinct but quaternary veins more or less visible. Inflorescence distinctly elongate spike; peduncle 4.5-6 cm long, densely tomentellous; rachis very long up to 13 cm, densely rufous tomentellous. Flowers 4-6 cm long densely tometellous. Fruit ovoid or ovoid-ellipsoid, 5-6 x 3.5 mm, densely pubescent, rounded at base and usually with persistent calyx at apex. (Fig. 9/29).

Geographical range: Central America from southern Mexico to Guatemala and Honduras. (Map 9/8).

Comments: This species is very close to some specimens of Bucida buceras but it differs in its larger leaves with more secondary veins and more conspicuous venation and in its longer inflorescences

9.2.3. Doubtful species of Bucida

B. megapotamica Sprengel, Syst. Veget. 4 Cur. Post. : 177 (1827). Type?

B. palustris Borh. & Muñiz, Act. Bot. Acad. Sci. Hung. 21: 224 (1976).
Type: Borhidi, Risco & Oviedo s.n. (holotye: SV; isotype SV, BP,not seen).

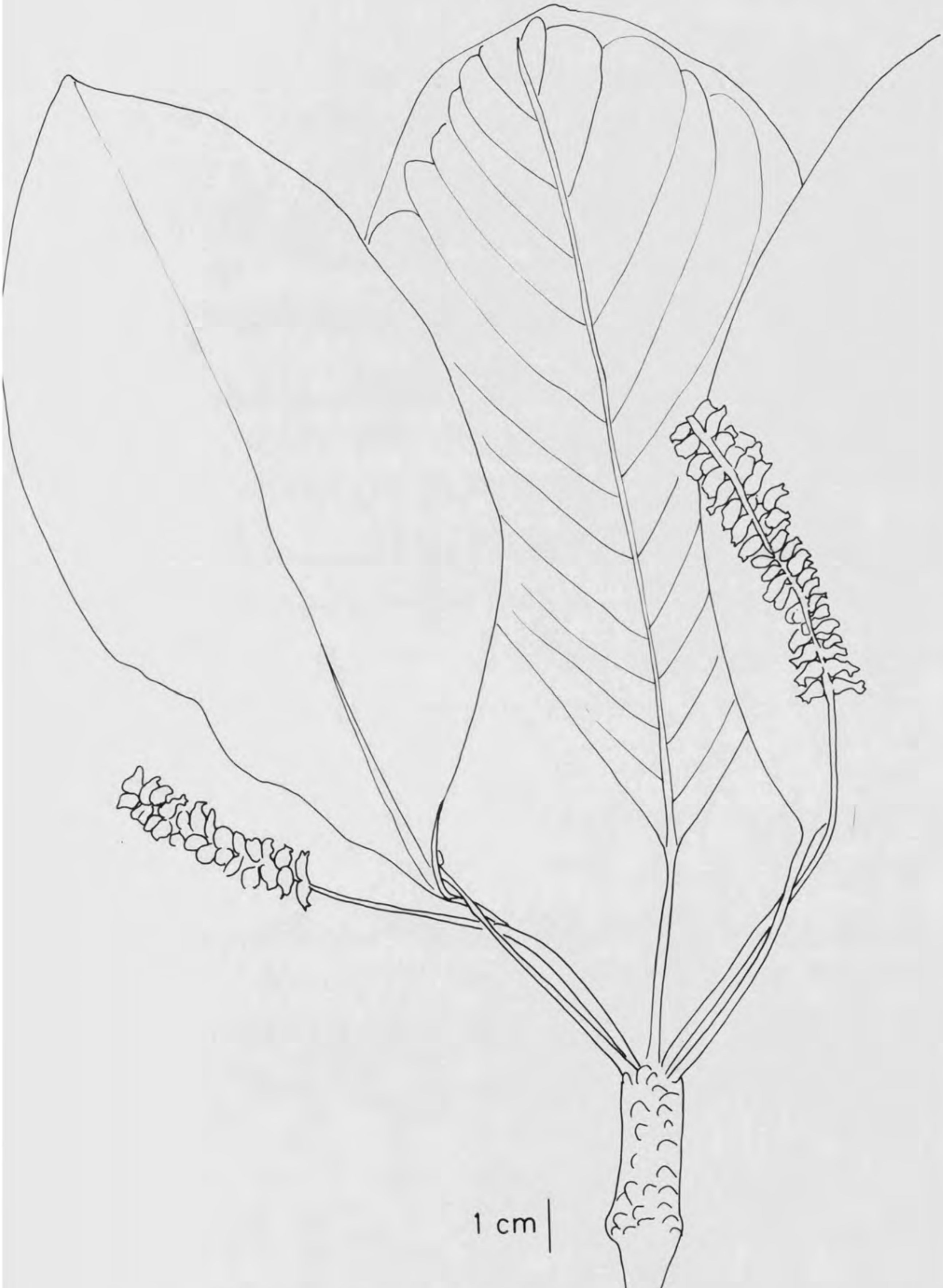


Fig. 9/29: Bucida macostachya

Perhaps a synonym of B. molineti. Described from Cuba.

B. umbellata Sessé & Moc., Pl. N. Hispan.: 71 (1887-90). Type? not seen. Described from Mexico.

9.2.4. Species excluded from Bucida.

B. angustifolia DC. Prodr. 3: 10 (1828) = Terminalia amazonia (J. Gmel.) Exell.

B. angustifolia Spruce ex Eichler in C. Martius, Fl. Bras. 14, 2: 96 = Buchenavia tetraphylla (Aublet) Howard.

B. buceras Sieber ex Presl, Oken, Isis, 21: 272 (1828) = Terminalia catappa L. (fide Index Kewensis).

B. buceras var. angustifolia (DC.) Eichler, Fl. Bras. 14, 2: 95: (1867) = Terminalia amazonia (J. Gmel.) Exelll.

B. buceras Vell, Fl. Flum. 4 : 172 t. 87 (1825) = Laguncularia raceomosa (L.) Gaertner f. (fide Eichler 1867).

B. capitata Vahl, Ecolg. Am. 1 : 50 t. 8 (1796) = Buchenavia tetraphylla (Aublet) Howard.

B. comintata Blanco Fl. Filip.: 856 (1837) = Terminalia citrina (Gaertner) (fide Exell 1954).

B. nitida Hassk., Flora 27: 605 (1844) = Terminalia sp.

9.3. Buchenavia

9.3.1. Key to the species of *Buchenavia*

1 - Inflorescences capitate to subcapitate, with rachis shorter than peduncle and almost always less than 15 mm long 2

1 - Inflorescences elongate, with rachis up to 13 cm long, if occasionally subcapitate then elongating in fruit 5

2 - Fruit distinctly beaked, irregularly and markedly ridged, densely ferrugineous - pubescent . . . . 1. *B. ochroprumna*

2 - Fruit not beaked, rounded or obtuse or shortly apiculate, not or obscurely 5-ridged, glabrous or puberulous when mature 3

3 - Leaves chartaceous when mature, small, 1.5-4 x 0.5-2 cm, with 5-12 pairs of secondary veins; flowers often laxly arranged on the rachis; fruit 14-20 x 8-12 mm, glabrous . . . . 2. *B. parvifolia*

3 - Leaves subcoriaceous to coriaceous when mature, medium (occasionally small), 2-9 x 1-6 cm, with 2-8 pairs of secondary veins; flowers almost always densely arranged on the rachis; fruit 15-30 x 10-22, glabrous or puberulous 4

4 - Fruit glabrous or very sparsely pubescent . . . 3. *B. tetraphylla*

4 - Fruit densely but minutely puberulous . . . . . 4. *B. kleinii*

5 - Leaves relatively small to medium, up to 16 x 6 cm but usually 3-8 x 2-5 cm; venation brochidodromous to sometimes eucamptodromous - brochidodromous (except eucamptodromous in *B. pallidovirens*); domatia usually present (except entirely absent in *B. suaveolens*) 6

5 - Leaves relatively large to very large but sometimes medium to small, up to 40 cm long and 14 cm broad but usually 8-20 x 4-8 cm; venation eucamptodromous or sometimes eucamptodromous - brochidodromous, rarely brochidodromous; domatia usually absent 14

6 - Venation typically eucamptodromous with secondary veins usually originating at narrowly acute angles; tertiary veins regularly percurrent; areolation very close and more or less orthogonally arranged . . . . 5. B. pallidovirens

6 - Venation brochidodromous or eucamptodromous - brochidodromous; secondary veins diverging at moderately or widely acute or at right angles; tertiary veins randomly reticulate or weakly percurrent or inconspicuous; areolation (if present) incomplete or imperfect and wide (except B. amazonia) 7

7 - Venation brochidodromous to weakly brochidodromous, not raised below; secondary veins weak and often inconspicuous; domatia completely absent; fruit flattened or terete and distinctly apiculate, glabrous . . . . 6. B. suaveolens

7 - Venation brochidodromous - eucamptodromous or brochiodromous, raised to prominently raised below; secondary veins moderate and always conspicuous; domatia usually present; fruit various but often rounded at apex and pubescent, if distinctly apiculate or beaked then the body distinctly 4-6 angled 8

8 - Fruit distinctly 4-6 angled, distinctly apiculate or beaked, with projection 3-8 mm long, glabrous . . . . 7. B. oxycarpa

8 - Fruit not angled, not beaked but sometimes shortly apiculate with projection 1-2 mm long, pubescent or sometimes glabrous 9

9 - Secondary veins 3-5 pairs, widely spaced, prominently raised below; distal secondaries almost perpendicular to the primary veins; tertiaries raised below; areoles very large; domatia lebetiform . . . . 8. B. fanshawei

9 - Secondary veins usually more than 5 pairs (4-12), narrowly or moderately spaced, slightly or prominently raised below; tertiaries usually not raised, areoles various; domatia not lebetiform 10

10 - Leaf chartaceous, obovate - oblong or elliptic, long acuminate, fruit densely silvery-brown - tomentellous . . . . 9. _B_. _sericocarpa_

10 - Leaf subcoriaceous to thickly coriaceous, if chartaceous then the apex not acuminate, obovate to narrowly obovate or oblanceolate, rounded to obtuse or subacute rarely shortly acuminate; fruit pubescent or glabrous 11

11 - Leaves usually coriaceous or thickly coriaceous, densely or very densely clustered at the tips of the branchlets, up to 16 cm long and 7 cm broad; secondary veins (4)6-12 pairs 12

11 - Leaves usually chartaceous to subcoriaceous, not densely clustered at branchlet tips, usually less than 10 cm long and 4 cm broad; secondary veins 4-7 pairs 13

12 - Leaves usually very densely clustered at the tips of the branchlets; lamina coriaceous to thickly coriaceous, 6-14.5 x 1.5-3.5(5) cm, usually oblanceolate, apiculate or subacute at apex; fruit densely grey-tomentellous, 1.5-2.3 x 1-1.3 mm . . . . . 10. _B_. _hoehneana_

12 - Leaves often densely crowded at branchlet tips; lamina coriaceous when mature, 3-16 x 2-7 cm, obovate or narrowly obovate, round to obtuse at the apex; fruit often glabrous but sometimes sparsely to densely pubescent, 24-35 x 11-25 mm . . . . 11. _B_. _grandis_

13 - Lamina chartaceous, obovate or narrowly obovate; tertiary veins irregularly percurrent and conspicuous; higher-order venation usually distinct;areoles conspicuous and small; fruit sparsely puberulous to almost glabrous . . . . 12. _B_. _amazonia_

13 - Lamina subcoriaceous when mature, oblanceolate or narrowly elliptic to elliptic or sometimes obovate; tertiary veins randomly reticulate; higher-order venation and areoles not conspicuous or lacking; fruit densely-greyish-brown-tomentellous or glabrous . . . 13. _B_. _viridiflora_

14 - Leaves at flowering time usually densely rubiginous - to ferrugineous - pubescent to - tomentose below, pubescent and almost always drying reddish-brown above; tertiary and quaternary venation prominently raised below 15

14 - Leaves at flowering time usually sparsely pubescent to almost glabrous below, glabrous and greyish - or reddish-brown above; higher-order venation rarely raised below 16

15 - Fruit ellipsoid or more or less spherical, rounded at the apex, sparsely puberulous or glabrous when mature, 21-31 x 12-25 mm . . . . 14. B. tomentosa

15 - Fruit ellipsoid to narrowly ellipsoid or irregularly ridged, apiculate or acuminate or obtuse at the apex, densely rubiginous - to ferrugineous - tomentellous at least at the apex, 19-45 x 8-30 mm. . . . . 15. B. reticulata

16 - Fruit with an apical beak 10-20 mm long . . . . 16. B. megalophylla

16 - Fruit rounded to obtuse or subacute or rarely apiculate at the apex 17

17 - Fruit large, 3-6.5 x 1.3-4 cm, 5-6 angled, with 3 angles more prominent than the rest, obtuse to subacute or acuminate at the apex, glabrous but with rusty-coloured and scaley surface . . . . . . .17. B. guianensis

17 - Fruit smaller, 1.8-4 x 1-2 cm, various but not angled or ridged, rounded to obtuse at the apex, variously pubescent or glabrous 18

18 - Fruit glabrous or sparsely teommentellous, usually pseudostipitate but sometimes very short or absent; leaves usually densely clustered at branchlet tips 19

18 - Fruit densely tomentellous or velutinous, rounded at the base; leaves not densely clustered at branchlet tips 20

19 - Lamina coriaceous to thickly coriaceous, elliptic to oblong or oblanceolate, rounded to obtuse or subacute at the apex; fruit obovoid,

sparsely - densely roufous tomentellous, distinctly but shortly pseudostipitate at the base . . . . 18. B. nitidissima

19 - Lamina chartaceous or subcoriaceous, oblanceolate to narrowly obovate, abruptly acuminate or apiculate at the apex; fruit oblong to ellipsoid, usually glabrous, not or shortly stipitate . . . . 19. B. congesta

20 - Lamina 3-35 x 1.5-14 cm, oblanceolate or oblong to elliptic - oblong, often acuminate at the apex; fruit 10-30 x 6-13, densely ferrugineous tomentellous . . . . 20. B. macrophylla

20 - Lamina 16-29 x 4.5-10 cm, narrowly obovate to oblanceolate, abruptly acute to acuminate at the apex; fruit (immature) 12 x 8 mm, densely rufous-velutinous . . . . 21. B. pulcherrima

9.3.2. The species of Buchenavia

1. Buchenavia ochroprumna Eichler, Flora 49: 165 (1866). Type: Brazil: Pará, near Santarém, Jan. 1850, Spruce 309 (M, lectotype).

Buchenavia discolor Diels, Verh. Bot. Ver. Prov. Brandeb. 48: 192 (1907). Type: Amazonas, near Manáos, on the banks of Rio Negro, Dec. 1901, Ule 5979 (B, holotype, destroyed).

Shrub or small tree, 3-12 (20) m high, 10-25 cm diameter. Petiole 4-15 mm, usually rather stout. Lamina subcoriaceous, chartaceous when young, obovate or obalncolate; apex usually rounded, sometimes obtuse or retuse; base usually cuneate; upper and lower surfaces almost glabrous except on the major veins; domatia present. Venation brochidodromous; primary veins moderate, usually slightly raised below; secondary veins moderate or fine, 3-7 pairs; tertiary veins randomly reticulate, often not conspicuous; higher-order venation not distinct; areoles lacking. Inflorescence capitate; peduncle 6-30 mm long, slender at flowering time, stout in fruit. Fruit ovoid or ellipsoid, markedly and irregularly ridged, 18-30 x 7-17 mm (including beak), long-beaked at the apex, pseudostipitate or rounded at the base, densely ferrugineous - tomentellous; beak 4-10 mm long, straight or curved; endocarp irregularly ridged in section.

Geographical range: Brazil (Amazonas) and Colombia. (Map 9/9).

Ecology: Common in Amazonas forest (particularly around Manaus) at low altitude, often growing in flooded areas. Flowers July-August.

Comments: Buchenavia ochroprumna is a very distinct species characterized by its beaked, irregularly ridged and densely pubescent fruits, its inconspicuous higher-order venation and areolation, and by its characterstically brownish leaves (lower surface) when dry. However, the species can sometimes hardly be separated from B. tetraphylla at flowering time.

Exell & Stace (1963) did not see the type of B. discolor, but isotypes seen subsequently by C. A. Stace in G, L and RB show that this taxon belongs to B. ochroprumna.

2. Buchenavia parvifolia Ducke, Arch. Jard. Bot. Rio Janeiro 4: 150 (1925). Type: Brasil: Pará: Vila Braga , Rio Tapajoz, medium sized tree in non-flooded wood by waterfall, 23 Sept. 1922 and 24 May 1923, Ducke 17686 (lectotype MG, not seen; isolectotype K, S).

Buchenavia rabelloana Mattos, Cienc. Cult. XIX: 33 (1967). Type: Brasil: Estado de São Paulo: Salesópolis, Estação Biologica de Boracéia, Perto do Rio Claro, 27-IV-1966, J. Mattos 13570 (holotype SP, not seen; isotype IRRN*) (paratypes, J. Mattos 13855 SP, Kuhlmann 4335 SP).

Shrub or small tree, 5-8 m high, 10 cm diameter. Petiole very short and slender, 2-5 mm long, pubescent eglandular. Lamina chartaceous, rather small, 1.5-4 x 0.5-2 cm, narrowly obovate to obovate or oblanceolate; apex rounded to obtuse or retuse or acute; base cuneate; upper surface very

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*Instituto de Pesquisas de Recursos Natarais Renovaveis of the Secretaria da Agricultura, Porto Alegre, Rs. (Mattos personal com.)

sparsely pubescent or almost glabrous except the primary vein; lower surface usually sparsely pubescent except densely pubescent on the primary vein; domatia usually present. Venation brochidodromous; primary vein moderate or fine sometimes slightly raised below; secondary veins 5-12 pairs, fine, not raised, sometimes inconspcuous; tertiary veins ramified or reticulate; higher-order venation inconspicuous. Inflorescence capitate - subcapitate; peduncle 1-2 cm long, slender; rachis 2-4 mm long. Flowers 2-4 mm long, usually glabrous. Fruit ellipsoid or ovoid, 14-20 mm long, usually apiculate or acute but sometimes rounded or obtuse at the apex, acute or rounded at the base, glabrous; endocarp very slightly longitudinally ridged or furrowed. Circular in section. (Appendix 4 Pl. 15D).

Geographical range: Brazil, Venezuela, Colombia and Guyana. (Map 9/10).

Ecology: Frequent in the Amazon, growing in non-flooded, dense and low elevation forest (at altitude 100-300 m), flowers August and March.

Common name: Cumeiyo (in Venezuela); Amuvelinho (in Brazil).

Comments: This species is closely related to B. capitata but it can be easily distinguished from it by its smaller leaves, less dense inflorescences and glabrous ovary. The fruits are similar to those in B. capitata but they are usually smaller.

Although Buchenavia rabelloana occurs in the state of São Paulo in Brazil, which is very far from the main range of distribution of B. parvifolia, its inflorescence, flowers, fruits and leaf shape and size are identical to those in B. parvifolia. It differs only in having slightly more coriaceous leaves with fewer secondary veins, and accordingly I include it in B. parvifolia.

3. Buchenavia tetraphylla (Aublet) Howard, J. Am. Arb. 64: 266 (1983).
   Cordia tetraphylla Aublet, Hist. Pl. Guiana 1: 224, t. 88 (1775).
      Type: Loc. cit., t. 88 pro parte (leafy branch & fruits).

Buchenavia capitata (Vahl) Eichler, Flora 49: 165 (1866).

Bucida capitata Vahl, Ec log. Amer. 1 : 50, t. 8 (1796). Type: Montserrat, Ryan (holotype C; isotypes BM, C).

Hudsonia arborea A. Robinson ex Lunan, Hist. Jam. 2: 310 (1814). Type: ?

Terminalia obovata Cambess. in A. St. Hil, Fl. Bras. Merid. 2: 241 (1829), not T. obovata (Ruiz Lopez & Pavon) Steudel, Nom . Bot., ed. 2, 2: 668 (1841) = Terminalia amazonia. Type: Brasil; Minas Geraes, Vulgo Carascos, Montis Serra Negra, St. Hilaire (not seen).

Terminalia hilariana Steudel, Nom. Bot. ed. 2, 2: 668 (1841), nom. illegit. for T. obovata Cambess.

T. capitata Suavalle Fl. Cuba : 38 (1868).

Bucida angustifolia Spruce ex Eichler in C. Martius, Fl. Bras. 14 (2) 96 (1867), nom. synon. illegit.; non B. angustifolia DC. (1828) nec A. Rich. (Type: Brasil, prope manaos Olim Villa da Barra do Rio Negro, Spruce 1662 (syntypes A + GH, BP).

Buchenavia vaupesana Cuatrec. in Fieldiana, Bot. 27 (1): 108 (1950). Type: Colombia: Amazonas, Cuatrecasas 6828 (holotype U).

Buchenavia ptariensis Steyerm. in Fieldiana, Bot. 28: 423 (1952). Type: Venezuela, Steyermark 60038 (F, holotype, not seen).

Buchenavia gracilis Glaz., Mem. Soc. Bot. France 1 (3): 203 (1908), nom. nud.

Buchenavia macabensis Glaz. Mem. Soc. Bot. France 1 (3): 203 (1908), nom. nud.

Small to medium sized tree or shrub, 2-25 m high, 30-50 cm diameter. Petiole 4-20 mm long, usually rather stout, sparsely - densely pubescent, eglandular. Lamina subcoriaceous or coriaceous when mature, 2-10 x 1-5 cm, narrowly to broadly obovate; apex retuse or rounded, sometimes obtuse or subacute; base cuneate, sometimes decurrent into the petiole; upper surface usually glabrous; lower surface densely pubescent when very young, glabrous except on the primary and sometimes secondary veins when mature; domatia usually present. Venation brochidodromous; primary veins moderate and slightly raised below; secondary veins 2-7 pairs, usually fine, occasionally slightly raised below; tertiary veins randomly reticulate but sometimes irregularly percurrent; higher-order venation not distinct; areolation imperfect. Inflorescences capitate with peduncle usually longer than rachis; peduncle 6-26 cm long, usually rufous pubescent when young, almost glabrous when mature; rachis very short, up to 10 mm long, often less than 5 mm long. Bracts very small and caducous; flowers 2.5- 5 mm long; lower receptacle 1.5-3 mm long, densely rufous - sericeous; upper receptacle 1-1.5 mm long, glabrous or slightly pubescent. Fruit ellipsoid, ovoid or 5-ridged to subterete, 10-30 x 8-22, acute to broadly obtuse but sometimes rounded or apiculate at apex, usually shortly pseudostipitate at base, glabrous or rarely sparsely pubescent. Endocarp longitudinally ridged, usually 4 or 5 ridges more prominent than the rest. (Appendix 4 Pl. 15A).

Geographical range: Brazil, Bolivia, French Guiana, Surinam, Venezuela, Colombia, Panama and West Indies from Cuba to Trinidad. (Map 9/10).

Ecology: The most common species of Buchenavia. It grows in various habitats but it is common in lowland forest and along river banks. It is found at altitudes 50-1200 m. Flowers March-April and August.

Common name: Imirindiba, Cuirana, Tanibuca (in Brazil); Huapomocillo (in Bolivia); Toekadi, Gemberhout (in Surinam); Casabe, Amarillo (in Venezuela).

Comments: Buchenavia gracilis was based on Glaziou 5855 from Rio de Janeiro, Brazil. I have examined the specimens in C, P and S. Although all specimens consist of young sterile material, they certainly belong to Buchenavia and are almost certainly conspecific with B. tetraphylla.

Buchenavia macahensis was based on Glaziou 18218 from Rio de Janeiro, Brazil. I have examined the specimens in LE and P. They consist of only leaves and very young inflorescences. They differ from typical B. tetraphylla only in having slightly narrower leaves with subacute apex and this comes well within the range of variation of B. tetraphylla.

B. vaupesana falls within the range of variation shown by B. capitata.

B. ptariensis has not been seen by me; it is accepted as a synonym of B. tetraphylla by Exell & Stace (1963).

The leaves of B. tetraphylla show considerable variation in size and sometimes in the shape of the apex, but the general shape remains fairly constant. The inflorescences also show considerable variation in the length of the rachis and number and size of flowers.

The paper by Howard (1983) came to my notice at the last moment. Following correspondence with R. A. Howard it was decided to adopt the name B. tetraphylla for the present species in this chapter, although in all previous chapters the name B. capitata was used.

4. Buchenavia kleinii Exell, Ann. & Mag. Nat. Hist., Ser. 12, 6: 400 (1953). Type: Brasil: Santa Catarina: Mata do Hoffmann, Brusque, 13 Jan. 1951, Klein 22 (holotype S; isotype BM).

Buchenavia igaratensis N. Mattos, Loefgrenia 24: 1 (1967). Type: Brasil: Estado de São Paulo: Santa Isabel, Igarata, 12. XII. 1951, Moyses Kuhlmann 2751 (SP, holotype).

Medium sized tree, 8-30 m high, 25-50 cm diameter. Petiole 8-33 mm long. Lamina chartaceous to subcoriaceous, 2-10 x 1.5-6 cm, obovate to broadly obovate; apex rounded or obtuse or subacute or apiculate, base cuneate to narrowly cuneate; upper surface densely pubescent to glabrous; lower surface densely pubescent when young becoming glabrous except on the primary and secondary veins when mature; domatia present. Venation brochidodromous or eucamptodromous brochidodromous; primary vein moderate, slightly raised below; secondary veins 4-8 pairs, moderate; tertiary veins randomly reticulate or weakly percurrent; higher-order venation distinct or not; areolation incomplete or/and imperfect. Inflorescence capitate; peduncle 10-20 mm long; rachis very short. Flowers 2-4 mm long; lower receptacle densely pubescent; upper receptacle more or less glabrous. Fruit ellipsoid or obovoid 15-30 x 10-15 mm, apiculate or rounded at the apex, densely puberulous, becoming less hairy when very old. Endocarp slightly longitudinally ridged. (Appendix 4 Pl. 15 B & C).

Geographical range: Southern Brazil. (Map 9/10).

Ecology: This species is fairly common in the south-eastern corner of Santa Catarina and frequent in Parana and Sao Paulo. It may also occur in Rio Grande do Sul and farther north-east to Rio de Janeiro. Flowers March.

Common name: Garajuva, Guarajuba.

Comments: *Buchenavia igaratensis* (known only by its holotype from Sao Paulo) differs from typical *B. kleinii* only by having slightly longer petioles and slightly narrower leaves, but it comes within the range of variation of *B. kleinii*.

B. kleinii is very closely related to *B. capitata*.

5. *Buchenavia pallidovirens* Cuatrec. in Fieldiana, Bot. 27 (1) : 107 (1950).

Type: Colombia : Valle Costa del Pacífico, Bahia de Buenaventura, Quebrada de San Joaquin, 0-10 m., "Arbol grande. Racimes Péndulos verdoso amarillentos, Perianto verde amarillento claro. Anteras amarillas", 23 Feb. 1946, Cuatrecasas 19939 (holotype F, not seen; isotypes BM, U, US).

Small to large-sized tree, 2-35 m high, 20-40 cm diameter. Petiole 5-15 mm long, pubescent, usually biglandular. Lamina subcoriaceous or sometimes coriaceous, 3-16 x 1-3.5(4), oblanceolate to narrowly elliptic or oblong-lanceolate or narrowly obovate, abruptly apiculate or shortly acuminate or mucronate at the apex, narrowly cuneate but scarcely decurrent into the petiole at the base; upper surface more or less glabrous except the primary vein; lower surface sparsely and minutely pubescent or nearly glabrous except pubescent or sparsely pubescent on the primary and secondary veins; domatia usually present. Venation eucamptodromous; primary vein moderate; secondary veins 5-7 pairs, moderate, often prominently raised below, diverging at narrowly or sometimes moderately acute (20° - 50°) angles, curving abruptly inwards towards the apex; tertiary veins percurrent, not raised, higher-order venation often distinct; areoles well developed, very small and usually orthogonally arranged. Inflorescence distinctly elongate; peduncle 20-35 mm long, slender, sparsely pubescent; rachis 40-70 mm long, pubescent; flowers 2-3.5 mm long; lower receptacle densely pubescent; upper receptacle pubescent. Fruit ellipsoid, sometimes terete or slightly flattened, 10-17 x 6-13 mm, subacute to rounded or subtrancate at both ends, glabrous or pubescent.

Geographical range: Brazil (Amazonas), Venezuela, Colombia and Peru. (Map 9/9).

Ecology: Shrubs or large trees grow near rivers at low or high altitudes. Flowers February and October.

Common name: Yampig.

Comments: This species is characterized by its distinctive leaf-venation, particularly the secondary veins and areolation.

6. Buchenavia suaveolens Eichler, Flora 49: 166 (1866). Type Brazil: Rio Negro, between Barra and Barcellos, Nov. 1851, Spruce 1887 in part (lectotype LE; isolectotypes BM, BP, C, FI, K, NY, W).

Buchenavia oxycarpa Eichler, Flora 49: 165 (1866) pro parte, quoad Schomburgk 854.

Terminalia suaveolens Spruce ex Eichler, Fl. Brasil. 14 (2) : 97 (1867), nom. syn.

Terminalia vasivae Spruce ex Eichler, loc. cit. (1867) nom. syn.

Buchenavia pterocarpa Exell & Stace, Bull. Brit. Mus. (Nat. Hist.) Bot. 3 (1) : 23, fig. 3 and (1963). Type: Venezuela: Amazonas, occasional along Rio Yatua, near Laja Catipan, Casiquiare, 100-140 m., "flat-topped riverine tree, 6-8 m high, fruit green", 6 Feb. 1954, Maguire, Wurdack & Bunting 37543 (BM, holotype).

Small to medium-sized tree, 5-20 m tall, 10-20 cm diameter. Petiole 3-20 mm long, sparsely puberulous, eglandular. Lamina coriaceous or sometimes subcoriaceous, oblanceolate to narrowly obovate or narrowly elliptic or obovate; apex rounded to obtuse of retuse; base narrowly cuneate and scarcely decurrent into the petiole; both surfaces almost glabrous except the primary vein; domatia absent. Venation brochidodromous or weakly brochididromous; primary vein moderate, sometimes slightly raised below; secondary veins fine or weak, 6-10 pairs, inconspicuous, occasionally very scarcely raised below, diverging at moderately to widely acute angles; tertiary veins and higher-order venation not distinct and very inconspicuous; areoles lacking. Inflorescence slightly to distinctly elongate; peduncle 10-25 mm long, slender, sparsely pubescent or puberulous; rachis 15-65 mm long, slender, sparsely pubescent. Flowers 2-4 mm long, densely pubescent round the ovary, sparsely puberulous on the upper receptacle. Fruit ellipsoid to obovoid, more or less terete, or flattened often with two narrow lateral wing-like projections and one to three small ridges, 14-30 x 8-16 mm, apiculate or distinctly beaked at the apex, rounded or shortly pseudostipitate at the base, glabrous; beak short 1-4 mm long, straight or curved; endocarp ellipsoid ridged, circular or irregularly ridged but with 2 prominent lateral angles in section. (Fig. 9/30).

Geographical range: Brazil and Venezuela (Map 9/9).

Ecology: This is a riverine species of land liable to flooding. Flowers April and November to December.

Fig. 9/30: Buchenavia suaveolens

Comments: This is a very distinct species. It is characterized by its distinctive basic venation type and also fruits. The venation type is more or less similar to that in sections Pachyphylla and Ramatuella of Terminalia. The fruits show considerable variation in their shape varying from completely terete with straight beak to distinctly ridged or flattened with a curved beak. The leaves also vary considerably in shape.

B. pterocarpa, which differs from B. suaveolens in having narrower leaves and a strongly flattened, ridged fruit, falls within the wide range of variation of B. suaveolens.

7. Buchenavia oxycarpa (C. Martius) Eichler, Flora 49: 164, t. 3 figs. 17, 18, 20, 21 (1866), excl. Schomburgk 854

Terminalia oxycarpa C. Martius, Flora 24, Beibl. 2: 22 (1841). Type: Brasil: Amazonas: in inundations on the bank of the river Solimões, near Ega and elsewhere in the province of Rio Negro, 1820, Martius (M, lectotype).

Buchenavia punctata Eichler, Flora 49: 166 (1866). Type: Peru : San Martin, in rocky stream, near Tarapoto, "Arbore 25 pedalis ramis paucis longis validis brevi-ramulosis", 1855-56, Spruce 4945 (lectotype BR, not seen; isolectotype BM, G, K, NY, W).

Terminalia punctata Spruce ex Eichler in Martius, Fl. Bras. 14 (2): 98 (1867), nom. synon. illegit., non T. punctata Roth (1821), nec Eichler (1867).

Small or occasionally medium-sized tree, 2-8(20) m high, 8-15 cm diameter. Petiole 4-25 mm long, usually glabrous but sometimes pubescent to sparsely pubescent, eglandular. Lamina usually chartaceous but sometimes subcoriaceous - coriaceous, 1-15 x 0.5-5 cm, very narrowly obovate or oblanceolate or narrowly elliptic or obovate, rounde or acute to subacute at the apex, narrowly to very narrowly cuneate at the base, sparsely to very sparsely pubescent to almost glabrous on both surfaces except pubescent on the primary and secondary veins; domatia present. Venation brochidodromous or eucamptodromous - brochidodromous; primary vein moderate, slightly to sometimes prominently raised below; secondary veins (4) 6-9(12) pairs, moderate, tertiary veins weakly percurrent or randomly reticulate, not raised; higher-order venation often distinct; areoles imperfect, usually small. Inflorescence slightly to distinctly elongate spike, peduncle 3-6 cm long, pubescnet; rachis 3-7 cm long, slender, pubescent. Flower 2-4(5) mm long; lower receptacle usually sparsely pubescent to almost glabrous but sometimes densely pubescent on the ovary when young; upper receptacle glabrous. Fruit ellipsoid, distinctly 5-6 angled, 19-32 x 9-20 mm, long beaked or rarely apiculate at the apex, rounded to obtuse or shortly pseudostipitate at the base, glabrous; beak 3-10 mm long, pointed, straight or curved; endocarp distinctly longitudinally ridged, usually 5-angled in section.

Geographical range: Brazil, Peru, Colombia and Venezuela. (Map 9/9).

Ecology: Common in the Amazon, usually in flooded forest at low altitudes. Flowers January, April and October to November.

Comments; This is a very distinct species. The most distinctive character is the fruit, which is glabrous, distinctly beaked and almost 4-6 angled. Buchenavia punctata appears to be a distinctive specimen from the extreme west of the range.

8. Buchenavia fanshawei Exell & Maguire, Bull. Torr. Bot. Club 75: 648 (1948). Type: British Guiana; Riverside below Tukeit, Potaro River Gorge, rare, 16 May 1944, Maguire & Fanshawe 23499 (holotype NY, not seen; isotypes BM, K, MO).

Medium to large-sized tree, 10-30 m high, 15-40 cm diameter. Petiole 6-24 mm long, moderate, pubescent to slightly pubescent, almost eglandular. Lamina subcoriaceous to coriaceous (1) 3-15 x 0.5-6 cm, obovate or narrowly obovate or narrowly elliptic; apex rounded or slightly acuminate or acute; base cuneate; upper surface glabrous except slightly pubescent on the primary vein; lower surface very sparsely pubescent or glabrous except pubescent on the primary and secondary veins; domatia almost always present and lebetiform. Venation brochidodromous; primary veins moderate and prominently raised below; secondary veins 3-5 pairs, modererate and usually raised below; widely spaced, originating at acute or obtuse angles but the upper ones almost perpendicular to the primary vein; tertiary veins randomly reticulate or irregularly percurrent and raised below; higher-order venation sometimes distinct; areoles usually incompletely closed or lacking. Inflorescence slightly elongate; peduncle 6-30 mm long, slender, pubescent; rachis 0.7-4 cm long, densely puberulous. Flowers 2-4 cm long; lower receptacle densely rufous pubescent or puberulous; upper receptacle sparsely puberulous. Fruit ovoid or ovoid-ellipsoid or oblong-ovoid, 17-25 x 11-15 mm, rounded to acute or rarely apiculate or shortly acuminate at the apex, rounded or shortly pseudostipitate at the base, usually densely tomentellous but becoming almost glabrous when very old. Endocarp slightly longitudinally furrowed or ridged, acute to obtuse at both ends, more or less circular in section.

Geographical range: Guyana and Amazonian Brazil. (Map 9/9).

Ecology: This species grows on sandy soil along river banks and in woods. Flowers May to June.

Common name: Fukadi of Sand Fukadi.

Comments: *B. fanshawei* is very closely related to *B. macrophylla*. Sometimes the two species are hardly separable, particularly in the Manaus area, where they overlap. However, the distinctive domatia and the usually smaller leaves with fewer secondary veins make its identification usually possible.

9. Buchenavia sericocarpa Ducke, Bol. Técn. Inst. Agron. Norte 4: 23 (1945).
Type: Brasil: Amazonas: Manãos, Estrada do Bombeamento, "Capoeirão, terra firme, árvore pequena", 26 Nov. and 30 Dec. 1943, Ducke 1481 (holtype RB, not seen; isotype K).

Buchenavia acuminata Exell & Stace, Bull. Brit. Mus. (Nat. Hist) Bot. 3(1) : 29 (1963). Type : Brasil: Amazonas: humayta, near Livramento, on Rio Livramento, basin of Rio Madeira, on terra firma, "tree 60 ft. high", 12 Oct.- 6 Nov. 1934, Krukoff 6916 (holotype BM; isotypes F, K).

Small to medium-sized tree 5-20 m high, 10-25 cm diameter. Petiole 7-30 mm long, pubescent, often biglandular. Lamina chartaceous or subcoriaceous 2-13.5 x 0.8-6 cm, narrowly elliptic to elliptic; apex usually long acuminate or sometimes subacute or rarely obtuse; base narrowly cuneate; upper surface almost glabrous except slightly pubescent on the primary vein; lower surface very sparsely pubescent to almost glabrous except pubescent to sparsely pubescent on the major veins; domatia present; venation brochidodromous or eucamptodromous - brochidodromous; primary vein moderate, raised below; secondary veins 5-10 pairs, moderate, raised below; tertiary veins weakly percurrent or randomly reticulate; higher-order venation not distinct; areoles often lacking or incomplete and large. Inflorescence slightly to distinctly elongate; peduncle 7-30 mm long, sparsely appressed-pubescent; rachis 1.5-3 cm long, pubescent. Flower 2-3.5 mm long; ovary densely pubescent; upper receptacle, sparsely puberulous. Fruit ellipsoid to obovoid or ellipsoid-oblong, more or less terete, 15-25 x 50-10 mm, rounded at apex, rounded or shortly pseudostipitate at base, densely silvery-grey or brown-tomentellous.

Geographical range: Brazil and Colombia (Amazonas). (Map 9/10).

Ecology: This is a tree of terra firma in the Amazon basin.

Comments: In the key given by Exell & Stace (1963) this species falls under B. capitata group on the basis of possessing short rachis. In fact the species possesses a long rachis but the isotype at K examined by Exell and Stace had a broken one. B. sericocarpa is a distinct species characterized by its long acuminate leaf apex. B. acuminata has been recognized as a separate species from B. sericocarpa on the basis of its long rachis, but this difference no longer exists.

10. Buchenavia hoehneana N. Mattos, Loefgrenia 21: 1 (1967). Type: Brasil: São Paulo, Caraguatatuba, na estrada de São Sebastião, 8/XII/1939, Hoehne & Gehrt s.n. (holtype SP 41860, not seen; isotype LTR).

Tree, 10 m high, 25 cm diameter. Leaves usually very densely clustered at the tip of the branchlets; petiole 1-2 cm long, moderate, tomentellous, usually biglandular; lamina subcoriaceous to coriaceous, rather stiff, (4) 6-14.5 x 1.5-5 cm, oblanceolate or narrowly obovate oblong; apex rounded to apiculate or shortly and abruptly acuminate; base narrowly cuneate; upper surface pubescent to very sparsely pubescent; lower surface usually pubescent to sparsely pubescent except densely pubescent on the primary and secondary veins; domatia absent but tuffet of hairs sometimes present. Venation brochidodromous; primary vein moderate, prominently raised below; secondary veins (4)6-12 pairs, moderate, raised below; tertiary veins fine, percurrent and usually widely spaced, oblique or perpendicular to the midvein; higher-order venation often distinct; areoles small and well developed. Inflorescence slightly to distinctly elongate; peduncle (in fruit) 1-8 cm long, slightly to densely pubescent; rachis (in fruit) 3-4 cm long, densely pubescent. Flowers unknown. Fruit ellipsoid or ovoid-ellipsoid, 1.5-2.3 x 1-1.3 cm, rounded to obtuse or subacute at the apex, rounded at the base, sometimes very shortly pseudostipitate, densely silvery or grey-pubescent.

Geographical range: Southern and southeastern Brazil. (Map 9/11).

Comments: This species was until recently known only from its type from São Paulo, but another specimen has been collected from Bahia (Belem & Pinheiro 3280 in UB). The leaves of this species show some similarity with those of B. congesta but its fruits are densely pubescent and its distribution is far from that of B. congesta.

11. Buchenavia grandis Ducke, Arch. Jard. Bot. Rio Janeiro 4: 148 (1925).
    Type: Brazil: Pará, Oriximná by Rio Trombetus, 5 Feb. 1918, Ducke 16976 (lectotype MG, not seen; isolectotype P, US).

  Buchenavia huberi Ducke, Bol. Técn. Inst. Agron. Norte 4: 24 (1945).
    Type: Brazil, Amazonas: Manaos, vicinity of the Cachoeira do Mindu, on "terra firme", "árvore grande", 3 Dec. 1943, Ducke 1450 (lectotype RB, not seen; isolectotype K).

Medium to large-sized tree, occasionally shrub (in Venezuela), (3) 15-30 m high, 16-100 cm diameter. Petiole (5) 10-28 mm long, pubescent to sparsely pubescent, eglandular or biglandular near the apex. Lamina subcoriaceous to corieaceous when mature, 2.5-16 x (1.3) 2-7 cm, narrowly obovate or obovate or obovate elliptic; apex rounded to obtuse or subacute or rarely apiculate or retuse; base narrowly cuneate sometimes scarcely decurrent into the petiole; upper surface almost glabrous; lower surface usually glabrous sometimes sparsely pubescent or puberulous; domatia often present. Venation brochidodromous or eucamptodromous - brochidodromous; primary vein moderate and raised below; secondary veins 5-10 pairs, moderate, usually slightly raised below; tertiary veins randomly reticulate ro irregularly or regularly percurrent, not raised; higher-order veination usually indistinct; areolation imperfect. Inflorescence distinctly elongate; peduncle 12-24 mm long, greyish or rufous-puberulous; rachis slender 2.2-10 cm long, rufous or cano-puberulous; flowers 3-4 cm long glabrous or pubescent. Fruit ellipsoid to ellipsoid ovoid, more or less terete or slightly 4-5 angled, 24-35 x 11-16 (25) mm, apiculate at apex, shortly pseudostipitate at the base, glabrous or pubescent. Endocarp longitudinally ridged, acute to subacute at the apex rounded or acute at the base, more or less circular in section.

Geographical range: Brazil, Colombia, Venezuela, Guyana, Surinam and Peru. (Map 9/11).

Ecology: *B. grandis* is a very tall tree of forest on dry ground. Flowers August and September.

Common name: Tanibuca.

Comments: This species is very closely related to *B. congesta*. It differs from *B. congesta* in having smaller leaves which are rounded to obtuse at the apex while those of *B. convesta* are usually abruptly acuminate at the apex. However, *B. grandis* is a very variable species. Its fruits and leaves vary considerably in their shape, size and amount of indumentum.

The fruits of *B. grandis* vary from glabrous to densely pubescent. *B. huberi* represents the extreme form of pubescence.

12. *Buchenavia amazonia* Alwan, sp. nov.

Frutex vel arbor parva, 2-8 m alta. Folia spiraliter ordinata ad ramulorum apices congesta; petiolus 0.8-2 cm longus, dense rufo-pubescens, biglandulosus; lamina chartacea, (2) 3-8 (12.5) x 1.5-4(5.5)cm, obovata vel anguste obovata vel elliptica, apice rotundata - obtusata vel acuminata - subacuta, basi cuneata, supra fere glabra, subtus fere glabra venis primariis secondariisque sparse pubescentibus exceptis; venatio brochidodroma vel eucamptodromo - brochidodroma; costa media moderata, infra prominens; venae secondariae infra prominentes, 5-7 paribus; venae tertiariae irregulariter percurrentes sed conspicuae; areolae parvae, perfecte effectae. Inflorescentiae elongato - spicatae; pedunculus gracilis, 0.5-1.5 cm longus, rufo-pubescens; rachis 1.5-3 cm longa, pubescens. Flores 2-3 x 2.3 mm; receptaculum inferum 1-2 mm longum, infime tomentosum; receptaculum superum glabrum. Fructus ellipsoideo-ovoideus, 1.3-2 x 0.7-1.2 cm, apice rotundatao - obtuso vel subacuto vel breviter apiculato, basi rotundata - obtusa, sparse puberula.

Holotype: Colombia: Wet tropical forest of Amazon basin: Solano, 8 km. SE. of Tres Esquinas, on Rio Coquetá below mouth of Rio Orteguaza, Comisaria de Caquetá."Tree 8 m. high, 20. DBH. Bark brown, smoothish. Frts. green, oblong. Wet soil of old channel, near river. (Mature frts. No 4730.) Grass pasture of cleared lowland forest and in lowland forest. Trip on foot 1.km. N. of Solano. Altitude 200 meters", March 7 1945, Little and Little 9626 (US) (Isotype: COL).

Tree of shrub, 2-8 m high, 20 cm diameter. Petiole 0.8-2 cm long, densely rufous pubescent, often biglandular. Lamina chartaceous, (2)3-8(12.5) x 1.5-4(5.5) cm, obovate or narrowly obovate to elliptic; apex rounded to obtuse or acuminate to subacute; base cuneate; upper surface almost glabrous, lower surface almost glabrous except sparsely pubescent on the primary and secondary veins; domatia present or not. Venation brochidodromous or eucamptodromous - brochidodromous; primary vein moderate, raised below; secondary veins 5-7 pairs, moderate, usually prominently raised below; tertiary veins irregularly percurrent but conspicuous; higher-order venation distinct and conspicuous; areoles well-developed and very small. Inflorescence elongate spike; peduncle 0.5-1.5 cm long, rufous pubescent; rachis 1.5-3 cm long, pubescent. Flowers 2-3(4) x 2-3 mm; lower receptacle 1.2- mm long, tomentose round the ovary; upper receptacle glabrous. Fruit ellipsoid-ovoid, 1.3-2 x 0.701.2 cm, rounded to obtuse or subacute or very shortly apiculate at the apex, rounded to obtuse at the base, sparsely to very sparsely puberulous; endocarp very slightly longitudinally furrowed, circular in section.

Geographical range: Brazil (Amazonas), Colombia and Peru. (Map 9/11).

Ecology: A shrub or small tree growing in wet soil along edge of old channels in forests at low altitudes (200-275 m).

Comments: This species has some similarity with B. oxycarpa, particularly with respect to the general shape of the leaves, but it can be easily separated from it by its leaves, which have more conspicuous higher order venation and very close areolation, and by its fruits which lack a beak, are smaller in size, and are almost terete. The fruit of this species is somewhat similar to that of B. viridiflora

Specimen seen:

Colombia: same details as the holotype, Little & Little 9627 (COL, US); Little & Little 9730 (COL, US). Brazil: Basin of Rio Purus, Lábrea, Lago Preto, 3 km. north of Lábrea, Varzea forest" shrub 2 m. tall Fr-green. Growing on flooded bank", Oct. 29. 1968, Prance, Rames & Farias 8020 (A + GH, F, INPA, LTR, NY, US); Amazonas, Rio Tefé, Paxiubinha, Igapó, 12.6.1950, R. L. Fróes 26237 (BM). Perus: Loreto: Masisea "alt about 275 m. open woods. Tree 12-15 ft. fls pink", Killip & Smith 26866 (US); Loreto, Rio Tambor-Yaca., "Tree 6 m", 21 Sept. 1972, Croat 20596 (A + GH, MO).

13: Buchenavia viridiflora Ducke, Arch. Inst. Biol. Veg. Rio Janeiro 2: 63 (1935). Type: Brasil: Amazonas, Estrado do Aleixo, Manãos, in non-flooded forest, 15 July 1932, Ducke 25023 (lectotype MG, not seen; isolectotype K, S).

Small to large-sized tree 4-20(40) m high, 6-40 cm diameter. Petiole 4-16 mm long, pubescent usually eglandular but sometimes biglandular. Lamina subcoriaceous or chartaceous, 1-10 x 0.5-5.5 cm, oblanceolate to narrowly elliptic or elliptic or obovate; apex rounded or retuse to subacute or acute; base narrowly cuneate and often scarcely decurrent into the petiole; upper surface glabrous except sparsely pubescent on the primary vein; lower surface almost glabrous except pubescent to sparsely pubescent on the primary and secondary veins; domatia present. Venation brochidodromous or eucamptodromous - brochidodromous; primary vein moderate and raised below; secondary veins moderate 4-7 pairs, slightly raised below; tertiary veins randomly reticulate but sometimes weakly percurrent, not raised; higher-order venation not distinct and inconspicuous; areoles incomplete or lacking. Inflorescence slightly elongate, peduncle slender, 5-27 mm long, pubescent; rachis slender, 12-50 mm long, pubescent. Flowers 2.5-5 mm long; lower receptacle densely pubescent round the ovary; upper receptacle glabrous. Fruit terete or sometimes slightly flattened, rounded to subacute at both ends or sometimes shortly apciulate at the apex, densely greyish-brown-tomentellous or almost glabrous; endocarp longitudinally furrowed or ridged, more of less circular in section.

Geographical range: Brazil (Amazonas), Venezuela, Peru, Ecuador and Frech Guinana. (Map 9/11).

Ecology: A small to large tree of non-flooded forest. Flowers July-October.

Common name: Tanibouca, Yacushapana.

Comments: Much new material has been collected since Exell & Stace (1963) wrote their account, and it is now clear that this species is widely distributed and very variable.

14. Buchenavia tomentosa Eichler, Flora 49: 166 (1866). Type: Brasil: Minas Gerais, on sandy plains between Alegres and Rio Sao Francisco, "arbor 8-20 ped", Sept. 1834, Riedel 2641 (lectotype LE; isolectotypes BM, C, FI, K, W).

Terminalia tomentosa C. Martius ex Eichler in C. Martius, Fl. Bras 14, 2 (1867) nom. syn.

Buchenavia corrugata Ducke, Arch. Jard. Bot. Rio Janeiro 4: 150 (1925). Type: Brasil: Pará, Serra Pontada, in the Juthay region between Almeirim and Prainha "silva, arbor magna", 11 Sept. 1923, Ducke 17677 (holotype: MG, not seen; isotypes K,S).

Buchenavia callistachya Ducke, Arch. Inst. Biol. Veg. Rio Janeiro 2: 64 (1935). Type: Brasil: Amazonas, Manãos, near Estrada do Aleixo, in non-flooded wood. "Arbor. sat. magna, spicae anthesi pallide viridiflorae pedunculo brunneo-purpureo" 9 July and 26 Nov. 1932, Ducke 25021 (holotype MG, not seen; isotype K, S).

Small tree, 2-10 m tall, 5-35 cm diameter. Petiole stout, 3-18 mm long, densely rubiginous - or ferrugineous - velutinous at flowering time, eglandular or sometimes biglandular. Lamina chartaceous when young, subcoriaceous to coriaceous when mature, 3.5-24 x 1.5-10 cm, narrowly elliptic to elliptic or oblanceolate to obovate or oblong - elliptic, rounded or sometimes obtuse (when young) at the apex, cuneate at the base, inrolled at the margin when young; upper surface densely pubescent; lower surface ferrugineous - or rubiginous - tomentose but indumentum wearing off when very old; domatia absent. Venation eucamptodromous or eucamptodromous - brochidodromous; primary vein moderate or thick, prominently raised below; secondary veins moderate, 8-14 pairs, usually prominently raised below, diverging at moderately acute angles, tertiary veins percurrent or weakly percurrent rarely randomly reticulate, usually raised below; higher-order venation distinct, quaternary veins often raised below; areoles imperfect of well developed more or less orthogonally arranged. Inflorescence slightly or distinctly elongate, peduncle stout, 6-20 mm long, densely rubiginous - velutinous at flowering time; rachis (1.5) 3-12 cm long, densely rubiginous - velutinous when young. Flowers similar to those of B. reticulata; lower receptacele 2-3 mm long; upper receptacle 1.5-2 x 2.5-4, glabrous. Fruit ellipsoid to more or less spherical, often wrinkled when dry, 21-31 x 12-25 mm, nearly rounded at both ends or sometimes very shortly pseudostipitate at the base, very sparsely ferrugineous - to rubiginous - puberulous or glabrous when mature. (Appendix 4 Pl. 16 A-C).

Geographical range: Brazil (Central Brazil from Minas Gerais to Pará). (Map 9/11).

Ecology: A tree of dry ground to the south of the Amazonian area, growing in sandstone soil on Foothills at 500-600 m altitudes. Flowers September.

Buchenavia tomentosa is closely related to B. reticulata, although its distribution does not extend up to the Amazon. Its leaves show considerable variation in their size and the inflorescences vary considerably in the length of the rachis. B. callistachya differs from typical B. tomentosa only in possessing slightly shorter rachis but this comes well within the variation of B. tomentosa.

15. Buchenavia reticulata Eichler, Flora 49: 166 (1866). Type: Venezuela: Amazonas, on the Rivers Casiquiare, Vasiva and Pacimoni, 1853-54, Spruce 3453 in Part (lectotype BR, not seen; isolectotypes BM, K, LE, W).

Small to large tree, 3-35 m high, 15-100 cm diameter. Petiole stout, usually short, 0.6-3.2 cm long, ferrugineous or rubiginous - tomentose, usually biglandular. Lamina usually chartaceous but sometimes coriaceous, 4-30 x 1-9(12) cm, narrowly elliptic to oblanceolate; apex obtuse to acute or apiculate; base narrowly cuneate; upper surface sparsely pubescent becoming glabrous when very old except rufous tomentose or pubescent on the primary and secondary veins; lower surface usually ferrugineous - tomentose over the whole surface; domatia absent. Venation eucamptodromous - brochidodromous or eucamptodromous; primary vein moderate or thick, prominently raised below; secondary veins 5-15 pairs, prominently or very prominently raised below, diverging at acute angles; tertiary veins percurrent to weakly percurrent or sometimes randomly reticulate, usually raised below; higher-order venation distinct, quaternary veins often raised below; areoles imperfect or well developed. Inflorescence distinctly elongate; peduncle 2-4 cm long, stout, rufous tomentose rachis 3-14 cm long, rufous tomentose. Flower 3-5 mm long; lower receptacle ferrugineous - to rubiginous tomentose on the ovary, almost glabrous above it; upper receptacle almost glabrous. Fruit ellipsoid to narrowly ellipsoid often irregularly furrowed or ridged, sometimes slightly flattened, 19-45 mm x 8-30, apiculate or acuminate or more or less rounded at the apex, shortly pseudostipitate at the base, rubiginous to ferrugineous - tomentellous; endocarp slightly to markedly longitudinally furrowed, circular or irregularly ridged in section, sometimes with 2 lateral angles. Appendix 4 Pl. 16D).

Geographical range: Brazil, Venezuela and Colombia (Map 9/12).

Ecology: Common in the upper Amazon region, mainly on river banks. It occurs also in virgin forests and deep ravine at 200-400 m altitude. Flowers April-June and November-January.

Comments: This is a very distinct species characterized by its rather prominently raised venation and densely tomentellous fruits. However it shows considerable variation in the shape and size of the leaves and fruits.

16. Buchenavia megalophylla Van Heurck & Muell. Arg. in Van Heurck, Obs. Bot.: 211 (1870). Type: unknown.

Shrub or small tree, 3 m high. Petiole 12-23 mm long, thick, puberulous,biglandular. Lamina subcoriaceous, 14-35 x 5-14 cm, narrowly obovate to oblanceolate; apex shortly acuminate or apiculate; base narrowly cuneate but not decurrent into the petiole; upper surface more or less glabrous except sometimes pubescent on the primary and secondary veins; lower surface glabrous to sparsely puberulous except minutely pubescent on the primary and secondary veins; domatia absent. Venation eucamptodromous; primary vein thick and promently raised below; secondary vein moderate, prominently raised below, 9-14 pairs, slightly curved and widely spaced; tertiary veins percurrent, often sinuous; higher-order venation often distinct but not raised; areolation usually imperfect. Inflorescence long; peduncle 2-3 cm, rather stout, densely and minutely pubescent; rachis 7-13 cm long, moderate, tomentellous. Flowers 3-4 mm long; lower receptacle densely puberulous; upper receptacle glabrous. Fruit markedly and

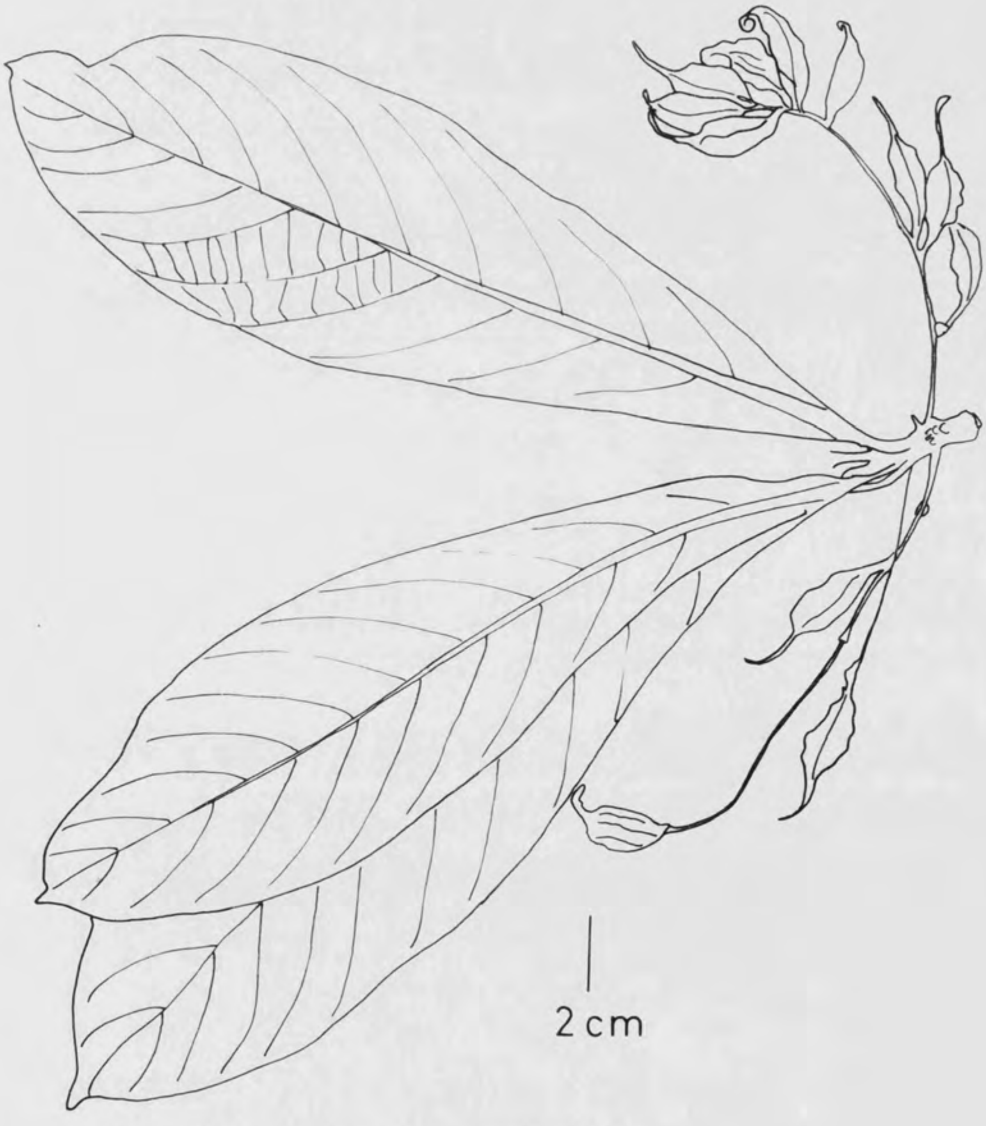


Fig. 9/31: Buchenavia megalophylla

irregularly 5-ridged, rather abruptly narrowed into a long acumen at the apex and into a pseudostipe at the base; body of fruit 18-26 x 11-13 mm; acumen 10-20 mm long, straight or markedly curved, slender or rather stout; pseudostipe 2-7 mm long. (Fig. 9/31 and Appendix 4 Pl. 17B).

Geographical range: Guyana (Map 9/12).

Comments: This species seems closely related to *B. macrophylla* and in the absence of fruits they often cannot be separated on any characters. The extremely distinctive fruits however, make its identification very definite.

17. *Buchenavia guianensis* Alwan, Comb. nov. Based on *Pamea guianensis* Aublet, Hist. Pl. Guiane 2: 946. t. 359 (1775). Type: Ex Herbarium Aublet (BM, holotype).

Terminalia pamea DC., Prod. 3: 13 (1828), based on *Pamea guianensis*.

Myrobalanus pamaea (DC.) Kuntze, Rev.. Gen.: 237 (1891).

Medium sized tree, 6-25m tall, 15-45 cm diameter. Leaves densely to very densely crowded at the end of the branchlets; petiole (0.5)2-7 cm long, moderate or rather thick, usually glabrous, often eglandular but sometimes conspicuously biglandular; lamina coriaceous (6)13-40 x (2) 4-9.5 cm, oblong-obovate to narrowly oblong-obovate or oblanceolate; apex long to short acuminate or sometimes apiculate; base narrowly or very narrowly cuneate, sometimes decurrent into the petile; upper surface almost glabrous except slightly pubescent or ciliate at the margins; lower surface usually glabrous or very sparsely pubescent except sometimes slightly pubescent on the primary vein and ciliate at the margin; margin often slightly revolute; domatia absent. Venation eucamptodromous; primary vein often thick, or moderate, prominently raised below;secondary veins 8-20 pairs, moderate, prominently raised below, diverging at moderately -widely acute angle; distal secondary veins usually more obtuse than the rest, often joining each other before the margin; tertiary veins oppositely or irregularly

Fig. 9/32: Buchenavia guianensis

percurrent, usually not raised below but conspicuous; higher-order venation usually distinct; areoles often well developed and small. Inflorescence distinctly elongate; peduncle 2-3 cm long, glabrous or slightly pubescent; rachis 5-13 cm long, rufous pubescent. Flowers 3-5 mm long; lower receptacle 2-3.5 mm long, densely pubescent becoming glabrous soon; upper receptacle 1-15. x 3 mm, glabrous outside, densely pubescent inside; calyx teeth very small. Fruit ovoid or ellipsoid or ellipsoid-oblong or oblong, with 6 angles of which 3 are more prominent than the others, 3-6.5 x 1.3-4 cm, obtuse to acute or sometimes shortly and bluntly acuminate at the apex, rounded to obtuse at the base, without pseudostipe, glabrous but not shiny, with scaley and rusty coloured surface. Endocarp distinctly longitudinally angled, rounded at base, subacute at apex, trinagular in section. (Fig. 9/32).

Geographical range: Brazil (Amazonas) and French Guiana. (Map 9/12).

Common name: Tanimbuca, Guirana, Tanimbuca f. Grande.

Comments: This very distinct species differs from all the others in its characteristic fruits, and can also be distinguished by its large leaves with long petioles. We have not been able to trace a specimen in P, and the type in BM lacks fruits.

18. Buchenavia nitidissima (Rich.) Alwan, Comb. nov.

Terminalia nitidissima Rich., Act. Soc. Hist. Nat. Par. 1: 109 (1792).

Type: Guyane Francaise, M. Le Blond, 1792 (G, holotype).

Myrobalanus nitidisssima (Rich.) Kuntze, Rev. Gen.: 237 (1891).

Large-sized tree, 30-45 m high, up to 200 cm diameter. Leaves crowded at the end of the branchlets; petiole 1.5-3 cm long, rather thick, almost glabrous, eglandular; lamina coriaceous to thickly coriaceous, (8) 12-23 x 4.5-8.5, elliptic to elliptic oblong or oblanceolate or oblong. Apex rounded to obtuse or apiculate orsubacute; base attentuate or narrowly cuneate, slightly decurrent into the petiole; upper surface glabrous and shiny; lower surface glabrous and shiny except very sparsely pubescent on the primary vein; domatia absent. Venation eucamptodromous; primary vein moderate, prominently raised below; secondary veins 5-9 pairs, moderate, slightly raised below; tertiary veins percurrent, occasionally randomly arranged; higher-order venation distinct; areolation usuallly orthogonally reticulate. Infructescence distinctly elongate, peduncle 5 cm long, rather stout; rachis 7-11 cm long, rather stout. Fruit oblong ellipsoid or ovoid to ovoid ellipsoid, 2.8-4 x 1.5-1.8 cm, rounded at the apex, distinctly pseudostipitate at the base, densely rufous tomentellous, with slightly longitudinally furrowed surface. Endocarp distinctly longitudinally furrowed or slightly ridged, very hard to cut through, more or less circular in section. (Fig. 9/33 and Appendix 4 Pl. 17C).

Geographical range: French Guiana Map 9/13.

Ecology: A large tree with buttresses to 2.5 m high, grows in tropical moist forest at 200-400 m altitude.

Common name: Amanier Sauvage.

Comments: Terminalia nitidissima was based on a sterile specimen collected by Le Blond (1792) from French Guiana. Although the specimen at G is not annotated by Richard, it agrees completely with the original description. Since it is sterile it is quite difficult to place the specimen in its correct genus. However, the two specimens (Olde man 2473 and Lescure 122) collected recently from Cayenne (and identified as Terminalia pamea), possessing leaves very similar to those of the Le Blond specimen and fruits, clearly show that T. nitidissima is a species of Buchenavia.

Buchenavia nitidissima is a very distinct species characterized by its pseudostipitate densely rufous tomentellous fruits and its large, coriaceous, glabrous, brownish leaves when dry.

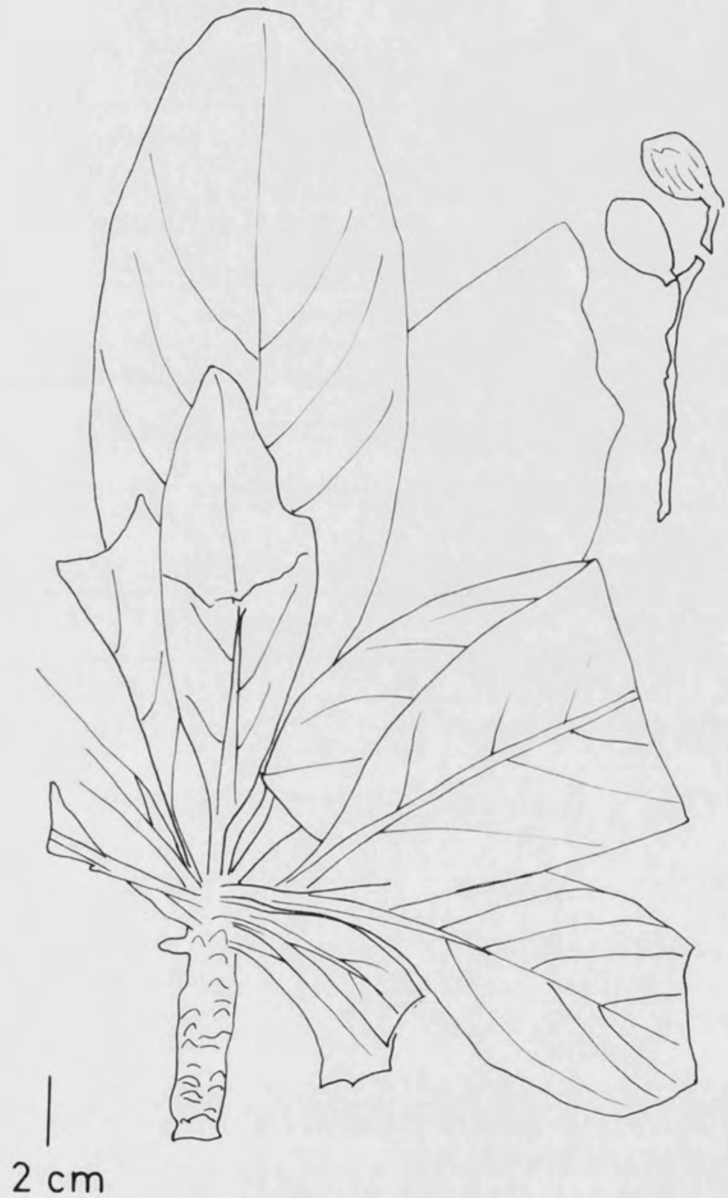


Fig. 9/33: Buchenavia nitidissima

19. Buchenavia congesta Ducke, Trop. Woods 90: 24 (1947). Type: Brasil: Amazonas, Manáos, near Cachoeira do Mindú in a non-flooded wood in a humid spot, "arbor sat. magna", 3 Dec. 1943, Ducke 2003 (lectotype RB, not seen; isolectotype INPA).

Buchenavia longibracteata Fróes, Bol. Técn. Inst. Agron. Norte 20:53, t. 16 (1950). Type: Brasil: Amazonas, Cachoeira das Araras, Rio Vaupés, "arvore, 5 m", 1 Nov-1945, Fróes 21308 (holotype IAN, not seen; isotypes K, NY, US).

Small to medium-sized tree 5-20(30) m high, 15-30 cm diameter. Petiole (6)10-30 mm long, moderate, minutely pubescent, eglandular or biglandular. Lamina chartaceous or subcoriaceous, 8-23 x 3-9 cm, oblanceolate, narrowly obovate or obovate; apex shortly and abruptly acuminate or apiculate; base narrowly cuneate sometimes decurrent into the petiole; upper surface almost glabrous; lower surface usually sparsely pubescent to almost glabrous except minutely rufous pubescent on the primary and secondary veins; domatia absent. Venation eucamptodromous; primary vein moderate - thick and prominently raised below; secondary veins 9-16 pairs, moderate and usually raised below; tertiary veins always percurrent and usually narrowly spaced; higher-order venation often distinct; areoles imperfect or sometimes well developed. Inflorescence distinctly elongate; peduncle 18-37 mm long, rather slender, densely rubiginous-puberulous at flowering time; rachis long, usually 5-11 cm long, rather slender, densely pubescent. Bracts small or sometimes large up to 13 mm long. Flowers 3-4 cm long; lower receptacle densely-puberulous or pubescent; upper receptacle glabrous or very sparsely puberulous. Fruit oblong-ellipsoid, terete or sometimes slightly flattened, 18-25 x 7-15 mm, rounded to broadly obtuse or sometimes acute or rarely apiculate at the apex, often shortly pseudostipitate at the base, usually glabrous even when young. Endocarp longitudinally slightly furrowed, subcircular in section. (Fig. 9/34).

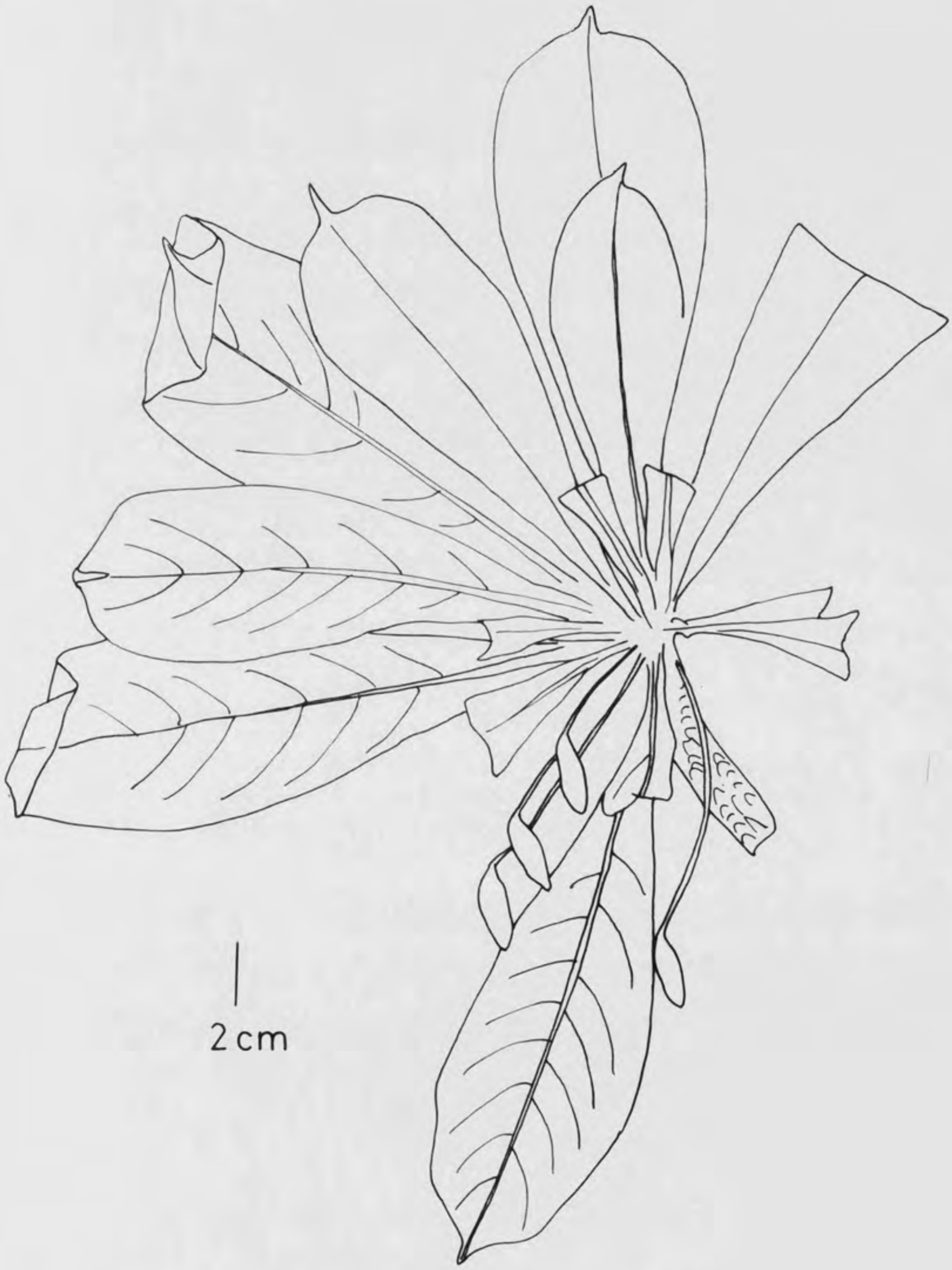


Fig. 9/34: Buchenavia congesta

Geographical range: In the Amazon basin of Brazil, Venezuela and Colombia (Map 9/13).

Ecology: A lowland tree, growing in open areas, secondary forest and patches of primary forest. Flowers September.

Comments: *B. longibracteata* differs from *B. congesta* and all the other species of the genus in having large leafy bracts. Exell & Stace (1963), who did not see the fruit of *B. longibracteata*, believed that it was probably an abnormal form of *B. macrophylla*. I have seen fruiting specimens of *B. longibracteata* in which the leaves and fruits are very similar to those of *B. congesta*. The fruits are glabrous, while those of *B. macrophylla* are densely tomentellous. I believe that the large leafy bracts (which are not seen except in the type) are an abnormal character and insufficient to keep *B. longibracteata* separate.

20. *Buchenavia macrophylla* Eichler, Flora 49: 166 (1866). Type: Brasil: Amazonas: Near Panuré on Rio Vaupés, Oct. 1852-Jan. 1853, Spruce 2507 in part (lectotype BR, not seen; isolectotypes BM, C, K, LE, NY, US, W; lectoparatype K).

Terminalia macrophylla Spruce ex Eichler in Martius, Fl. Brasil, 14 (2): 98 (1867), nom. syn. illegit.

Buchenavia stellae Cuatrec. in Fieldiana, Bot. 27 (1): 109 (1950). Type: Colombia: Caqueta: Florencia, in the Cerros La Estrella, 400 m, 30 Mar. 1940, Cuatrecasas 8863 (holotype, F, not seen: isotypes U, US).

Shrub or small tree, 3-20 m high, 5-60 cm diameter. Petiole 6-35 mm long, slender or stout, very variable in length, densely to sparsely pubescent, almost biglandular. Lamina subcoriaceous to coriaceous, 3-35 x 1.5-14 cm, oblanceolate to narrowly obovate or oblong to elliptic oblong; apex long acuminate to short apiculate or rarely rounded; base very narrowly cuneate often decurrent into the petiole; upper and lower surfaces almost glabrous except pubescent on the primary and secondary veins; domatia absent. Venation eucamptodromous or eucamptodromous - brochidodromous; primary vein moderate to thick, prominently raised below secondary veins 6-14 pairs, usually moderate and prominently raised below, often widely spaced; tertiary veins percurrent, often raised below; higher-order venation distinct, with conspicuous quarternary and quinternary veins; areoles imperfect and usually large. Inflorescence distinctly elongate; peduncle 6-32 mm long, puberulous; rachis 2-10 cm long densely puberulous. Flowers 2-4(5) cm long; ovary densely pubescent; upper receptacle almost glabrous. Fruit oblong ellipsoid to ovoid ellipsoid, sometimes terete or slightly flattened, 10-30 x 6-13 mm, rounded to subacute or apiculate at apex, rounded to very shortly pseudostipitate at the base, densely ferrugineous - tomentellous. Endocarp slightly ridged, subcircular or elliptical in section. (Appendix 4 Pl. 17A).

Geographical range: Brazil (Amazonas), Peru, Colombia, Venezuela, Guyana, French Guiana. (Map 9/13).

Ecology: A small tree of river banks. Flowers June-July, September and October.

Comments: This species is a very distinct one, although it shows considerable variation in the size of its leaves.

21. Buchenavia pulcherrima Exell & Stace, Bull. Brit. Mus. (Nat. Hist) Bot. 3 (1) : 33 (1963). Type: British Guiana: Essequibo: 172 km. along Bartica-Potaro Road, "60 ft. tree 10 in diam. basally swollen from Clump Wallaba forest - lvs. tufted to branch ends, thinly leathery, primary nerves prominent beneath - Young fr. on drooping stalks from below lvs., oval, rusty-velvety pubescent", 15 Nov. 1943, Field No. F 1485, Record No 4221 (holotype K; istotype FDG).

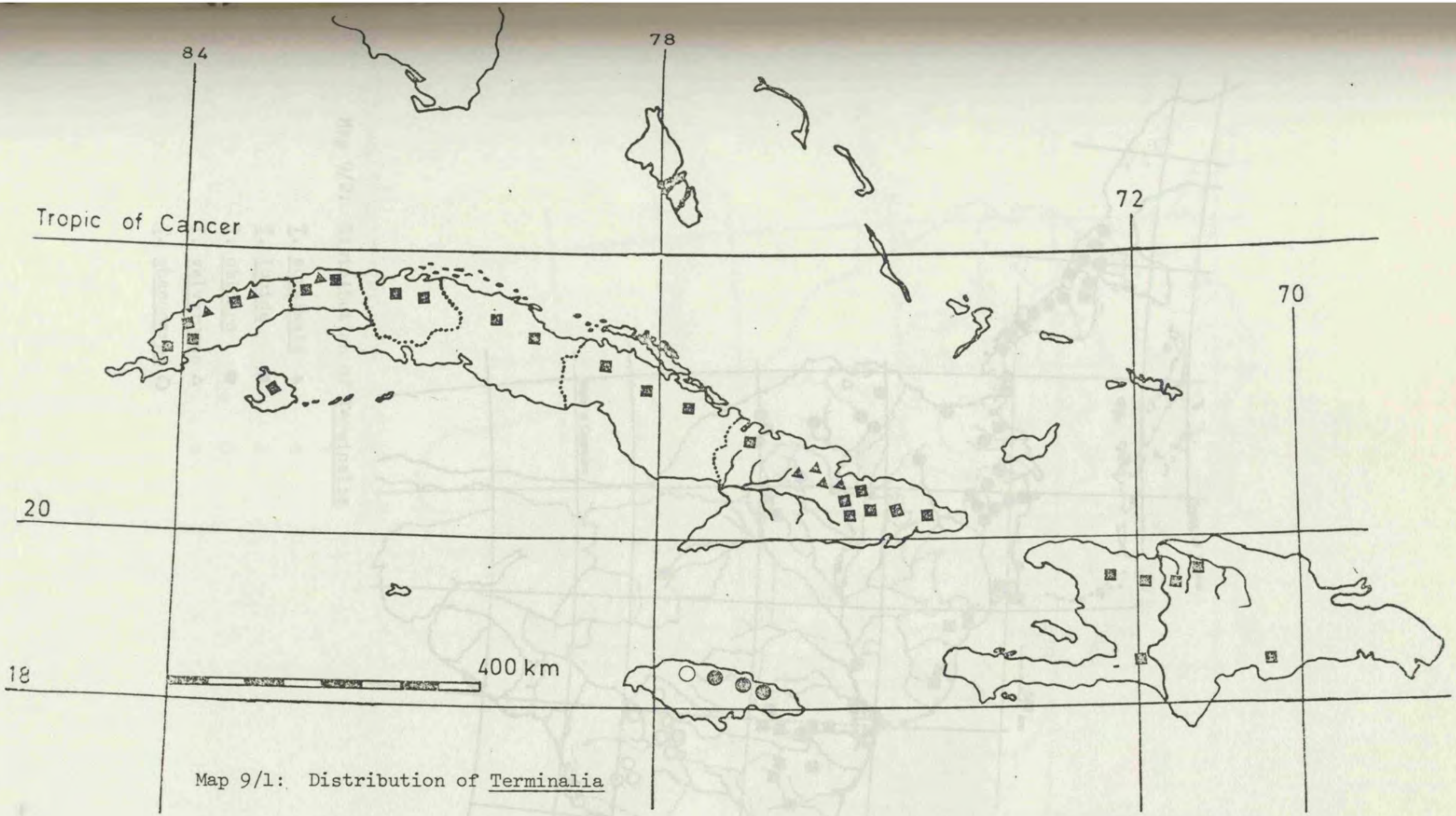
Large tree, 20 m high, 25 cm diameter. Leaves crowded at the tip of the branchlets; petiole 3-3.8 cm long, moderate, eglandular or inconspicuously biglandular; lamina subcoriaceous, 16-29 x 4.5-10 cm, narrowly obovate or oblanceolate or narrowly oblong obovate; apex abruptly acuminate or apiculate or acute or mucronate;base narrowly cuneate; upper surface glabrous and shiny; lower surface almost glabrous except sparsely pubescent on the primary vein; domatia absent. Venation eucamptodromous; primary vein moderate to thick, prominently raised below; secondary veins 9-11 pairs, prominently raised below, more or less straight and parallel; tertiary veins oppositely percurrent, very conspicuous; higher-order venation distinct quaternary veins often slightly raised; areoles imperfect or well developed. Inflorescence distinctly elongate; peduncle slender, 3-4.2 cm long, sparsely rufous pubescent; rachis 7-11 cm long, rufous pubescent. Fruit (immature) ellipsoid, 12 x 8 mm, rounded to obtuse at the base and apex, densely rufous velutinous. (Appendix 4 Pl. 17D).

Geographical range: Guyana. (Map 9/13.)

Comments: This species shows some similarity to *B. nitidissima* but its fruits are closer to those of *B. macrophylla*,

9.3.3. Species excluded from Buchenavia

Buchenavia fluminensis Glazio, Mem. Soc. Bot. France 1, 3 : 203 (1908), nom. nud. = *Terminalia riedelii* Eichler.



Map 9/1: Distribution of Terminalia

T. latifolia

T. arbuscula

T. eriostachya

T. chicharronia

Map 9/2: Distribution of Terminalia

T. acuminata ▲

T. lucida ■

T. oblonga ●

T. valverdeae △

T. phaeocarpa ○

Map 9/3: Distribution of Terminalia

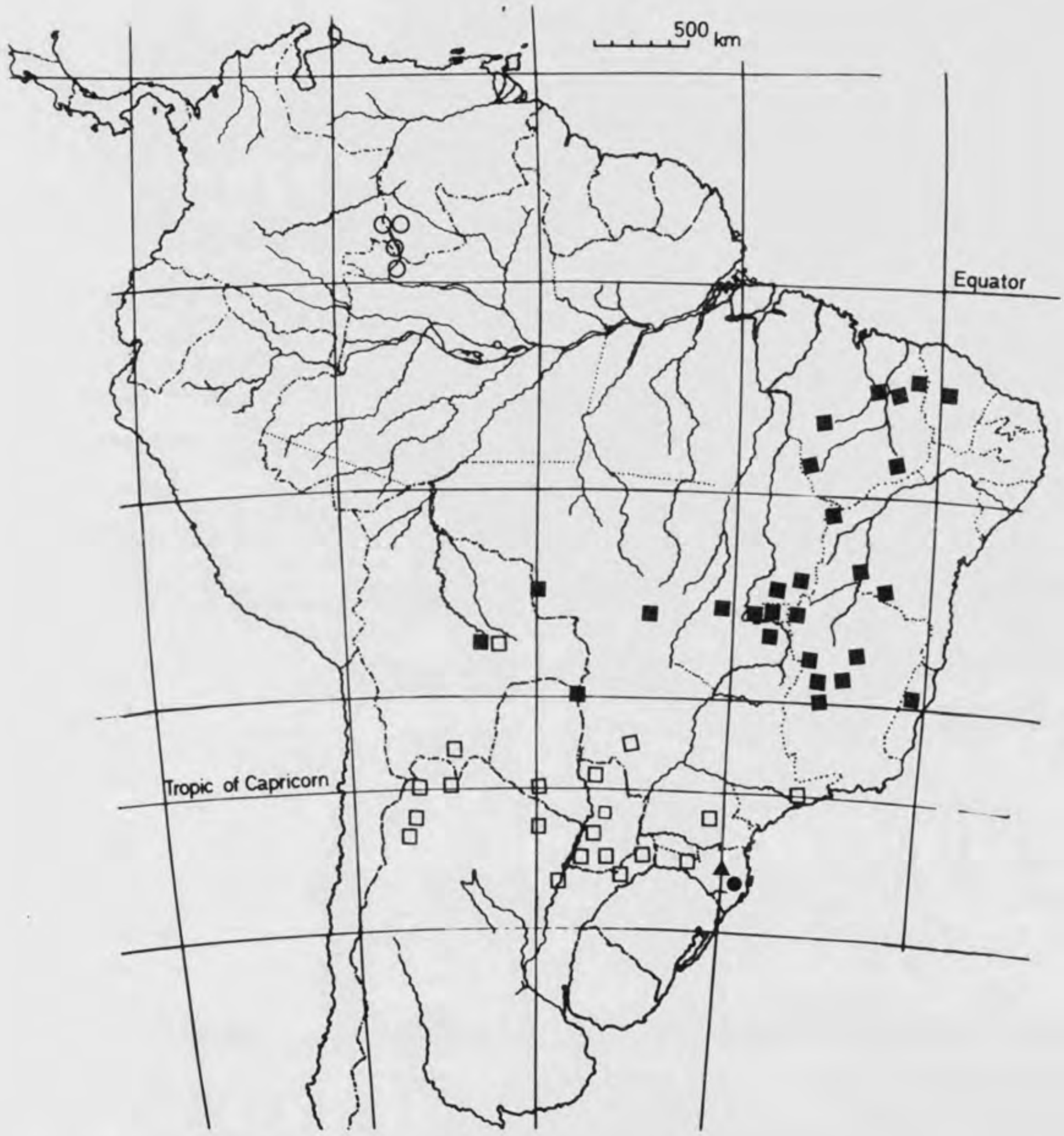
T. dichotoma	●
T. argentea	■
T. kuhlmannii	▲
T. januariensis	□
T. guyanensis	△

Map 9/4: Distribution of Terminalia

T. eichleriana ▲

T. australis ■

T. actinophylla ●



Map 9/5: Distribution of Terminalia

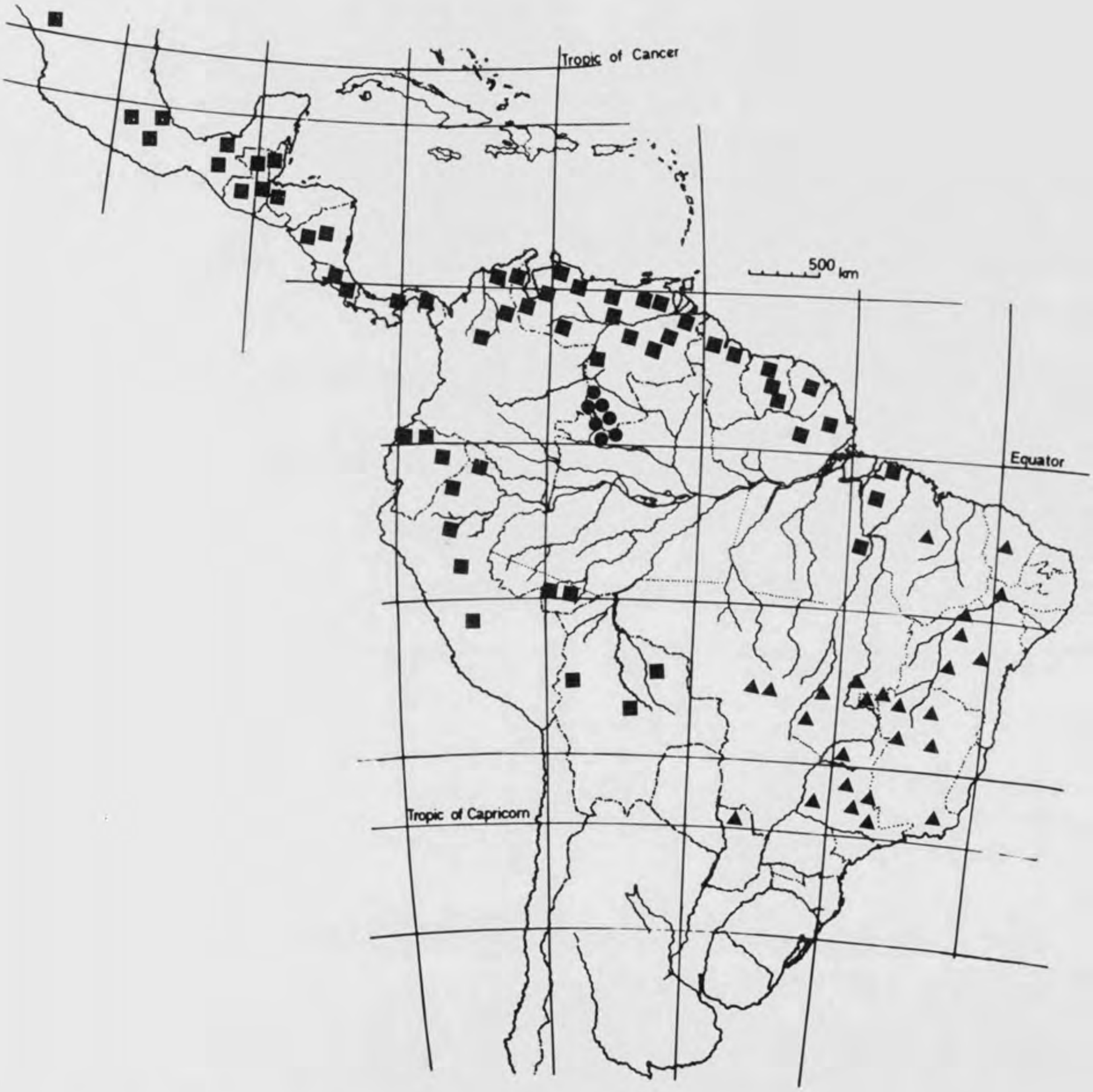
T. fagifolia ■

T. triflora □

T. uleana ●

T. reitzii ▲

T. ramatuella ○

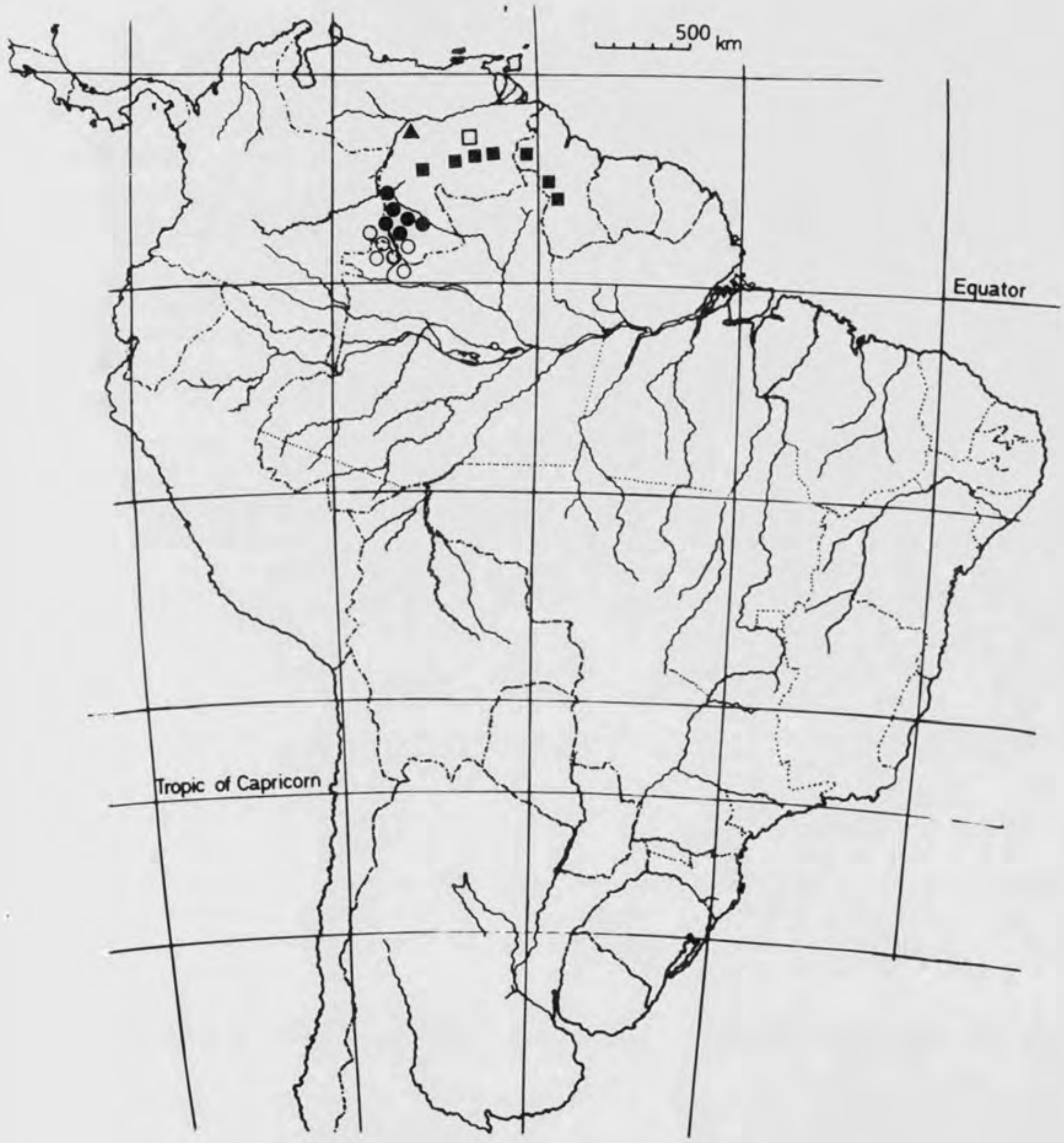


Map 9/6: Distribution of Terminalia

T. amazonia ■

T. glabrescens ▲

T. virens ●



Map 9/7: Distribution of Terminalia

T. quintalata ■

T. yapacana ●

T. guaiquinimae □

T. steyermarkii ▲

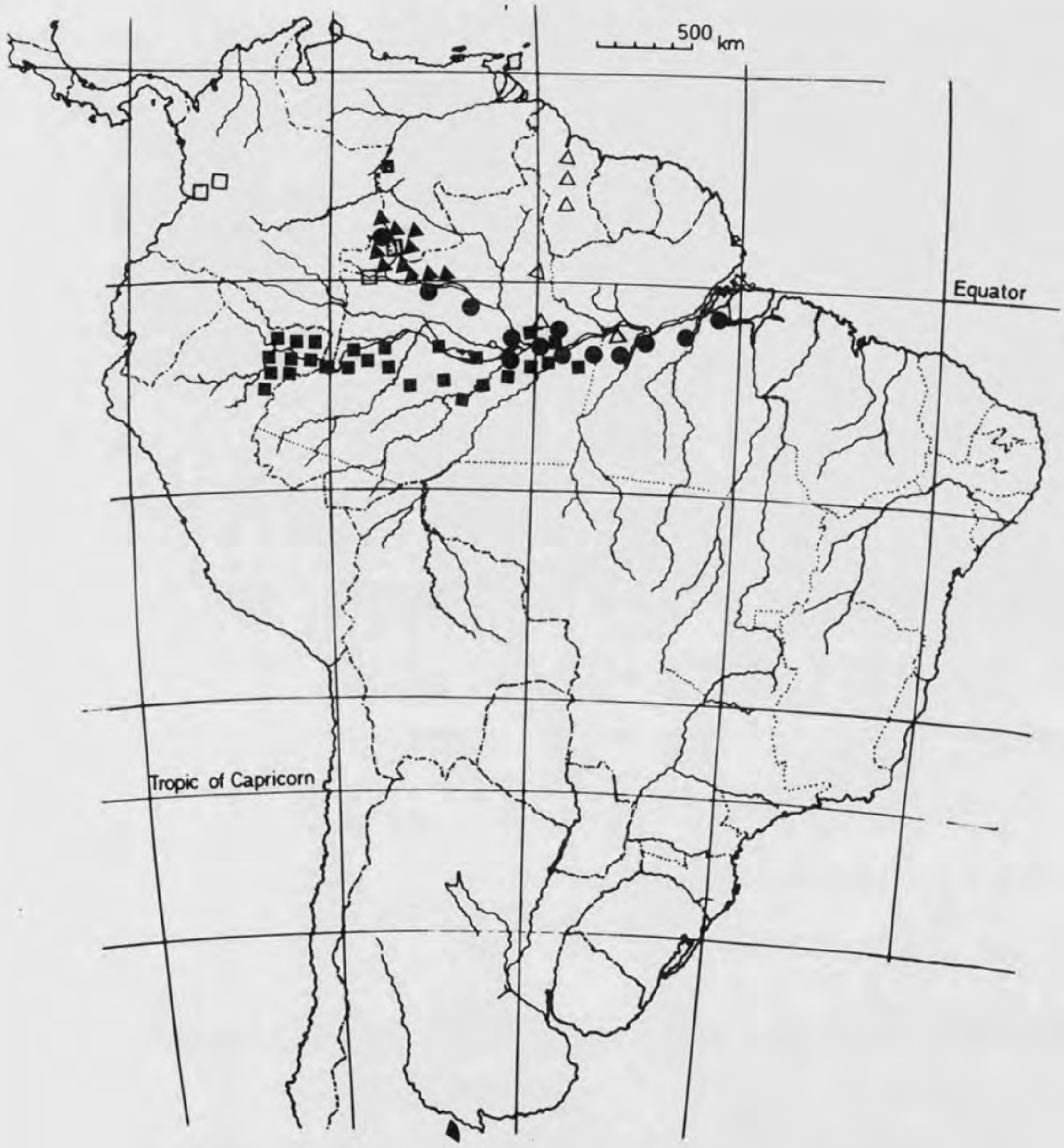
T. crispialata ○

Map 9/8: Distribution of Bucida

B. molineti ●

B. buceras ▲

B. macrostachya ■



Map 9/9: Distribution of Buchenavia

B. ochroprumna ●

B. pallidovirens □

B. suaveolens ▲

B. oxycarpa ■

B. fanshawei △

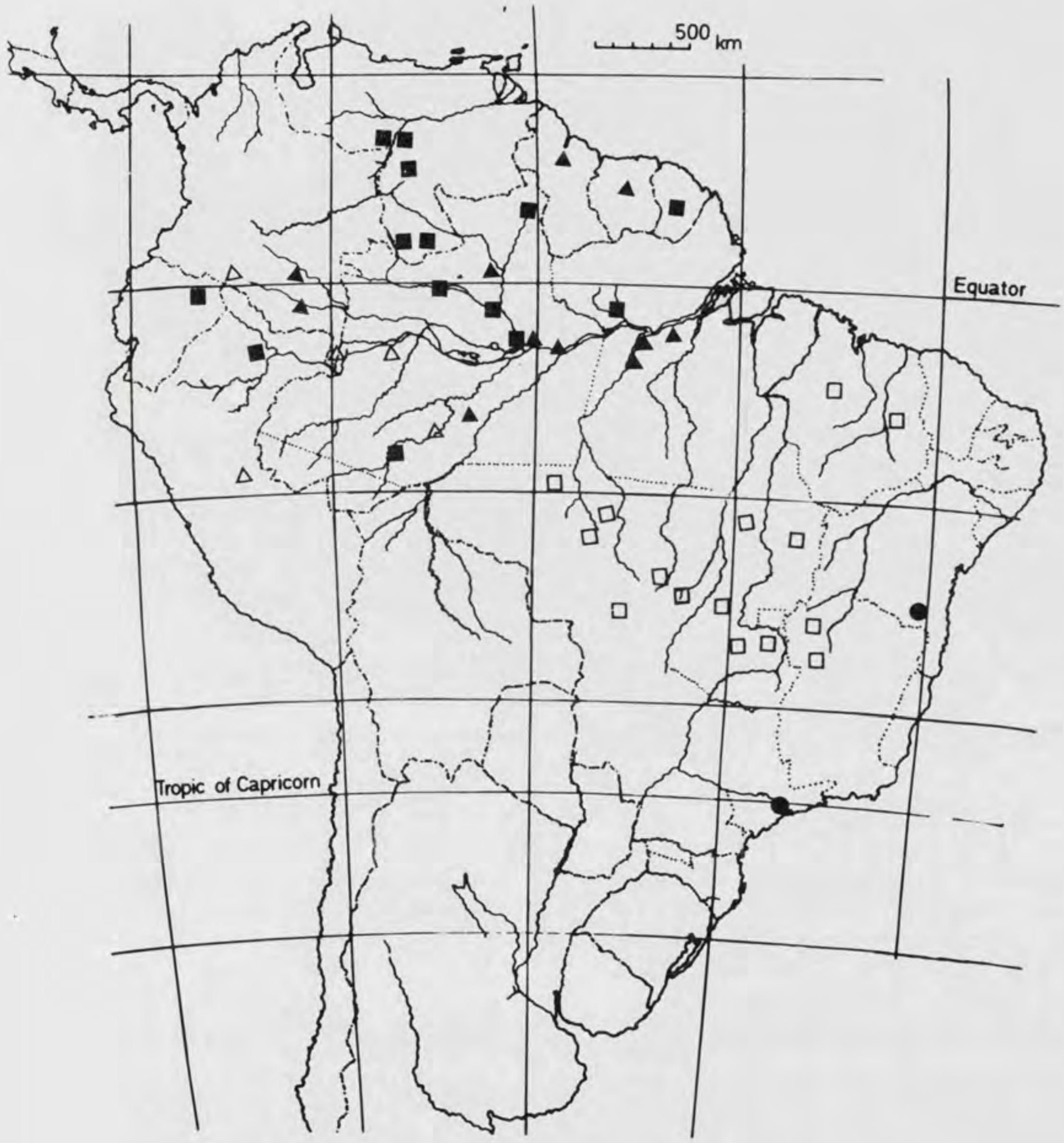
Map 9/10: Distribution of Buchenavia

B. parvifolia ●

B. tetraphylla ■

B. kleinii △

B. sericocarpa ▲



Map 9/11. Distribution of Buchenavia

B. hoeheana ●

B. grandis ▲

B. amazonia △

B. tomentosa □

B. viridiflora ■

Map 9/12: Distribution of Buchenavia

B. reticulata ●
B. megalophylla ▲
B. guianensis ■

Map 9/13: Distribution of Buchenavia

B. nitidissima ■

B. congesta ●

B. macrophylla ▲

B. pulcherima □

CHAPTER 10

GENERAL DISCUSSION AND CONCLUSIONS

This research was initiated because of the widespread taxonomic confusion existing within the genus Terminalia at both species and sectional levels, particularly in America. It is hoped that the American species of Terminalia have been treated objectively in this thesis.

In the preceding chapters of this work detailed information has been presented on the variation in morphology, anatomy, pollen morphology, distribution and ecology of the species of Terminalia, Ramatuella, Bucida Buchenavia. Also, information on the leaf architecture for the whole family have been provided. These results give a more complete idea about the circumscription of the taxa investigated than has been available hitherto.

The data also assist in elucidating relationships and permit clear interpretation of the systematic position of the genera studied within the Combretaceae.

The taxonomic importance and the evolutionary significance of the leaf architecture, anatomy and pollen morphology have been discussed in chapters 5, 6 and 7 respectively. The taxonomic treatment presented in chapters 8 and 9, which is often supported by anatomical and palynological evidence, is to some extent a conclusion to this study. However, some speculation on the evolutionary relationships among the sections recognized within Terminalia, and the relationship between Terminalia and the other genera in subtribte Terminaliinae, is desirable and will be discussed in this chapter.

10.1. Morphological trends

In order to evaluate relationships and deduce phylogenetic sequences in a plant group, the direction of the trends within the group under study should be first determined. The primitiveness or advancedness of a character vary from genus to genus, and there is not definite way to recognize it in the absence of fossils. However, and in spite of the difficulties, botanists should not give up attempting to construct phylogenies (Stebbins 1974). A cladistic analysis of the family would be very desirable, but must await the accumulation of more complete data.

Evidence from the morphological variation presented in chapters 4, 5 and 7 suggest the following trends:

1. Leaf entire ⟶ leaf serrate
2. Venation brochidodromous ⟶ eucamptodromous ⟶ craspedodromous
3. Inflorescence simple spike ⟶ inflorescence paniculate spike
4. Inflorescence elongate ⟶ inflorescence capitate
5. Flowers pentamerous ⟶ flowers tetramerous
6. Flowers hermaphrodite ⟶ flowers unisexual
7. Flowers monoecious ⟶ flowers dioecious
8. Calyx lobe distinct ⟶ calyx lobe obscure
9. Calyx deciduous ⟶ calyx persistent
10. Stamens of two whorls ⟶ stamens of one whorl
11. Stamens exserted ⟶ stamens included
12. Pollen psilate ⟶ verrucate ⟶ echinulate
13. Wings 5 ⟶ wings 4 ⟶ wings 3 ⇄ wings 2 ⟶ 1
    Wings 5 ↘ wings 6
14. Body of fruit large ⟶ body of fruit small
15. Wings absent ⟶ wings present
16. Wings coriaceous ⟶ wings papyraceous

Although these morphological trends have been found to be of significance at the specific level, they can also be applied to higher taxa. These trends have been followed in the formulation of the model of relationships among the sections of Terminalia shown in Figure 10/1. The characters used to construct Figure 10/1 are listed in the key opposite to it.

The most significant character at sectional level is the morphology of the fruits, on the basis of which the genus can be divided into 2 major groups: Sections I-IV and V-XXII.

Key to Figure 10/1

1 + Fruits unwinged (rarely narrlowly winged) drupaceous

1 - Fruits distinctly winged

2 + Flowers all hermaphrodite

2 - Flowers male and hermaphrodite

3 + Drupaceous fruit compressed

3 - Drupaceous fruit not compressed

4 + Leaves large, obovate or broadly obovate

4 - Leaves not of this type

5 + Inflorescences simple spike

5 - Inflorescences paniculate

6 + Flowers pentamerous

6 - Flowers tetramerous

7 + Fruits with 5 equal wings

7 - Fruits not of this type

8 + Fruits with 2 or 3 equal wings

8 - Fruits with 4 or 5 equal or unequal wings

9 + Fruits longer than broad

9 - Fruits broader than long

10 + Fruits pedicellate

10 - Fruits not pedicellate

11 + Flowers large

11 - Flowers small

12 + Leaves in fascicles on short spur shoots

12 - Leaves not of this type

13 + Fruits suborbicular

13 - Fruits not suborbicular

14 + Bark peeling off in cylindrical or hemi-cylindrical papery flakes

14 - Bark not peeling as above

15 + Inflorescences distinctly elongated

15 - Inflorescences capitate or subcapitate

16 + Body of fruit suborbicular, wider than wing

16 - Body of fruit not of this type

17 + Leaves coriaceous with typical brochidodromous venation

17 - Leaves not as above

18 + Inflorescences with few flowers

18 - Inflorescences with numerous flowers

19 + Fruits large

19 - Fruits small

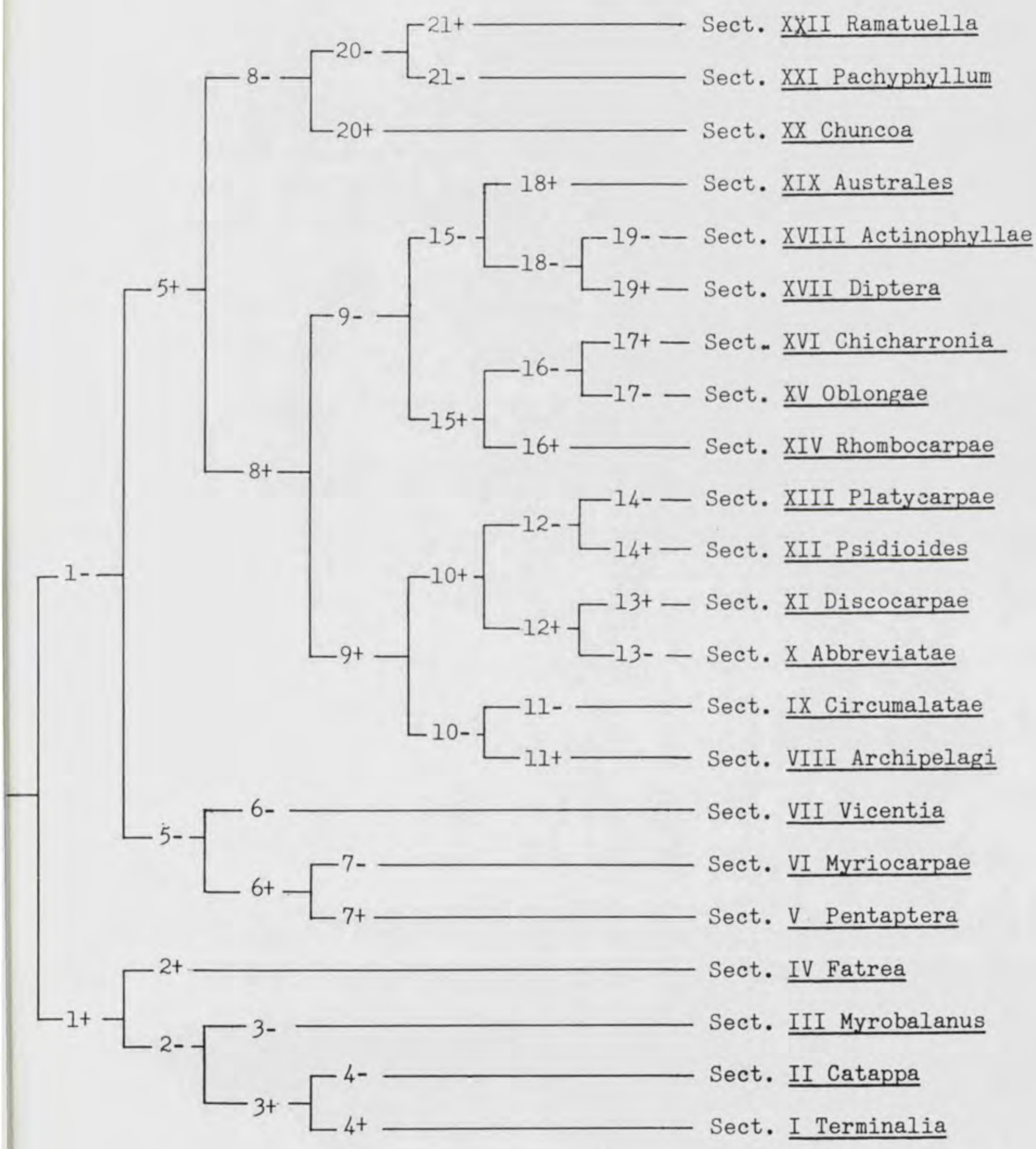
20 + Fruits with 3 rudimentary and 2 distinct wings

20 - Fruits with 4 or 5 equal wings

21 + Fruits grouped into a hemispherical mass

21 - Fruits not of this type

Fig. 10/1 Schematic key of relationships between the sections of Terminalia



Although presented in the form of a dendrogram, this schematic key is not intended to present a modern phenogram or cladogram, and there is no significance in the length of the lines.

Sections I Terminalia, II Catappa, III Myrobalanus and IV Fatrea form a group distinct in possessing unwinged (rarely narrowly winged) drupaceous fruits. More than half of Terminalia species possess unwinged fruits (Table 10/1). Within sections Terminalia and Catappa development of a narrow wing can be clearly seen in some species.

The other major grouping is the Sections V Pentaptera to XXII Ramatuella, which are distinct in having distinctly (rarely narrowly) winged fruits.

Section V Pentaptera, VI Myriocarpae, and VII Vicentia form a group distinct in having a paniculate inflorescence, 3 - 5 winged fruits and usually subopposite leaves. This group, which shows a tendency towards subopposite leaves and almost always has hermaphrodite flowers, is the closest to the genus Combretum. In America perhaps the closest species to Combretum is T. acuminata, the only species in section Vicentia, but in Asia there are several species which seem to have closer affinities with Combretum. The reduction in number of wings is clear in many species of this group. The primitive character is considered to be the 5-winged fruit, as this is found in most species, and the 6-, 4- or 3-winged fruit is the most derived. In T. brassii the fruits possess 5 wings but 3 of them are rudimentary. In T. myriocarpa there are 3 wings but one of them is rudimentary, and in T. monaptera there are three wings but two of them are rudimentary. In T. polyantha the commonest case is a 4-winged fruit, but 3, 2 or 5-winged fruits can occasionally be found.

Sections VIIIArchipelagi to XXII Ramatuella form another group within the second major group, distinct in having a simple spicate inflorescence, 2-5 winged fruits and spiral or alternate leaves. On the basis of shape, size and number of wings of fruits these taxa can be divided into two further subgroups. Sections VIII Archipelagi to XIX Australes form a subgroup distinct in possessing 2- or rarely 3-winged fruits, sections XX Chuncoa to XXII Ramatuella form a subgroup characterized by having 5- or 4-winged fruits. The former subgroup can be further divided into two. Sections VIII Archipelagi to XIII Platycarpae are distinct in having 2-winged fruits almost always longer than broad, although Sections VIII Archipelagi and IX Circumalatae are very different from the other four sections. Section Archipelagi (endemic to South-east Asia) has affinities with some species of section Terminalia, while section Circumalatae (endemic to Australia) has some similarities with section Oblonga through T. oblongata. The other four Sections, X Abbreviatae, XI Discocarpae, XII Psidioides and XIII Platycarpae, are closely related to each other. They possess the same type of fruits (almost always pedicellate) but they are different vegetatively, these four sections are closer to American sections, especially section oblonga, than to the Asian sections.

Sections XIV Rhombocarpae to XIX Australes are distinct from the previous six sections in having 2-winged fruits which are almost always broader than long. The latter six sections are closely related. Sections XIV Rhombocarpae and XV Oblongae are mainly concentrated in Central and South America, but both occur in the western coast of Africa. Section Oblongae is also distributed in Asia (Burma to New Guinea) and northern Australia.

Sections XVII Diptera, XVIII Actinophyllae and XIX Australes are distinct from the other closely related sections XIV Rhombocarpae to XVI Chicharronia in possessing capitate or subcapitate inflorescences and 2- or 3-winged fruits.

Section XX Chuncoa which shares the same fruit character (5 wings) with sections XXI Pachyphullum and XXII Ramatuella, shows close similarity to section Oblongae with respect to its habit, distribution, leaves and flowers. Furthermore the fruits of section Chuncoa, although with five wings, have only 2 of them distinctly developed.

Sections Pachyphyllum and Ramatuella are closely related and form a group distinct in having 5- or 4-merous flowers, 5- or 4-winged fruits and coriaceous leaves with weakly brochidodromous venation.

10.2. Sections or subgenera

From Figure 10/1 one may suggest why the genus should not be divided into two subgenera, one with unwinged drupaceous fruits and the other with distinctly winged fruits. The difficulties which may face this idea are that, although the fruit morphology is the most significant character at infrageneric level, it is not always the best character to interpret relationships. In some species and sections the fruits are very different while their vegetative characters and pattern of distribution are very similar.

Giving the rank of subgenus to the two major fruits types perhaps carries some descriptive advantage but gives too much emphasis to a single character, and therefore obscures relationships between the subgenera so recognized. For example, section Fatrea is closer to the African sections X-XIII than to section Myrobalanus and Terminalia on the basis of vegetative morphology. Similar examples can be found at the species level: Terminalia dichotoma possesses fruits with very narrow wings similar to those in some species of sections Catappa and Terminalia, but the affinity of T. dichotoma is clearly with T. lucida, which possesses distinct wings. Also T. australis and T. triflora (both endemic to temperate South America) are very closely related species but have different fruits.

10.3. The origin of *Terminalia*

In order to understand the origin of *Terminalia*, one may first consider the age of the angiosperms and the order Myrtales to which the family Combretaceae belongs. Although the age, place and biological origin of the angiosperms are still uncertain, the oldest fossil pollen certainly determined as an angiosperm is from the uppermost part (Albian) of the Lower Cretaceous (of Africa, South America, Eurasia and North America) some 125 million years ago (Raven & Axelrod 1974, 1975; Beck 1976; Brenner 1976; Haegi 1981; Muller 1981). But Ramshaw *et al* (1972) claimed that the amino acid sequence differences in cytochrome C suggest the origin of angiosperms between 400-500 million years ago.

Most palynological workers believe that the flowering plants originated in the tropics. Takhtajan (1969) suggests South-east Asia as a centre of origin for the angiosperms, but there is more evidence today suggesting West Gondwanaland (South America and Africa) (Schuster 1972, 1976; Raven & Axelrod 1972, 1974; Haegi 1981).

The order Myrtales, represented by its oldest family Myrtaceae (Muller 1981), is known from the Cenomonian (Upper Cretaceous). This means that Myrtales have existed before the full opening of the Indian Ocean. According to Raven & Axelrod (1974) Combretaceae existed when South America and Africa were much closer.

Palaebotanical evidence for the origin of *Terminalia* and the Combretaceae is scanty. The information available in the literature is summarized in Table 10/2.

The oldest fossil combretaceous pollen (*Terminalia* type) is believed to be from the upper Eocene (Muller 1981). *Heterocolpites laevigatus* from the upper Eocene-lower Miocene of Cameroon is compared with pollen of *Terminalia superba* (Salard-Cheboldaeff 1978).

Terminalia cf. Catappa pollen and Lumnitzera littorea type pollen are recorded from the lower Miocene - upper Miocene of the Marshall Islands, and "cf. Combretum pollen" is recorded from the upper Miocene of the Marshall Ilands (Leopold 1969). A photomicrograph of "cf. Laguncularia pollen" from the upper Miocene of Mexico is presented by Graham (1976), but appears to me to belong to some other genus of Combretaceae. A fossil pollen of Terminalia amazonia has also been recorded from the upper Miocene of Veracruz, Mexico.

In the absence of a detailed pollen morphological survey of the whole family Combretaceae the identification of fossil Combretaceous pollen remains uncertain. And because many genera of Combretaceae possess the same pollen type it seems that the identification of certain genera such as Terminalia, Bucida, Anogeissus and Combretum on pollen characters is impossible. Further, the same pollen type (similar to Heterocolpites laevigatus) occurs in Melastomataceae and Crypteroniaceae (Salard-Cheboldaeff 1978, Muller 1981).

With regard to fossil woods, twelve species of Terminalioxylon and one species of Anogeissusoxylon (A. indica) have been described from the Tertiary of India (Boureau 1950; Navale 1955, 1962; Ramanujam 1956, 1966; Prakash 1965; Prakash & Navale 1962; Prakash & Awasthi 1971). According to Prakash (1973) the modern comparable form to Terminalioxylon is Terminalia and to Anogeissusoxylon is Anogeissus.

The earliest fossil Combretaceous wood (Terminalioxylon tomentosum Mahabale & Deshpande, which is comparable to Terminalia tomentosa) is from the early Eocene of Ghala, Gujarat state, India (Prakash 1973). But fossil woods of Terminalia tomentosa are described from the Miocene of southern and eastern India (Prakash 1965, 1966b).

Prakash (1973) said that there is definite evidence that Combretaceae (Terminalia) appeared during the Palaeogene (almost exclusively of Eocene age or very marginally earlier) in India and continued till the present time. Paleobotanical evidence shows that Terminalia became abundant in the Neogene (Miocene, Pliocene) deposits of India (Table 10/2). However, whether this evidence suggests an Indian origin for Terminalia remains to be confirmed.

Cytological information on Terminalia and other related genera investigated in this work is very scanty. There is no chromosomal information available on Ramatuella, Bucida and Buchenavia. The cytological information available on subtribe Terminaliinae is restricted to some chromosome counts, and these are presented in Table 10/3.

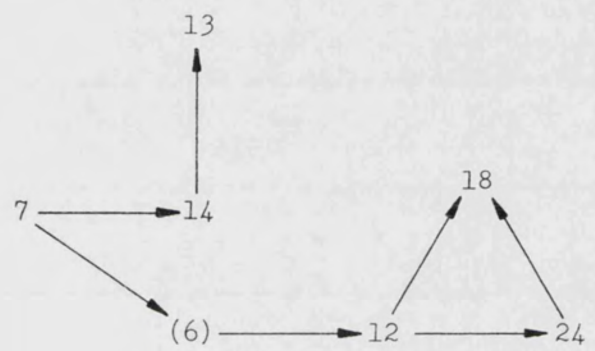
Chromosome numbers of n = 7, 12, 13, 14, 18, 24 and 36 have been reported in Terminalia and n = 12 in Anogeissus and Conocarpus. The original basic chromosome number for Terminalia and subtribe Terminaliinae is more likely to be x = 7, although Raven (1975) proposed a basic number of x = 12 for the family on the basis that n = 7 and n = 13 have not been reconfirmed.

However, there are also counts of n = 14 in Terminalia, and elsewhere in the family of n = 28, 26 and 52. These numbers taken together suggest a base number of x = 7, as illustrated in Fig. 10/2. Moreover, the 2n = 36 in Terminalia phanerophlebia (Africa) and T. braziliensis (South America) suggest that these two species are based on x = 6 rather than x = 12.

Although data derived from chromosome cytology are very useful in elucidating relationships, particularly in woody plants (Darlington, 1956; Ehrendorfer 1976), inaccurate and inadequate information is of no help. However, in general the relatively high number of chromosomes recorded in species of Terminalia suggests polyploid speciation.

Fig. 10/2 Diagram showing derivation of chromosome number of Terminalia based on possible x = 7.

( ) = not recorded



10.4. Geographical distribution

The greatest concentration of the genus Terminalia is in Asia (particularly South-East Asia), where 81 species occur (Table 10/1). Most of these species belong to sections Catappa and Terminalia. The second largest number of species occurs in Madagascar, with 36 species, most of which belong to sections Fatrea, Catappa and Myrobalanus. About 30 species occur in each of the other 3 continents, Africa, America and Australia

Figure 10/3 shows the geographic distribution of Terminalia, based on section. Eight sections are endemic to America and West Indies, five to Africa and Madagascar, three to Asia and New Guinea and one to Australia. Two sections are common to Australia, Asia and Madagascar, two have representatives in all main continents, and one is found in America and Africa. It is clear that the number of sections (18) in America and Africa (including Madagascar) is much greater than that (8) in Asia and Australia. But the number of species in the former two continents (96) is slightly less than than (110) in Asia and Australia. This indicates a good correlation between the number of sections and the surface area occupied.

Section Chuncoa in America is widely distributed throughout Central and South America but has only two species, T. amazonia, which is concentrated in Central America and northern South America, and T. glabrescens which is concentrated in eastern Brazil. On the other hand, section Pachyphyllum is concentrated in a very small area of the border between Venezuela, Colombia and Brazil yet has four species, and section Fatrea in Madagascar has twelve species. It seems that there is no close correlation between the size and the geographical range of some sections of Terminalia. The greatest concentration of species is in S. E. Asia, where there are only 7 sections.

In order to understand the present-day intercontinental distribution of Terminalia, one should consider the mechanisms by which the dispersal could have taken place.

All species of Terminalia which possess fruits with 2 wide wings have the ability to be transported aerially by wind, and this adaptation may explain why sections Chuncoa, Oblonga and Diptera (each with rather few species) are so widely distributed in America. Species which have fruits with 3-5 wings are also dispersed by wind but for a much shorter distance.

In the case of comparatively heavy fruits, they may be rolled along for a distance on the ground. This may explain why sections Pachyphyllum, Ramatuella and Vicentia are distributed in so limited an area. Ridley 1930 mentions that the 5-winged fruits of Terminalia tomentosa (section Pentaptera) are dispersed by rain-wash.

Long-range transport by ocean currents is a way that fruits of some species, for example, T. catappa (a widely distributed seashore species) are dispersed. Many species of Terminalia are river dispersed, such as those with wingless corky drupaceous fruits, like T. foetidissima. Also some species which have fleshy fruits are animal dispersed. River and animal dispersal are also common in Buchenavia, while long-range transport by birds is known in Bucida buceras (Ridley 1930).

Most species in Asia, New Guinea, Australia and Madagascar are water or animal dispersed, while the African and American species are wind dispersed, especially in savanna or other open habitats. It seems that there is a tendency in many sections for the evolution of wind dispersal. But the evolution of wings from unwinged drupaceous fruits is most obvious in sections Catappa and Pentaptera.

There are some examples of present day distribution of species and sections of Terminalia which suggest a link between the continents.

T. lucida (which has distinctly winged fruits) occurs in Central and South America and in West Africa; T. boivinii of section Fatrea occurs in Madagascar and East Africa; and T. complanata and T. subacroptera occur in North Australia and New Guinea. Also, within a section, some closely related species occur in different continents, such as the West African species T. superba which has affinities with T. oblonga from America, and some species of section Myrobalanus which occur in Madagascar and India. Most of the above examples cannot sufficiently be explained by long-range dispersal, but can be tentatively explained in terms of the continental drift theory.

According to the continental drift theory, India was once connected with the southern part of Africa and they formed a large southern continent with South America, Australia and Antarctica known as Gondwanaland. South America began to separate from Africa in the mid Cretaceous, and, by the beginning of the Tertiary, Liberia was separated from Paraiba (Brazil) by about 800 km. At that time the Atlantic was relatively shallow and provided with numerous islands (Axelrod & Raven 1978).

The exact time of the separation of Madagascar-India from Africa is unknown, but according to most workers could have occurred in the late Cretaceous. India separated from the Madagascar-Mascarene subcontinent in the Palaeocene and reached its recent position by the middle Eocene (Raven & Axelrod 1974, Axelrod & Raven 1978).

To explain the distribution of species and sections which occur in different continents on the basis of the continental drift theory one can assume that the genus Terminalia had originated in Madagascar-India when this area was connected with Africa, and South America was not far from Africa and direct migration through land bridges was possible.

On the basis of the high number of species in South-east Asia one may suggest this area as a place of origin for the genus, but geological and palaeobotanical evidence are against it, since this area came to existence in the Miocene (Raven & Axelrod 1972, Axelrod & Raven 1972; Schuster 1972).

Australia also is not likely to be a place of origin since all the other genera of the tribe Combreteae and the genus Strephonema (perhaps the most primitive genus in the family) are missing there. In addition the genus Terminalia in Australia shows much less diversity than in Asia and Africa.

Madagascar-India perhaps is the most likely place of origin for Terminalia because both unwinged drupaceous fruited species and variously winged fruited species occur there and also it is in agreement with fossil evidence available at present and with geographical distribution of the genus and the tribe Combreteae.

10.5. Terminalia and other related genera (Ramatuella, Bucida and Buchenavia)

Table 10/4 shows the characters of Terminalia compared with those of the other genera of Combretaceae mentioned above. From the Table it is obvious that both Ramatuella and Bucida share almost all their characters with Terminalia, and Buchenavia shares about half of its characters with Terminalia.

10.5.1. Ramatuella

In the absence of fruits, Ramatuella, unlike Bucida cannot be separated from section Pachyphullum of Terminalia. Its leaves and floral morphology are almost identical to those in Terminalia guaiquinimae, T. yapacana and T. steyermarkii. The main character which has been used to separate Ramatuella from Terminalia is the capitate infructescence.

However, the same character occurs in some species of Terminalia, e.g. T. eichleriana, and it is possible to separate Ramatuella from Terminalia only by a combination of fruit characters (Exell & Stace 1963, 1966). Anatomically Ramatuella are very similar to Terminalia section Pachyphyllum and palynologically they have the same pollen type (Terminalia type). Its geographical distribution is within the range of Terminalia in South America and adjacent to that of section Pachyphyllum. In fact the differences between section Pachyphyllum and Ramatuella are less than those between section Pachyphyllum and, for example, section Vicentia or section Oblongae.

Therefore Ramatuella has been relegated to Terminalia section Ramatuella in this work.

10.5.2. Bucida

As mentioned before, Bucida also shares almost all its characters with Terminalia. The most diagnostic character which is used by all workers in distinguishing Bucida from Terminalia is the persistence of the calyx on the mature fruit. But this character has also been found in some species of Terminalia in Madagascar, e.g. T. tetrandra. In addition not all species of Bucida always have fruit with persistent calyx; B. spinosa quite often has no persistent calyx.

However Bucida species can be distinguished from Terminalia by their floral (calyx lobes) and leaf morphology, although leaves with a similar morphology are present in some species of section Fatrea and Catappa in Madagascar. Anatomically Bucida differs from Terminalia mainly in having a subepidermal layer of sclerenchymatous tissue. Palynologically Bucida has the same pollen type as Terminalia. Geographically Bucida is confined to the West Indies and Central America. If the closest relatives of Bucida are certain Madagascan species of Terminalia, then those form another example of the interesting phytogeographical connection between these two areas (Stearn 1971, Leroy, 1978).

Until more information is available the two genera are best kept separated.

10.5.3. Buchenavia

Although the leaves of Buchenavia are often very similar to those in Terminalia, Buchenavia is a distinct genus. It is distinct in having characteristic flowers with adnate anther and echinate pollen, neither of which has been found elsewhere in the Combretaceae. Fruits of Buchenavia, however, are unwinged drupaceous and similar to those in sections Catappa, Myrobalanus, Terminalia and Fatrea of Terminalia in Madagascar, Asia and Australia. The only American species of Terminalia which has fruits similar to those in Buchenavia is Terminalia latifolia from the West Indies (Jamaica). Anatomically Buchenavia is similar to Terminalia. Ecologically and geographically both genera grow in the same situations and occupy the same geographical range in America.

However, there is not any doubt that Buchenavia is closely related to Terminalia. Exell & Stace (1972) said "It seems as if all the wingless fruited American Terminalias have become Buchenavias".

In fact there is no evidence that Buchenavia and Bucida have originated in America; unfortunately, fossil and cytological evidence concerning the origin of Buchenavia is absent.

Exell (1962) said that it is obvious in the Combretaceae that winged fruits are normally developed along evolutionary lines from non winged fruits (and not vice versa), though there may be occasional retrogression in certain circumstances, such as change in environment favourable to dispersal by water. There is some evidence available from modern geomorphologists and biogeographers to suggest the possible occurrence during the Quaternary of considerably drier climates than today in the Amazon basin. Hammen (1974) stated that palynological evidence supports the former existence of savannas in areas of S. America at present covered with tropical forest.

From the above, and since Buchenavia is concentrated in the tropical forest of the Amazon today, it is possible that the unwinged-fruited Buchenavia initiated from a winged-fruited Terminalia ancestor as an adaptation for water dispersal when the climate turned wetter.

10.6. Conclusion

1 - The species of Terminalia fall into 22 sections, of which section Archipelagi Alwan is a new section and section Chicharronia (A. Rich) Alwan has a new status and combination.

2 - Thirty one species of Terminalia are recognized in America and West Indies, of which three species (T. kuhlmannii Alwan, T. steyermarkii Alwan and T. uleana Engler ex Alwan) are newly described; T. eichleriana Alwan is a new name; two species (T. crispialata (Ducke) Alwan and T. virens (Spruce ex Eichler) Alwan are new combinations; and one species (T. ramatuella Alwan) is a new name.

3 - Ramatuella is relegated to Terminalia section Ramatuella (Kunth) Alwan.

4 - Twenty one species of Buchenavia are recognized, of which B. amazonia Alwan is a new species, B. guianensis Alwan and B. nitidissima Alwan are new combinations.

5 - Bucida is very closely related to Terminalia but is best kept separated. Three species are recognized.

Table 10/1: Distribution of fruit characters of _Terminalia_ in the four continents

Continent	Number of species which have distinctly winged-fruit								
	No. of species with 2 wings			No. of species with 3-5 wings			Total for winged-species	No. of species with unwinged-drupaceous fr.	Total number of species
	fr. longer than broad	fr. sub-orbicular	fr. broader than long	3 wings	(3)4 wings	(4)5 wings			
America and West Indies	2	0	15	1	1	9	28	3	31
Africa and Madagascar	31	5	3	0	0	0	39	26	65
Asia as far as Fiji and New Guinea	5	0	7	3	2	5	22	59	81
Australia	3	0	3	0	0	0	6	23	29
	41	5	27*	4	3	14	94*	107*	201*

* These figures are less than the sums of the vertical rows because one species (_T. lucida_) with fr. broader than long occurs in America and Africa, one species (_T. catappa_) with unwinged-fruits is common to all continents and species (_T. comblanata_) also with unwinged fruits occurs in Australia and New Guinea.

Table 10/2: List of fossil woods and pollen grains of <u>Terminalia</u> and genera compared with <u>Terminalia</u>

Fossil species	Modern Comparable Species	Fossil: Pollen	Fossil: Wood	Locality	Tertiary (65-2.5 m.y.BP): Eocene	Oligocene	Miocene	Pliocene	
<u>Terminalioxylon</u>	<u>Terminalia</u>								
<u>T. annamense</u>	<u>Terminalia</u>		W	Annam, Indochina			+		Boureau, 1950
<u>T. chowdhurii</u>	<u>Terminalia</u>		W	Cachar Hills, India			+		Parakash & Navale 1962
<u>T. coriaceum</u>	<u>T. coriacea</u>		W	Namsan R., India				+	Parakash & Awasthi 1971
<u>T. coromandelinum</u>	<u>Terminalia</u>		W	Murtandichaudi, India				+	Ramanujam 1966
<u>T. felixi</u>	<u>Terminalia</u>		W	Murtandichaudi, India				+	Ramanujam 1956
<u>T.grandiporosum</u>	<u>Terminalia</u>		W	Murtandichaudi, India				+	Ramanujam 1966
<u>T. mortandrense</u>	<u>Terminalia</u>		W	Murtandichaudi, India				+	Navale 1955
<u>T. sahnii</u>	<u>Terminalia</u>		W	Murtandichaudi, India				+	Navale 1955
<u>T. speciosum</u>	<u>Terminalia</u>		W	Tiruchhitambalam, India				+	Ramanujam 1956
<u>T. taraumaticum</u>	<u>Terminalia</u>		W	Murtandichavdi, India				+	Ramanujam 1966a
<u>T. tertiarum</u>	<u>Terminalia</u>		W	Namsang R., India				+	Parakesh 1966
<u>T. tomentosum</u>	<u>T. tomentosa</u>		W	Chala, India	+				Mahabale & Deshpande 1965

Fossil species	Modern Comparable Species	Fossil Pollen	Fossil Wood	Locality	Tertiary (65-2.5 m.y.BP) Eocene	Oligocene	Miocene	Pliocene	
Terminalia									
T. sp.	T. sp.		W	Balugoloa, India			+		Lakhanpal 1970
T. tomentosa	T. tomentosa		W	Nagaland, India			+		Parakash 1966a
T. amazonia	T. amazonia	P		Veracruz, Mexico			+		Graham 1976
T. cf. catappa	T. catappa	P		Marshall Islands			+		Leopold 1969
Heterocolpites									
H. laevigatus	T. superba	P		Cameroon	+				Salard-Cheholdaeff 1978

Table 10/3: List of chromosome counts in subtribe Terminaliinae

Species	Chromosome number n	2n	Locality	Author
<u>Terminalia arjuna</u>		24	India	Janaki Ammal 1962
		26	India	Sen 1955
	12		India, Bangalore	Mehra 1976, Sanjaba 1979
<u>T. bellirica</u>		26	India	Sen 1955
		48	India	Janaki Ammal 1962, Sobti 1962
		24	India	Mehra 1976
		28	India	Mehra 1976
	12		India	Mehra 1976, Mehra & Khosla 1969
<u>T. braziliensis</u>		36	Brazil	Gibbs 1982
<u>T. catappa</u>		24		Simmondar 1954, Sen 1955, Riley 1960, Chuang <u>et al</u> 1963
	7			Nanda 1962
<u>T. chebula</u>		24	India	Janaki Ammal 1962
		48	India	Sobti 1962
		26	India	Sen 1955
	12		India	Mehra 1976, Mehra & Khosla 1969
	36		India	Gill <u>et al</u> 1979

T. crenulata	12		India	Mehra 1976, Sanjaba 1979, Mehra & Kholsa 1969
T. ivorensis		24	Africa	Mangenot & Mangenot 1957
T. muelleriana		24		Janaki Ammal 1962
T. myriocarpa	12		India	Mehra & Kholsa 1969, Mehra 1976
T. phanerophlebia		36	Africa	Riley 1960
T. tomentosa	7		India	Nanda 1962
		24	India	Janaki Ammal 1962, Sobti 1962, Mehra 1976
	12		India	Mehra 1976
Anogeissus latifolia	12		India	Mehra 1976
A. leiocarpus		24	Africa	Mangenot & Mangenot 1962
A. schimperi		24	Africa	Mangenot, Mangenot 1958, Miege 1960
A. sericea	12		India	Gill et al 1979
Conocarpus erecta		24	Africa and Bahama Islands	Mangenot & Mangenot 1962, Semple 1970

Figure 10/3: The distribution of sections of Terminalia

Section		America	West Indies	Africa	Madagascar	Asia, as far as Fiji and New Guinea	Australia
I	Terminalia		x		x	x	x
II	Catappa				x	x	x
III	Myrobalanus				x	x	x
IV	Fatrea			x	x		
V	Pentaptera					x	
VI	Myriocarpae					x	
VII	Vicentia	x					
VIII	Archipelagi					x	
IX	Circumalatae						x
X	Abbreviatae			x	x		
XI	Discocarpae			x	x		
XII	Psidioides			x			
XIII	Platycarpae			x			
XIV	Rhombocarpus	x		x			
XV	Oblongae	x		x		x	x
XVI	Chicharronia	x					
XVII	Diptera	x					
XVIII	Actinophyllae	x					
XIX	Australes	x					
XX	Chuncoa	x					
XXI	Pachyphyllum	x					
XXII	Ramatuella	x					

Table 10/4: A comparison of Terminalia, Ramatuella, Bucida and Buchenavia

Character	Terminalia	Ramatuella	Bucida	Buchenavia
Spike	simple or branched	simple	simple	simple
Flowers	5 or 4-merous	5 or 4-merous	5-merous	5-merous
Upper receptacle	deciduous	deciduous	persistent	deciduous
Calyx lobes	distinct (conspicuous)	distinct	short	obscure
Stamens	10, 8, 5 or 4	10 or 8	10	10
Anthers	versatile	versatile	versatile	adnate
Pollen type	heterocolporate	heterocolporate	heterocolporate	tricolporate
Styles	exserted	exserted	exserted	included
Fruit wings	present or absent	present	absent	absent
Arrangement or fruits	variously arranged	in spherical head	along the rachis	along the rachis

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APPENDIX 1

List of genera and species, with authorities mentioned in the thesis. American species of Terminalia, Bucida and Buchenavia are excluded (see Chapter 9).

Adamaram Adans.

Agathisanthes Blume (Nyssaceae)

Anogeissus (DC.) Guill., Perr. & A. Rich.

A. leiocarpus (DC.) Guill. & Perr.

A. pendula Edgew.

A. schimperi Hochst. ex Hutch. & Dalziel

A. sericea Brandis

Anogeissusoxylon Navale

A. indica Navale

Aristotelia Comm. ex Lam.

Badamia Gaertner

B. commersonii Gaertner

Badhamia Berkeley (Myxomycetes)

Bobua DC. (Symplocaceae)

Bruguiera Thouars (Rhizophoraceae)

Cacoucia Aublet

Calopyxis Tul.

C. eriantha Tul.

C. subumbellata Baker

Calycopteris Lam.

Catappa Gaertner

C. benzoin Gaertner

Ceratostachys Blume (Nyssaceae)

Combretum Loefl.

C. glutinosum Perr. ex DC.

C. grandiflorum G. Don

C. leprosum C. Martius

C. micranthum G. Don

C. obscurum Tul.

C. pisonioides Taub.

C. pyramidatum Desv.

C. vernicosum Rusby

Conocarpus L.

C. erecta L.

Croton L.

C. bentzoe L.

Dansiea N. Byrnes

Dimocarpus Lour. (Sapindaceae)

Fatrea A. L. Juss.

F. buxifolia A. L. Juss.

Finetia Gagnepain

Garcinia L. (Clusiaceae)

Getonia Roxb. = Calycopteris

Glossopteris Rafin. (Aspleniaceae)

Guiera A. L. Juss.

Gyrocarpus Jacq. (Gyrocarpaceae)

Heterocolpites Van der Hammen

H. lavegatus Salard-Cheboldaeff

Hibbertia Andrews (Dilleniaceae)

Illigera Blume (Hernandiaceae)

Kniphofia Scop. (non Moench)

Laguncularia Gaertner f.

L. racemosa (L.) Gaertner f.

Lumnitzera Willd.

L. littorea (Jack) Voigt

L. racemosa Willd.

Macropteranthes F. Muell.

Meistemon Exell & Stace

Myrobalanifera Houtt.

M. citrina Houtt.

Myrobalanus Gaertner

M. bellirica (Gaertner) Kuntze

M. scutifera (Planchon ex Lawson) Kuntze

Panel Adans.

Pentaptera Roxb.

P. angustifolia Roxb.

Poivrea Comm. ex A. L. Juss. = Combretum

P. obscura (Tul.) Perrier

Pteleopsis Engl.

P. anisoptera (Welw. ex Lawson) Engl. & Diels

P. apetala Vollesen

P. diptera Engl. & Diels

P. myrtifolia (Lawson) Engl. & Diels

P. pteleopsoides (Exell) Vollesen

P. suberosa Engl. & Diels

Quisqualis L.

Q. indica L.

Resinaria Comm. ex Lam.

Sparattanthelium C. Martius (Hernandiaceae)

Sphalanthus Jack = Quisqualis

Strephonema Hook. f.

S. pseudocola A. Chev.

Terminalia L.

T. angustifolia Jacq.

T. angustifolia Roxb.

T. archipelagi Coode

T. arjuna (Roxb. ex DC.) Wight & Arn.

T. arostrata Ewart & Davies

T. avicinnioides Guill. & Perr.

T. bellirica (Gaertner) Roxb.

T. bentzoë (L.) L.f.

T. boivinii Tul.

T. brassii Exell

T. brownii Fresen.

T. calcicola H. Perrier

T. canescens (DC.) Radlk.

T. capitulata Exell

T. chebula Retz.

T. circumalata F. Muell.

T. crenulata Roth

T. divaricata H. Perrier

T. fatraea (Poiret) DC.

T. glaucescens Planchon ex Benth.

T. grandiflora Benth.

T. ivorensis A. Chev.

T. kaernbachii Warb.

T. laxiflora Engler & Diels

T. macroptera Guill. & Perr.

T. mauritiana Lam.

T. monaptera Roth

T. monoceros H. Perrier

T. mucronata Craib & Hutch.

T. "*muelleriana*" = *T. muelleri* Benth.

T. myriocarpa Van Heurck & Muell. Arg.

T. neotaliata Capuron

T. oblongata F. Muell.

T. orbicularis Engler & Diels

T. paniculata Roth

T. parvula Pampan.

T. pellucida C. Presl

T. perrieri Capuron

T. phanerophlebia Engler & Diels

T. pierrei Gagnepain

T. platyptera F. Muell.

T. polyantha C. Presl

T. prunioides Lawson

T. pteleopsoides Exell

T. pterocarya F. Muell.

T. scutifera Planchon ex Lawson

T. sericea Burchell ex DC.

T. sericocarpa F. Muell

T. subserrata H. Perrier

T. sulcata Tul.

T. superba Engler & Diels

T. tetrandra (Danguy) Capuron

T. tomentosa (Roxb.) Wight & Arn.

T. triptera Stapf

Terminaliopsis Danguy

T. tetrandra Danguy

Terminalioxylon Schönfeld

T. annamense Boureau

T. chowdhurii Parakash & Navale

T. coriaceum Parakash & Awasthi

T. coromandelinum Ramanujam

T. felixi Ramanujam

T. grandiporosum Ramanujam

T. mortandrense Navale

T. sahnii Navale

T. speciosum Ramanujam

T. tertiarum Parakash

T. tomentosum Mahable & Deshpande

T. traumaticum Ramanujam

Thiloa Eichler

T. glaucocarpa (C. Martius) Eichler

T. gracilis (Schoot) Eichler

T. paraguariensis Eichler

Trigonella L. (Leguminosae)

APPENDIX 2

Specimens of American Terminalia, and Ramatuella, examined for leaf anatomy

Species	Country	Collector and number	Herbarium
T. actinophylla			
	Brazil	Martius s.n.	M
	Brazil	Sucre 9294	LTR
	Brazil	Gardner 2068	NY
	Brazil	Alberto 41	LTR
	Brazil	Anderson 7257	LTR
T. acuminata			
	Brazil	Sello s.n.	C
	Brazil	Glaziou 11947	K
	Brazil	Glaziou 6521	K
	Brazil	Glaziou 6143	C
	Brazil	Allemao	BR
T. adamantium			
	Brazil	St. Hiliaire 2065	P
T. amazonia			
	Venezuela	Aristequieta 4835	VEN
	Venezuela	Aristequieta et al 77276	VEN
	Venezuela	Bernardi 6937	VEN
	Venezuela	Bernardi 7096	VEN
	Venezuela	Davidse & Gonzalez 13605	VEN
	Venezuela	Ijjasz 63	VEN
	Venezuela	Little 17670	VEN
	Venezuela	Marcano Berti 296	VEN
	Venezuela	Steyermark 108793	VEN
	Venezuela	Steyermark 101597	VEN

Species	Country	Collector and number	Herbarium
	Venezuela	Steyermark & Aristequieta 58489	VEN
	Venezuela	Williams 12948	(A + GH)
T. amazonia			
	Brazil	Ducke 17678	VEN
	Brazil	Prance et al 7717	P
	Costa Rica	Barbour 1002	MO
	Guatemala	Standley 73131	F
T. arbuscula			
	Jamaica	Swartz s.n.	S
T. argentea			
	Brazil	Hatschabach 36400	LTR
	Brazil	Hatschabach 34813	LTR
	Brazil	Hatschabach 33359	LTR
	Brazil	Irwin et al 25193	LTR
	Brazil	Irwin & Soderstrom 6169	LTR
T. australis			
	Brazil	Hatschabach 35171	LTR
	Brazil	Smith & Reitz	US
	Brazil	Mealme 344	R
	Uruguay	Puerto 5411	F
	Argentina	Pedersen 2917	BR
T. biscutella = T. argentea			
	Brazil	Mealme 2468	US
	Brazil	Reidel 1095	A + GH
	Paraguay	Rolas & Coll. 56	BAF
	Paraguay	Balansa 2234	P
	Paraguay	Hassler 7243	P
	Paraguay	Fiebrig 4788	K

Species	Country	Collector and number	Herbarium
T. brasiliensis = T. glabrescens			
	Brazil	Martius s.n.	M
	Brazil	Glaziou 19680	P
	Brazil	Hoehne s.n.	K
	Brazil	Mealme 2365	S
	Brazil	Glaziou 11946	G
	Brazil	St. Hilaire 873	P
	Paraguay	Hassler 11364	BAF
T. bucidioides = T. oblonga			
	Costa Rica	Allen 6282	US
	Costa Rica	Godfrey 66873	MO
	Panama	Loa & Holdridge 15	MO
T. catappa			
	Venezuela	Rodrigues 5	VEN
	Brazil	Klein & Bresolin 8525	LTR
T. chicharronia			
	Cuba	Sagra 185	G
	Cuba	Wright 2570	G
	Cuba	Sagra 164	P
	Cuba	Ekman 4780	NY
T. dichotoma			
	Brazil	Silva et al AS77	NY
	Brazil	Irwin et al 47845	LTR
	Brazil	Prance et al 1566	NY
	Brazil	Irwin et al 47154	LTR
	Brazil	Prance et al 16376	LTR
	Brazil	Pries et al 50335	R

Species	Country	Collector and number	Herbarium
	Vnezuela	Steryermark 87513	VEN
	Venezuela	Wurdack 335	VEN
	Venezuela	Steyermark 114417	VEN
	Guyana	Mora & Bolter 8153	NY
	French Guiana	Sagot s.n.	S
T. domingensis = T. chicharronia			
	Dominican Rep.	Alain & Liogier 19026	K
	Dominican Rep.	Alain & Liogier 23105	NY
	Haiti	Ekman 4419	S
T. eichleriana			
	Brazil	Blanchet 2794	G
T. eriostachya			
	Cuba	Leon 17734	A + GH
	Cuba	Ekman 508	S
	Cuba	Ekman 18157	S
	Cuba	Riog 1727	NY
T. fagifolia			
	Brazil	Anderson et al 36428	LTR
	Brazil	Anderson 7678	LTR
	Brazil	Irwin et al 8481	LTR
	Brazil	Irwin et al 27469	LTR
	Brazil	Irwin et al 14572	LTR
	Brazil	Irwin et al 9928	LTR
	Brazil	Irwin et al 10564	LTR
	Brazil	Pires 58157	NY
	Brazil	Hatschabach 28046	LTR

Species	Country	Collector and number	Herbarium
T. glabrescens			
	Brazil	Luschnath s.n.	P
	Brazil	Riedel s.n.	C
	Brazil	Warming s.n.	C
	Brazil	Ducke & Lima 77	SP
	Brazil	Irwin et al 8879	LTR
	Brazil	Irwin & Soderstrom 5349	LTR
	Brazil	Irwin & Soderstrom 6147	LTR
	Brazil	Irwin et al 18007	LTR
	Brazil	Prance & Silva 58638	LTR
	Brazil	Maguire et al 56955	LTR
	Brazil	Hatschabach 34811	LTR
	Brazil	Hatschabach 24979	LTR
	Brazil	Lisboa 2267	M
T. grandialata = T. januariensis			
	Brazil	Martius s.n.	M
	Brazil	Glaziou 8668	C
T. guaiquinimae			
	Venezuela	Maguire 33008	VEN
	Venezuela	Maguire 33008A	VEN
T. guyanemsis			
	French Giana	Poiteau s.n.	U
	Guyana	Forest Dept. 4811	U
	Venezuela	Berti 187	VEN
T. guyanemsis			
	Venezuela	Steyermark 62174	VEN
	Venezuela	Delgado 328	VEN
	Venezuela	Smith 5506	VEN

Species	Country	Collector and number	Herbarium
T. hassleriana = *T. triflora*			
	Paraguy	Hassler 866	G
T. hylobates = *T. phaeocarpa*			
	Brazil	Warming s.n.	F
T. januariensis			
	Brazil	Raddi s.n.	G
	Brazil	Curran 18	A + GH
	Brazil	Schott s.n.	W
	Brazil	Heringer 1490	SP
	Brazil	Widren s.n.	S
T. latifolia			
	Jamaica	Kramer 1712	U
	Jamaica	Procter 36256	U
	Jamaica	Procter 22209	A + GH
	Jamaica	Moneague 890	K
	Jamaica	Swartz s.n.	S
	Jamica	Miller 1281	US
T. lucida			
	Brazil	Silva 4822	LTR
	Brazil	Rosa & Vilar 3005	LTR
	Brazil	Berg & Henderson BG 682	LTR
	French Guiana	Pols 158	
	Trinidad	Carrick 1203	K
T. neglecta = *T. chicharronia*			
	Cuba	Wright 2569	P
	Cuba	Ekman 16920	S
	Cuba	Leon & Clement 6642	NY
	Cuba	Ekman 16920	S
	Cuba	Sumidero 13478	K

T. nipensis = T. chicharronia			
	Cuba	Leon & Alain 19237	NY
	Cuba	Ekman 3098	S
	Cuba	Leon & Alain 19204	NY
	Cuba	Crosby & Mathews 9216	F
T. nyssacfolia = T. lucida			
	Trinidad	Broadway 7466	K
	Trinidad	Britton & Britton 2177	US
T. obidensis = T. oblonga			
	Brazil	Ducke 25020	K
T. oblonga			
	Venezuela	Jimenez Saa 1257	LTR
	Venezuela	Steyermark & Fernadez 99632	VEN
	Venezuela	Steyermark et al 101958	VEN
	Venezuela	Veillon 141	VEN
	Venezuela	Steyermark et al 102066	VEN
	Venezuela	Steyermark 101696	VEN
	Venezuela	Little 16132	VEN
	Venezuela	Steyermark 79490	VEN
	Venezuela	Medind 42354	VEN
	Venezuela	Blanco 8479	VEN
	Venezuela	Little 16206	VEN
	Venezuela	Aristiquieta et al 6774	VEN
	Brazil	Steward et al P13206	LTR
	Peru	Spruce 4507	K
T. opacifolia = T. guaiquinimae			
	Venezuela	Maguire 32951	VEN
T. orientensis = T. chicharronia			
	Cuba	Grosby & Mathews 64	NY
	Cuba	Alain et al 3568	A + GH

Species	Country	Collector and number	Herbarium
	Cuba	Auna 12587	US
	Cuba	Leon & Clement 20232	US
T. phaeocarpa			
	Brazil	Irwin et al 18036	LTR
	Brazil	Irwin et al 15427	LTR
	Brazil	Irwin et al 8705	NY
	Brazil	Irwin et al 9058	LTR
	Brazil	Irwin et al 15710	NY
	Brazil	Prance & Silva 59560	LTR
	Brazil	Pires 58128	LTR
	Brazil	Riedel 2521	G
T. quintalata			
	Venezuela	Steyermark et al 109793	VEN
	Venezuela	Steyermark et al 113430	VEN
	Venezuela	Steyermark et al 108860	VEN
	Venezuela	Steyermark et al 108911	VEN
	Venezuela	Steyermark et al 109739	VEN
	Venezuela	Steyermark et al 117401	VEN
	Venezuela	Maguire 33094	VEN
	Venezuela	Bernardi 1689	VEN
	Venezuela	Rosa & Cordeire 1565	NY
	Guyana	Tillet & Tillet 45805	NY
	Guyana	Cardona 1791	VEN
	Guyana	Cardona 1793	VEN
	Guyana	Cardona 2612	VEN
	Guyana	Cardona 2365	VEN
T. reitzii			
	Brazil	Reitz & Klein 16138	G
	Brazil	Reitz & Klein 12194	NY
	Brazil	Reitz & Klein 7076	US

Species	Country	Collector and number	Herbarium
	Brazil	Kuhlmann & Concalues 1336	SP
	Brazil	Kuhlmann 4234	US
	Brazil	Kuhlmann 503	US
T. riedelii			
	Brazil	Riedel s.n.	G
	Brazil	Riedel 1162	K
T. steyermarkii			
	Venezuela	Steyermark 117521	LTR
T. subsericea = *T. argentea*			
	Brazil	Hatschabach 30425	C
	Brazil	Riedel 429	A + GH
	Brazil	Prance et al 59230	NY
	Brazil	Irwin & Soderstrom 6505	NY
	Brazil	Irwin & Soderstrom 7204	NY
T. subsericea			
	Bolivia	Schmidt 135	M
	Bolivia	Steinbuch 7160	G
T. triflora			
	Argentina	Venturi 5316	A + GH
	Argentina	Lorentz & Hieranymus s.n.	P
	Paraguy	Pederson 4233	P
	Brazil	Hatschabach 39279	LTR
	Brazil	Hatschabach 25172	LTR
	Brazil	Klein & Bresolin 8428	LTR
	Brazil	Klein & Bresolin 8495	LTR
T. uleana			
	Brazil	Ule 1004	US

Species	Country	Collector and number	Herbarium
T. virgata = T. guaiquinimae			
	Venezuela	Maguire 33000	VEN
T. yapacana			
	Venezuela	Maguire, Wurdack & Keith 41512	LTR
	Venezuela	Steyermark & Bunting 102847	LTR
	Venezuela	Huber 1689	LTR
	Venezuela	V. V. Y. Km 42984	VEN
	Venezuela	Maguire 50590	VEN
	Venezuela	Maguire 36582	VEN
R. argentea = T. ramatuella			
	Venezuela	Maguire & Wurdack 35542	VEN
	Venezuela	Williams 14791	MO
	Venezuela	Maguire & Wurdack 35549	VEN
	Venezuela	Maguire et al 41879	LTR
	Venezuela	Maguire et al 36264	VEN
	Venezuela	Spruce 3498	NY
R. crispialata = T. crispialata			
	Brazil	Frões 28040	LTR
	Brazil	Prance et al 16186	LTR
	Brazil	Prance et al 15471	LTR
	Brazil	Prance et al 15504	LTR
	Venezuela	Maguire et al 37562	VEN
R. latifolia = T. virens			
	Venezuela	Maguire 29258	VEN
R. maguirei = T. virens			
	Venezuela	Maguire & Wurdack 34606	VEN

Species	Country	Collector and number	Herbarium
R. obtusa = T. crispialata			
	Venezuela	Maguire et al 30796	VEN
	Brazil	Froēs & Addison 29040	LTR
R. virens = T. virens			
	Venezuela	Williams 14127	VEN
	Venezuela	Williams 14078	VEN
	Venezuela	Maguire et al 36556	VEN
	Venezuela	Steyermark & Bunting 102965	LTR
	Venezuela	Medina 544	VEN
	Venezuela	Huber 1555	LTR
	Venezuela	Huber 3126	LTR
	Venezuela	Maguire et al 41493	LTR
	Venezuela	Maguire et al 41501	LTR
	Venezuela	Maguire et al 30764	VEN
	Venezuela	Vareschi & Saffe 8000	VEN
	Venezuela	Spruce 3758	W
	Brazil	Froēs 22340	BM

APPENDIX 3

Specimens of Combretaceae studied with respect to pollen characters.

Species	Collector and number	Country	Herbarium
T. actinophylla	Ule 7469	Brazil	K
T. acuminata	Glaziou 11974	Brazil	C
T. adamantium	St.Hilaire 1716a	Brazil	P
T. amazonia	Carlos Blanco 90	Venezuela(Bolivar)	VEN
T. amazonia	Liebmann 3400	Mexico	C
T. amazonia	Schunke 6251	Peru	LTR
T. amazonia	Davidse & Gonzalez 16353	Venezuela	LTR
T. arbuscula	Procter 24870	Jamaica	US
T. argentea	Hatschabach and Kunmrow 34813	Brazil(S.Paulo)	LTR
T. argentea	Irwin et al 18333	Brazil(Federal Dist.)	LTR
T. australis	Hatschabach 35171	Brazil	LTR
T. australis	Cristobal & Krapouiskas 1729	Argentina	G
T. bipleura	Borhidi 4374	Cuba	BP
T. biscutella	Riedel 1095	Brazil	LE
T. camuxa	J.Coelho 1336	Brazil	SP
T. catappa	Busey 744	Panama	F
T. chicharronia	Richard 185	Cuba	G
T. dichotoma	Kartaleo 141	B. Guiana	A+GH
T. domingensis	Alain & Liogier 23105	Rep.Dominican	NY
T. eichleriana	Blanchet 2794	Brazil	G
T. eriostachya	Leon 17734	Cuba	A+GH
T. fagifolia	Irwin et al 8481	Brazil	LTR
T. fagifolia	Martius 1818	Brazil(Mg.)	M
T. glabrescens	Irwin & Soderstrom 5349	Brazil	LTR
T. guaiquinimae	Maguire 33008	Venezuela	NY
T. guyanensis	Breteler 4952	Venezuela	U

T. hylobates	Warming s.n.	Brazil	C
T. januariensis	Schott	Brazil	W
T. lucida	Cowan & Forster 1387	Trinidad	P
T. mameluco	J.Coelho de Moraes 1338	Brazil	SP
T. neglecta	Leon 11491	Cuba	P
T. nipensis	Borhidi,Capote &Oiedo s.n.	Cuba	BP
T. oblonga	Steyermark & Fernandez 99632	Venezuela	LTR
T. oblonga	Skutch 3990	Costa Rica	K
T. oblonga	Pittier 5467	Panama	US
T. opacifolia	Maguire 32951	Venezuela	BM
T. quintalata	Steyermark et al 108860	Venezuela	LTR
T. quintalata	Caradona 2612	Venezuela	VEN
T. reitzii	Reitz & Klein 7076	Brazil	US
T. riedelii	Riedel 1162	Brazil	G
T. steyermarkii	Steyermark et al 117521	Venezuela	LTR
T. tarapotensis	Spruce 4507	Peru	K
T. triflora	Klein & Bresolin 8349	Brazil	LTR
T. triflora	Schreiter 8351	Argentina	W
T. virgata	Maguire 33000	Venezuela	BM
T. yapacana	Huber 1689	Venezuela	LTR
T. arjuna	Killip 43485	Florida	US
T. bellirica	No collector	India	US 1559075
T. fatraea	Glazio 2910	Brazil?	BR
T. grandiflora	Shultz 532	Australia	K
T. ivorensis	Hazlett 2924	W.Africa	F
T. myriocarpa	F. Cook s/n in 1967	Panama	F
T. paniculata	W.B.Sebr 163 in 1815	S.E.Asia	FI
T. perrieri		Madagascar	K
T. platycarya	Byrnes 1937	Australia	K
T. platyptera	Adams 1396A	Australia	K

T. polyantha	No collector 1439	Philippines	FI
Buchenavia callistachya	Ducke 25021	Brazil	S
B. capitata	Prance & Silva 58639	Brazil	LTR
B. capitata	Pires, Rodrigues & Irwine 50501	Brazil	LTR
B. capitata	Davidse & Gonzalez 16346	Brazil	LTR
B. grandis	Ducke 21349	Brazil	S
B. guianensis	Rodrigues & Colho 9251	Brazil	INPA
B. igaratensis	Kuhimann 2751	Brazil	SP
B. kleinii	Hatschbach 18512	Brazil	P
B. macrophylla	Berg et al	Brazil	LTR
B. megalophylla	Smith 2118	B.Guiana	U
B. ochroprumna	Ducke 21350	Brazil	S
B. ochroprumna	Cid,Ramos,Mota & Rosas 1525	Brazil(Para)	LTR
B. ochroprumna	Cid et al 192	Brazil(Amazon)	LTR
B. oxycarpa	Kuhlmann 4493	Brazil	R
B. oxycarpa	Ducke 7689	Brazil(Para)	S
B. oxycarpa	Krakoff 1241	Brazil(Para)	P
B. pallidovirens	Cuatrecasas 19939	Colombia	U
B. reticulata	Maguire & Wurdack 34709	Venezuela	VEN
B. reticulata	Davidse & Gonzalez 13765	Venezuela	LTR
B. suaveolens	Ducke 25018	Brazil	S
B. suaveolens	Liesner 8758	Venezuela	MO
B. suaveolens	Al Gentry & Ramos 12966	Brazil	LTR
B. tomentosa	Hatschbach & Kummrow 34965	Brazil	LTR
B. tomentosa	Irwin & Soderstrom 6349	Brazil	LTR
B. tomentosa	Maguire et al 56252	Brazil	LTR
B. viridiflora	Ducke 1378	Brazil	US
B. viridiflora	Ducke 25023	Brazil	S
B. viridiflora	Prance et al14057	Brazil	LTR

B. viridiflora	Ducke 1378	Brazil	LTR
Bucida buceras	Ostenfeld 479	St.Thomas	C
B. buceras	Crutiss 496	Florida	F
B. buceras	Ekman 14532	Santo Domingo	C
B. ophiticola	Borhidi & E.del Risco s.n.	Cuba	BP
B. spinosa	John & Northrop 502	Bahama	F
B. spinosa	Wright 2573	Cuba	BP
B. subinermis	Bisse & Rojas	Cuba	JE
Ramatuella argentea	Froes 28684	Brazil	UB
R. argentea	Madison et al 6215	Brazil	F
R. virens	Spruce 3758	Venezuela-Colombia	W
R. virens	Maguire et al 36556	Venezuela	VEN
R. virens	Medina 544	Venezuela	VEN
Anogeissus leiocarpus	Morten s/n. in 15/9/53	Ghana	BM
Conocarpus erecta	Vin Celli 579	Nicaragua	LTR
Combretum leprosum	Maguire et al 56874		LTR
Laguncularia racemosa	Hatschbach 35611		LTR
Lumnitzera littorea	Hoogland 4377	New Guinea	BM
Lumnitzera racemosa	Petlitt 767	Maldive Island	BM
Pteleopsis deptera	Gossweiler 7475	Angola	BM
Pteleopsis myrtifolia	No collector 13960 in 1948	Angola	BM
Quisqualis indica	Stace s/n in 1979	Nigeria	LTR
Strephonema pseudocola	Boldivin 7083	Liberia	K
Thiloa glaucocarpa	Mattos et al 262	Brazil	LTR
Thiloa gracilis	Anderson 12032	Bolivia	LTR
Thiloa paraguariensis	Buck et al 761	Brazil	LTR

Appendix 4

Photographs of the type specimens of Terminalia and Buchenavia seen during this study.

Plate 1

A T. paraensis (holotype, M)

B T. latifolia (lectotype, S)

C T. arbuscula (holotype, S)

D T. firma (holotype, M)

Plate 2

A T. lucida (lectotype, BR)

B T. hayesii (holotype, US)

C T. nyssaefolia (holotype, NY)

D T. dichotoma (holotype, GOET)

Plate 3

A T. eriostachya (holotype, P)

B T. canescens Borh. (isotype, BP)

C T. chicharronia (lectotype, P)

D T. domingensis (isotype, P)

Plate 4

A. T. orientensis (holotype, NY)

B T. nipensis (isotype, NY)

C Gimernatea oblonga (holotype, MA (Phot, F))

D T. tarapotensis (lectotype, G)

Plate 5

A *T. chiriquensis* (holotype, US)

B *T. obidensis* (lectotype, RBO

C *T. bucidoides* (holotype, US)

D *T. mameluco* (holotype SP)

Plate 6

A *T. valverdeae* (holotype MO)

B *T. phaeocarpa* (lectotype, LE)

C *T. hylobates* (lectotype, C)

D *T. kuhlmanii* (holotype, RB)

Plate 7

A *T. argentea* (holotype, M)

B *T. subsericea* (lectotype, LE)

C *T. sericea* (lectotype, P)

D *T. biscutella* (lectotype, LE)

Plate 8

A *T. januariensis* (lectotype, G)

B *T. grandialata* (holotype, BR)

C *T. camuxa* (holotype, SP)

D *T. guyanensis* (paratype, A + GH)

Plate 9

A *T. eichleriana* (lectotype, BR

B *T. fagifolia* (lectotype, M)

C *T. actinophylla* (lectotype, M)

D *T. australis* (lectotype, P)

Plate 10

A *T. triflora* (isolectotype, P)

B *Myrobalanus balansae* (lectotype, P)

C *T. hassleriana* (lectotype, G)

D *T. hassleriana* var. *bernardinensis* (holotype, G)

Plate 11

A *T. reitzii* (isotype, NY)

B *T. odontoptera* (holotype, G)

C *T. glabrescens* (holotype, BR)

D *Chuncoa braziliensis* (lectotype, P)

Plate 12

A *Chuncoa flavescens* (holotype, PRC)

B *T. yapancana* (holotype, NY)

C *T. quintalata* (holotype, NY)

D *T. guaiquinimae* (holotype, NY)

Plate 13

A *T. virgata* (holotype, NY)

B *T. opacifolia* (holotype, NY)

C *Ramatuella virens* (isotype, LE)

D *T. adamantium* (holotype, P)

Plate 14

A *T. riedelii* (lectotype, LE)

B *Buchenavia fluminensis* (C)

C *T. rotundifolia* (C)

D *T. micophylla* (lectotype, BR)

Plate 15

A <u>B</u>. <u>capitata</u> (holotype C)

B <u>B</u>. <u>kleinii</u> (holotype, S)

C <u>B</u>. <u>igaratensis</u> (holotype, SP)

D <u>B</u>. <u>parvifolia</u> (isolectotype, S)

Plate 16

A <u>B</u>. <u>tomentosa</u> (lectotype, LE)

B <u>B</u>. <u>currugata</u> (isotype, S)

C <u>B</u>. <u>callistachya</u> (isotype, S)

D <u>B</u>. <u>recticullata</u> (isolectotype, LE)

Plate 17

A <u>B</u>. <u>macrophylla</u> (isolectotype, LE)

B <u>B</u>. <u>megalophylla</u> (isotype?, FDG)

C <u>B</u>. <u>nitiddisima</u> (holotype, G)

C <u>B</u>. <u>pulcherrima</u> (isotype, FDG)

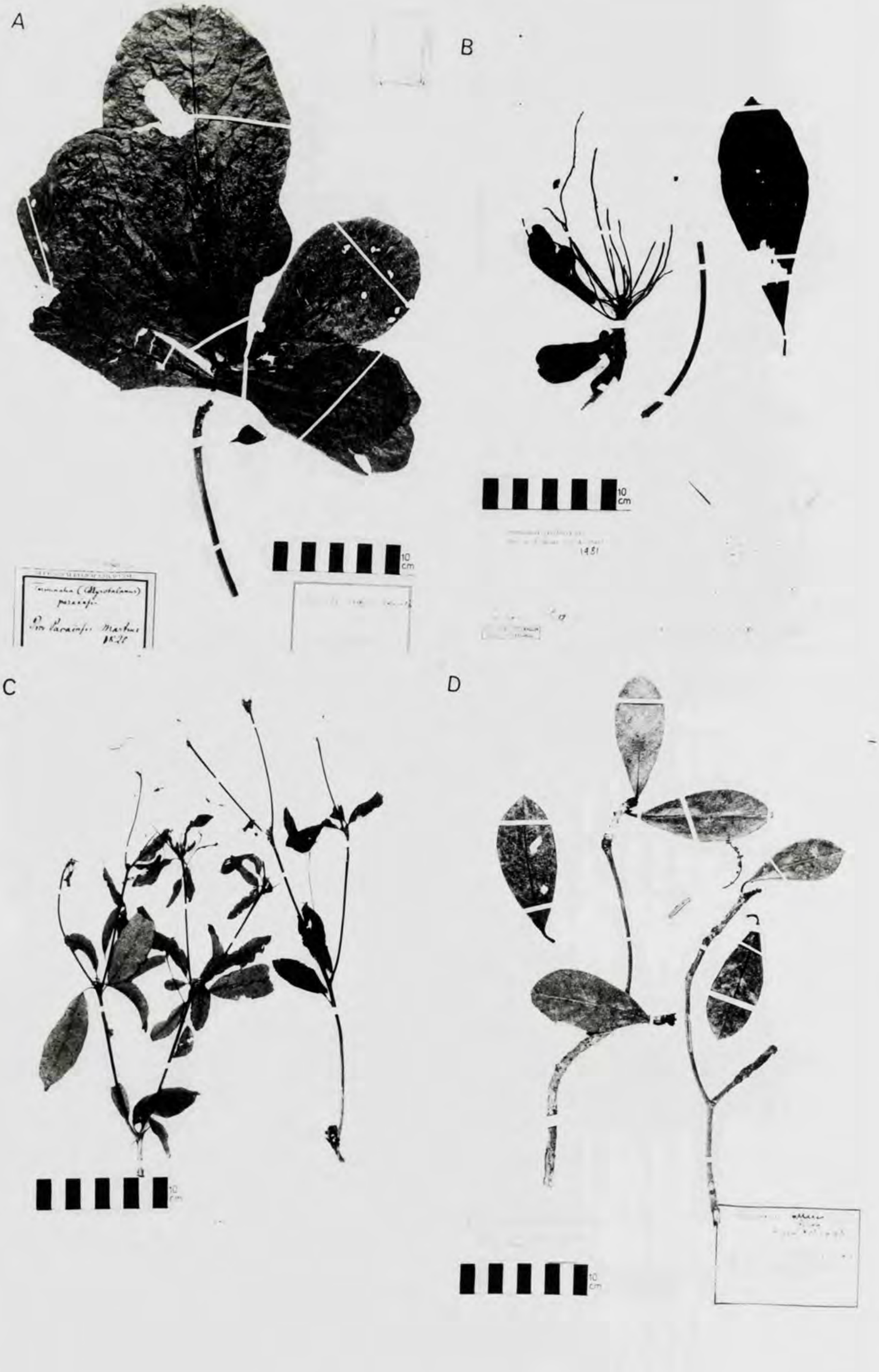

PLATE 1

PLATE 2

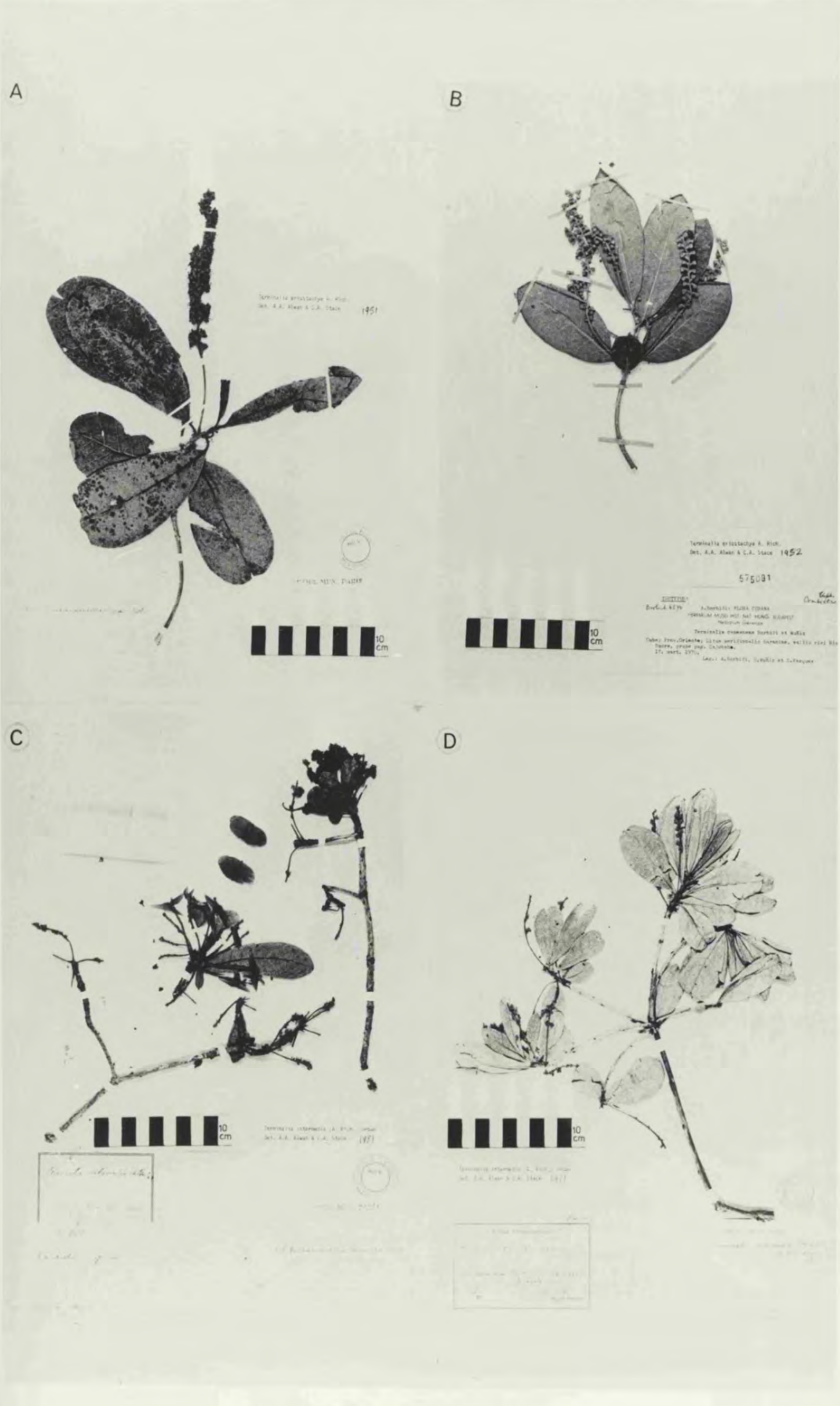
A
Terminalia eriostachya A. Rich.
Det. A.A. Alwan & C.A. Stace 1951
10 cm
B
Terminalia eriostachya A. Rich.
Det. A.A. Alwan & C.A. Stace 1952
575091
10 cm
C
10 cm
D
10 cm

PLATE 3

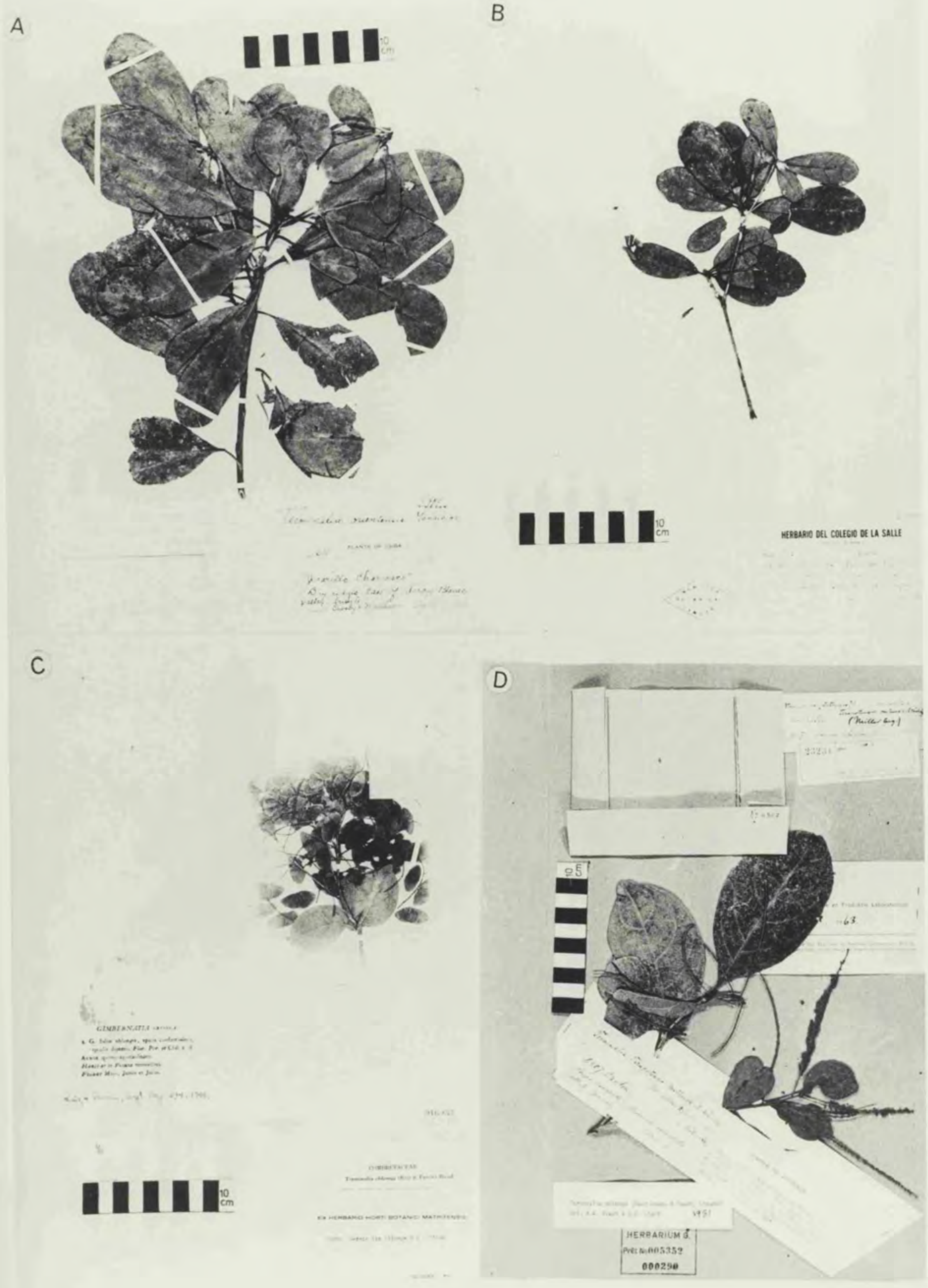
A
B
C
D
10 cm
HERBARIO DEL COLEGIO DE LA SALLE
EX HERBARIO HORTI BOTANICI MATRITENSIS
HERBARIUM

PLATE 4

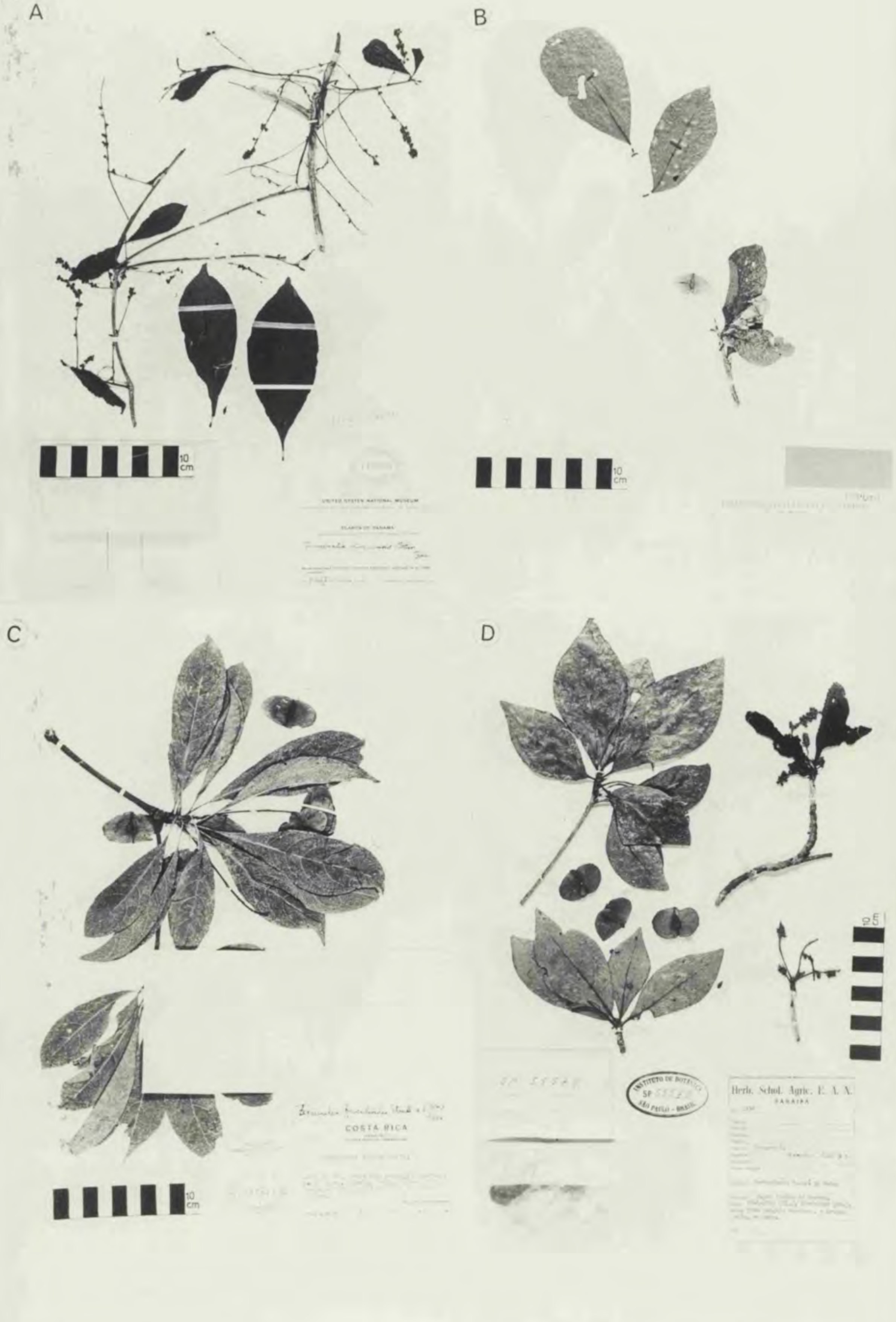
A
B
C
D
10 cm
10 cm
10 cm
UNITED STATES NATIONAL MUSEUM
PLANTS OF PANAMA
COSTA RICA
INSTITUTO DE BOTANICA
SÃO PAULO - BRASIL
Herb. Schol. Agric. E. A. N.

PLATE 5

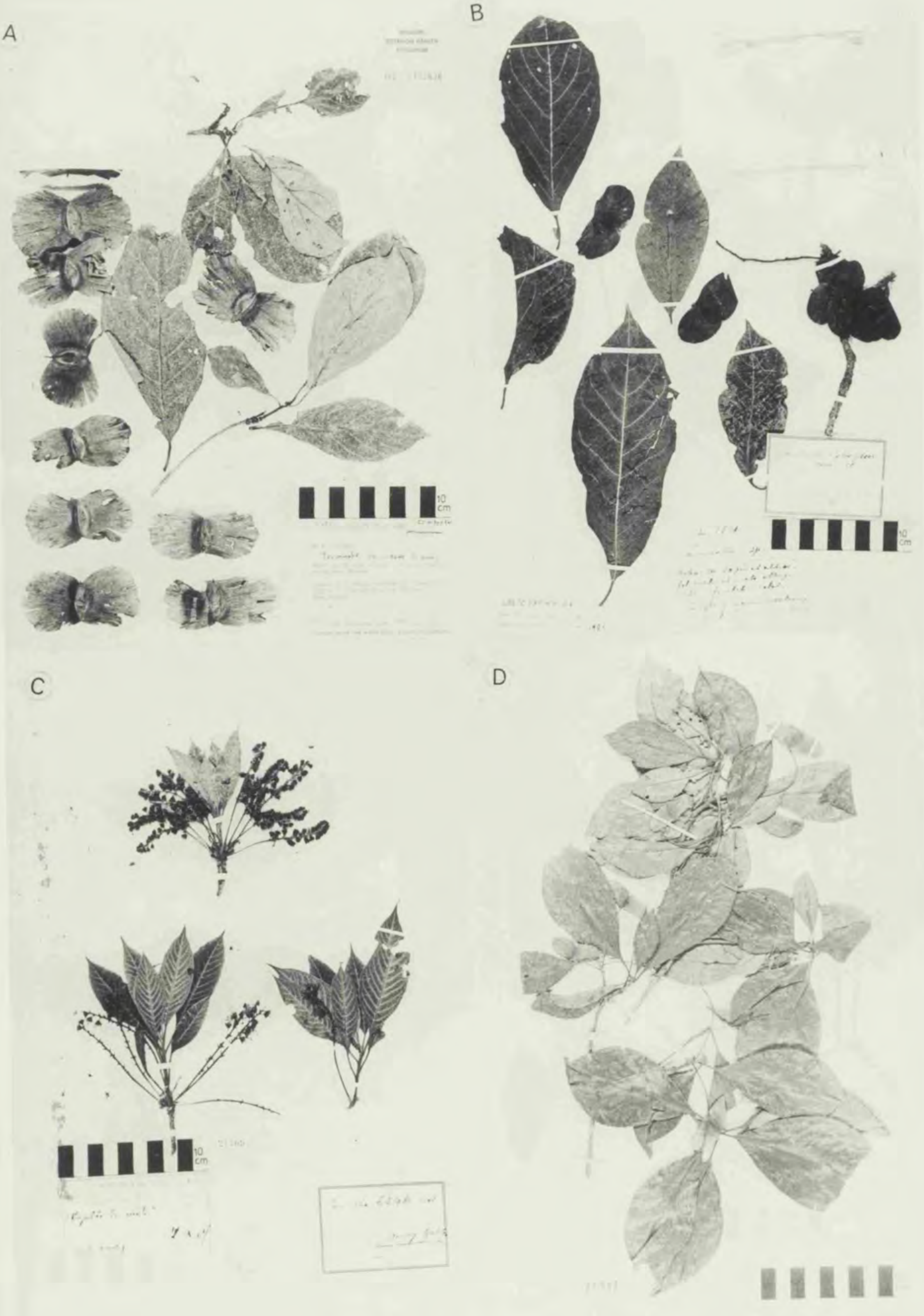

PLATE 6

PLATE 7

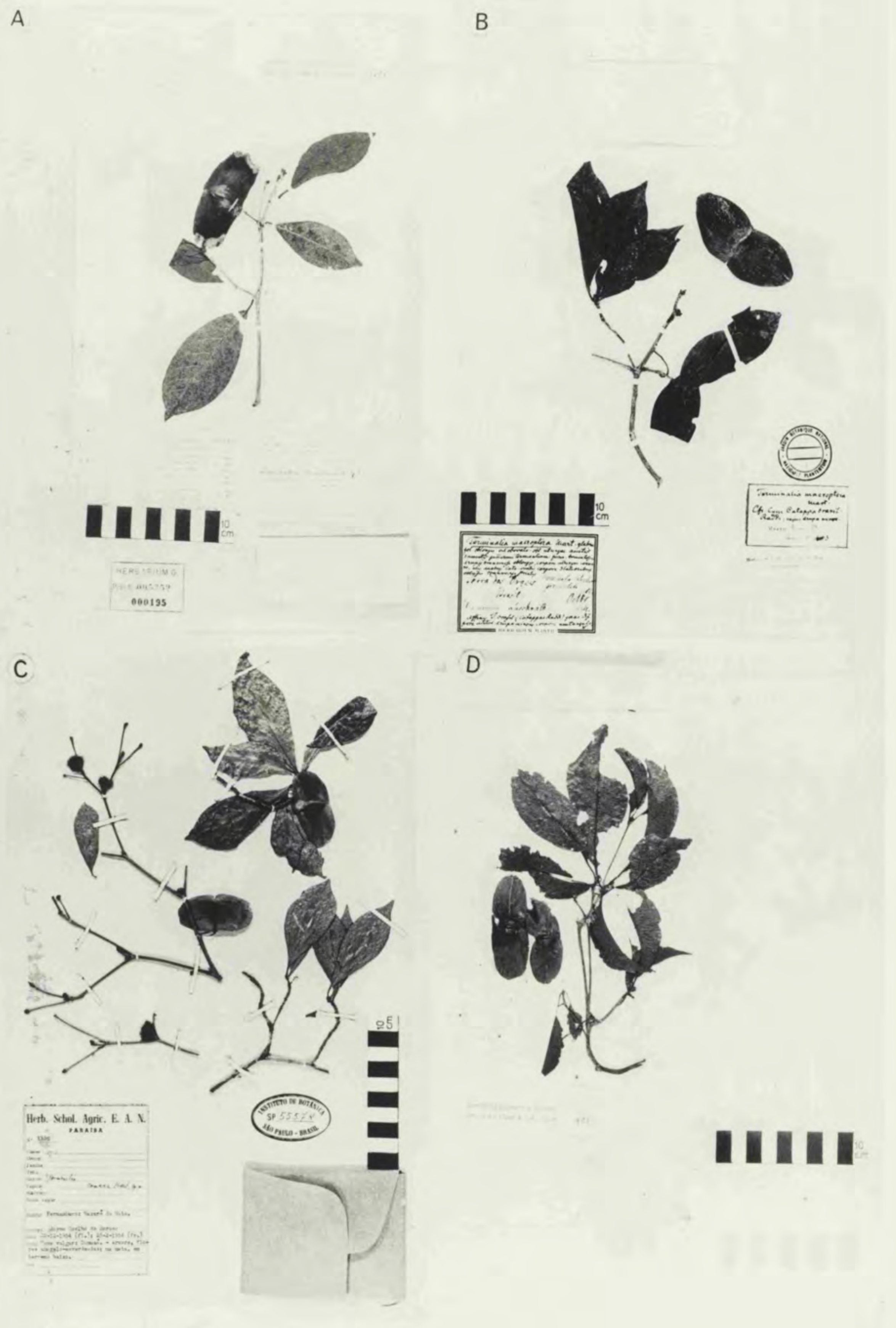

PLATE 8

PLATE 9

PLATE 10

PLATE 11

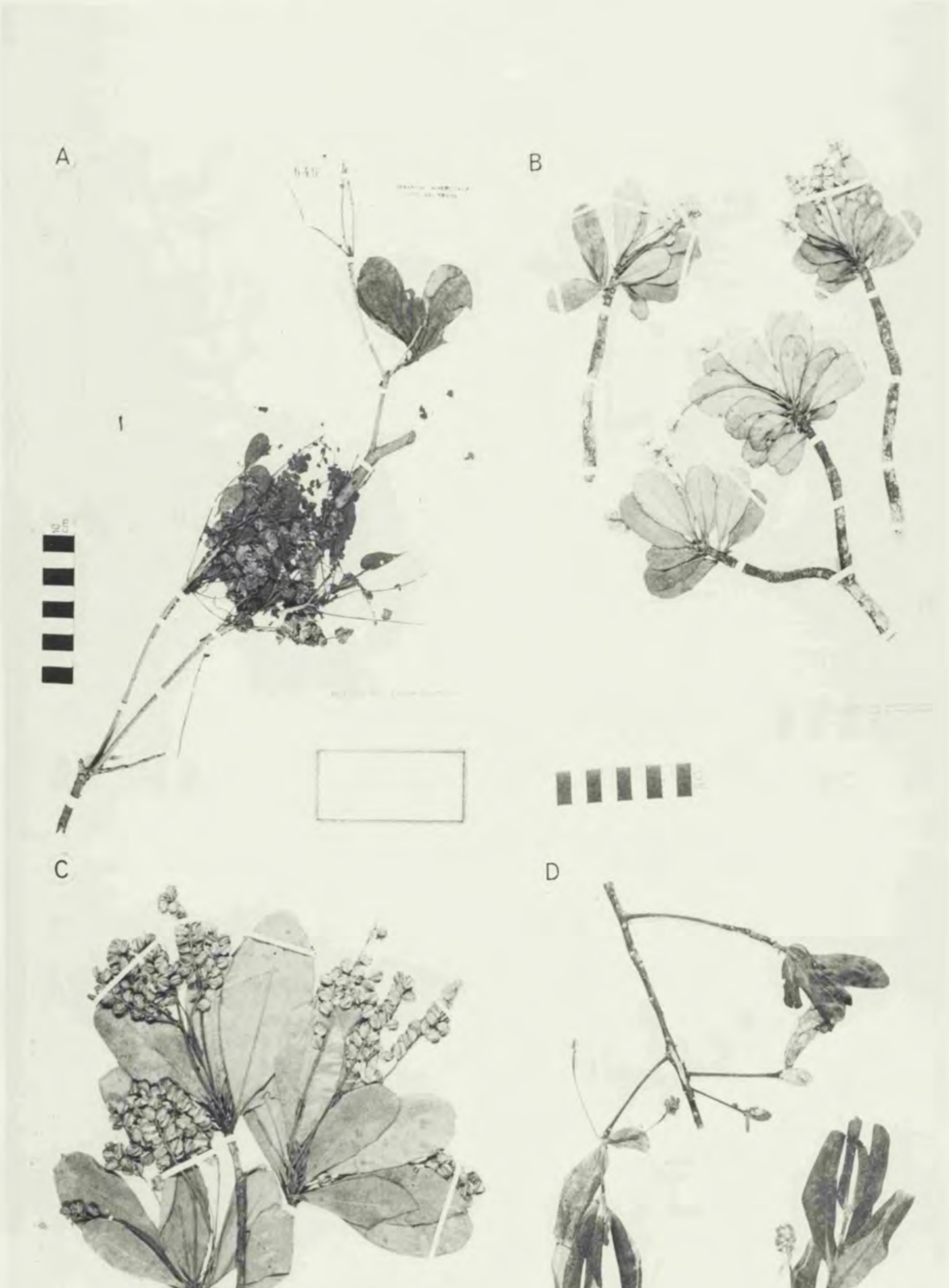

PLATE 12

PLATE 13

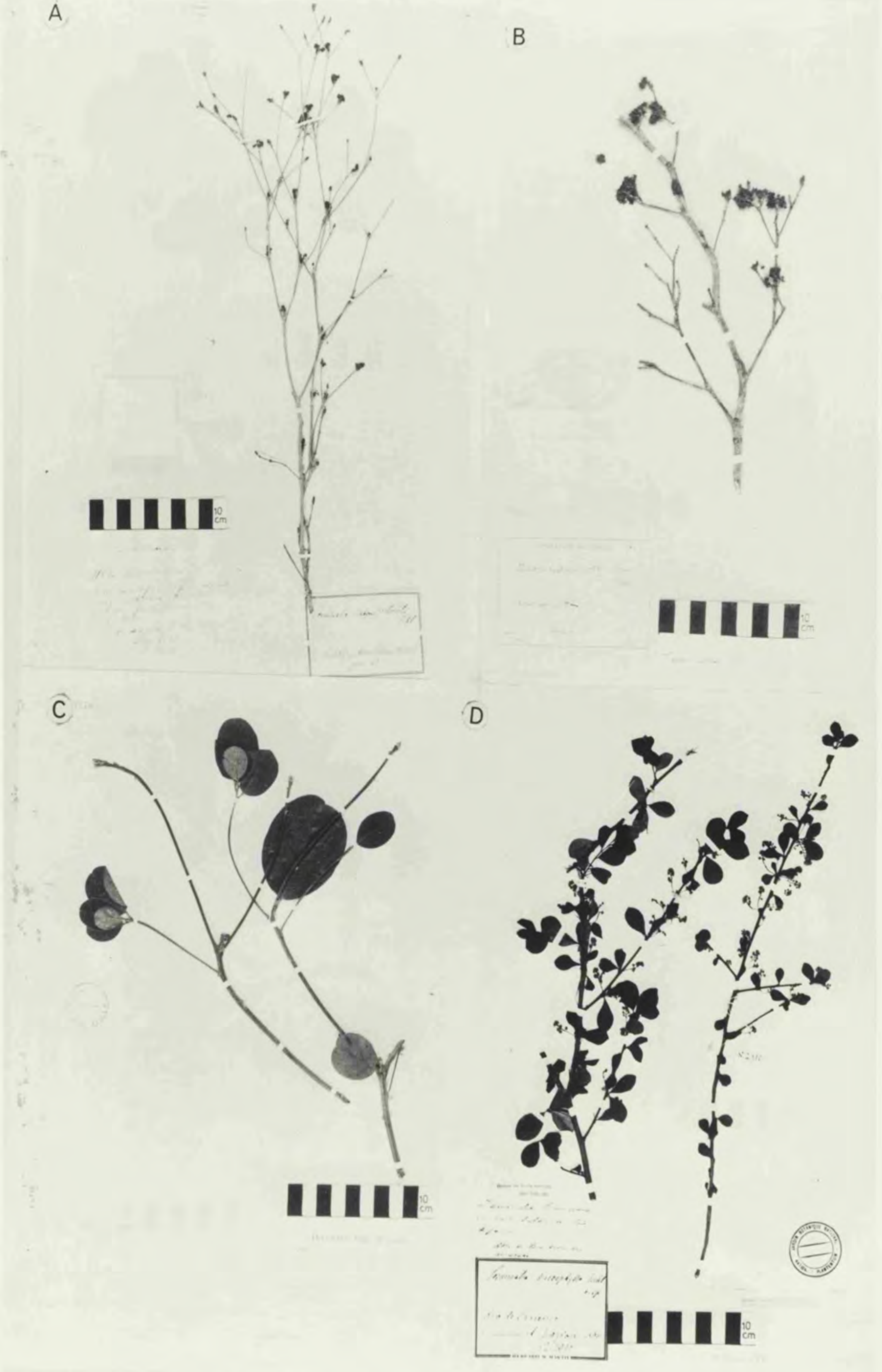

PLATE 14

PLATE 15

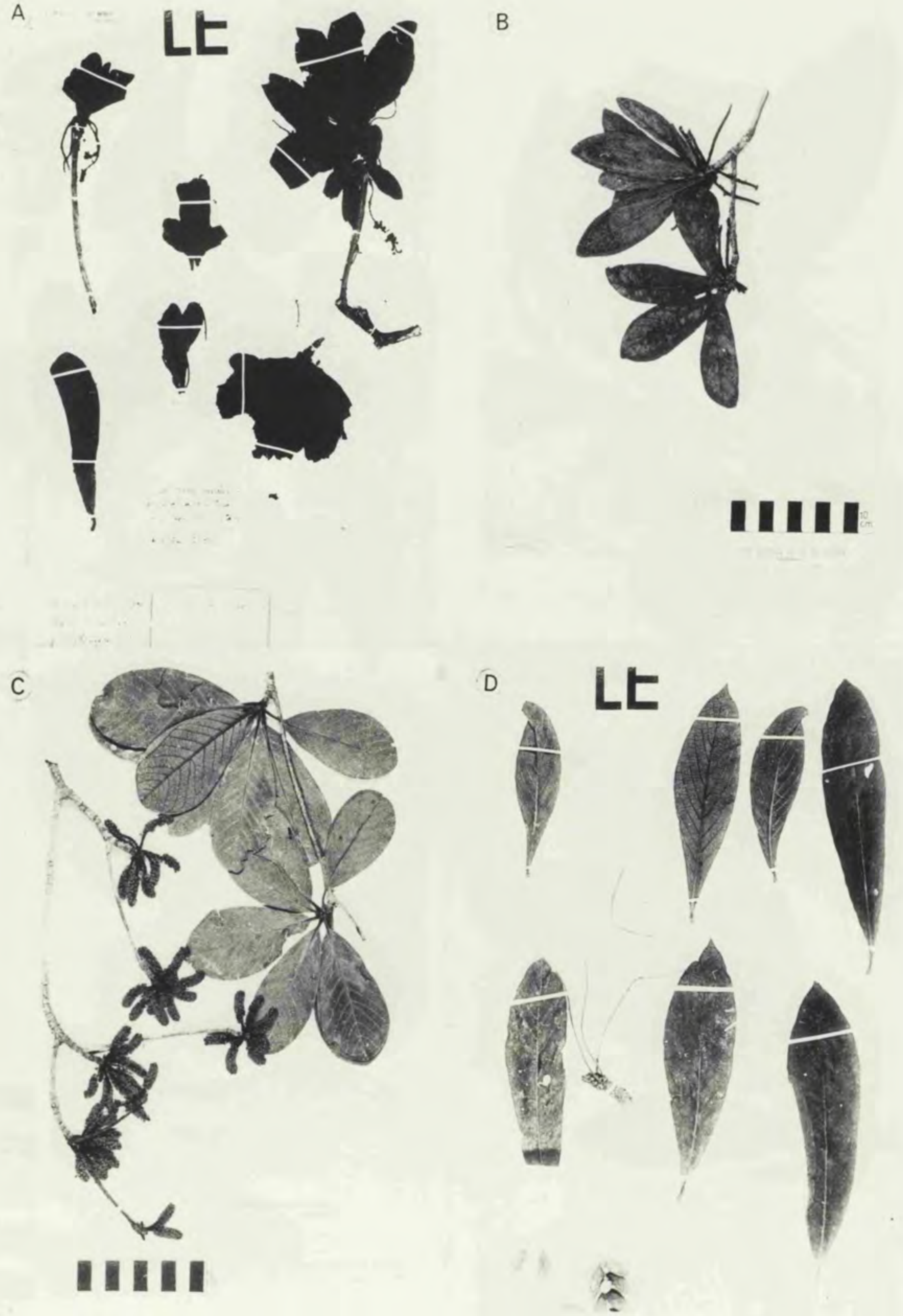

PLATE 16

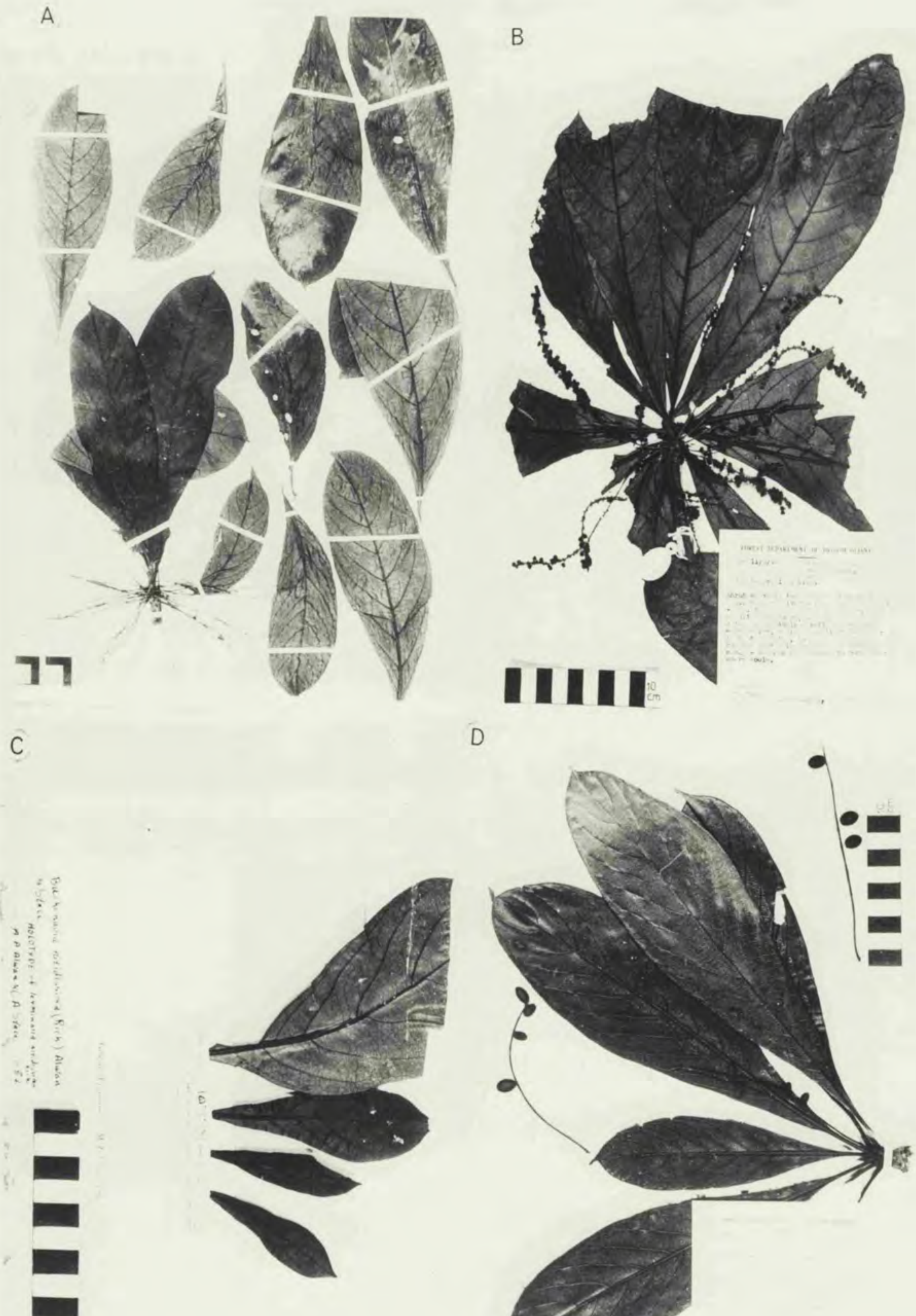

PLATE 17

APPENDIX 5

List of specimens of American Terminalia, Bucida and Buchenavia seen during this study.

A. Terminalia

1. TERMINALIA CATAPPA

BRAZIL: Brasilia, DF., Asa Norte Comercial (713), Mendonça 7(LTR). R. de Jan., Glaziou 1508 (BR, K, P). Belem, Mata da Serraria, 1952, Pires 4422 (IAN). Manaus, Rua Jamor Gabriel 18/7/1971, P.J.M., Mass 357 (INPA, MO, U, VEN). Guiabá, Mt., Macedo et al 1175 (INPA). Costcira do Ribcirão, St. Catarina, Klein & Dresolin 8525 (LTR). Belém, Pará, Pires 1122 (INPA). Fernando Do Noronha, Ridley et al 60 (BM). Paranaguá, Paraná, Dusen 13475 (A + GH, BM, F, NY, S). Mattogrosso, O. Kuntze (F297482). Seara, Curran 29 (A + GH, F, US). Sao Paulo, Gibbs et al 6654 (F, SP). Sao Paulo, Santos & Mosen 2849 (S). Antiquael aylvis umbrosis 1849, Wullschlaégel 202 (M). Prov. Paraensis 1820, Martius (M). Est. do Rio, Cupo Frio, Ule s.n. (R 91506). S. Jose, Sao Paulo, Carucago & Monini 89 (SP). Santos, S. Paulo, Gehrt 34341 (SP). Not localized, Hoehne 18290 (SP). Ilha Vitoria, São Paulo, Gomes 3686 (SP). S. Catarina, Reitz & Klein 2715 (BM, NY, US). Paranaguá, Paraná, Hatschabach 6413 (US). Parana, Hatschabach 21253 (BM). Belem, Pires 4422 (IAN, US). St. Catarina, Itaja, Reitz 4476 (US). Amazonas, Silva 1826 (NY).

BOLIVIA: Dpt. Beni., Ballivian, Espiritu en la Zona de influenciadel rio Yacuma (LTR).

PERU: Loreto, Killip & Smith 29001 (F, NY, US). Loreto, Williams 2315 (F, US). Rio Haullaga, Loreto, Williams 4935 (A + GH, F, S, US).

SURINAM: Hostmann, 812 a (G, GOET, P, S, U).Sndiser 90 (U). Paramaribo, Kegel 979 (GOET). Paramaribo, Focke 800 (U). Paramaribo, Went 484 (U). Braamspunt, Kramer & Hekking 2088 (U). Prope Albina, Marowyne (U).

GUYANA: Georgetown, Persaud 389 (F). Basin of Essequibo R., Smith 2118 (P, US). East Coast, Demerara, Omawale & Persaud 42 (NY).

FRENCH GUIANA: Karauany, Sagot 794 (G, K, P). Cayenne, Lescure 273 (CAY). Cayenne, Menten s.n. (K). Karauany, Benoitt 1256 (P). St - Larent, Lescure 689 (CAY). Guyaneni-Anlwanum, Richard Herb. (P), M. Gabriel 18002 (G).

VENEZUELA: Cultivado, muy Comun per les aveuidar, Parques y jardines de Camaue 7/7/1966, Torres 1833 (VEN). Élvigia, Merida, Little 16123 (VEN). Caraballeda, Dto. Fedral, Rodriqez, 5 (VEN). Jarodins de Caracas, Maxwell 227 (VEN). Arbusto de 2-3 m. hojas coriaceas, cultivadeo, Dtto Fedral, Zonas cercanos a la playa, a no más de 20 m. de la ovilla 14/7/1971, Morillo 1376 (VEN). Sa Vela de Caro, Carran & Haman 668, 1278 (VEN). Bello Monte, Caracass 16/7/1955, Reggio M. de Scorza s/n (VEN). Catia de mar, Voal 614 (F). Mocquerys, maracaileo, Drake 811, 22 (P). Chroroni, Vogl 45 (M). Aragua, Ocumare de la Costa, Oberwinkler 13334 (M).

COLUMBIA: Bolivar, Curran 255 (US, WIS). Antioquia, Barkley et al 17 (F), Riometa, Tanupe, Cuatrecasas 3648 (F, US). Riometa, Bocas del Tua, Cuatrecasas 4490 (US). Santander del Sur, Garganta 1252 (F). Savana, Rincon Hondo, Magdalena valley, Allen 445 (F, MO). Antioquia, Archer 600 (US). Del Hulia, Little & Little 9429 (NY, US). Norte de Santader, Kilip & Smith 21028 (US). Guataquie, Perez 384 (NY, US). Medellin, Toro 53 (US). Sta Marta, Perez 4817 (US). Choco, Warner 22 (A + GH). Valle Dagua, Pennell 5382 (A + GH, NY). Choco, Ducke 9675 (NY). Cundinamarca, La Mesa, Duque-Jaramillo 3689 (NY).

ECUADOR: Not localized, T.W. 836 (F). Not localized Shimpff 1104 (A + GH, G). Los Rios, Hacienda Clementina on Rio Pita (S). Los Rios, Little 6472 (U). Esmeraldos, San Lorenzo, Jativa & Epling 1118 (NY, U). Los Rios, Queredo-Sto Domingo, Dodson & Gentry 6573 (MO).

PANAMA: Canal zone, Forgeson 50983 (WIS). San Blas, Warner 197 (F, MO). Colon, Gogro 1906 (HBG). Not localized, Wilbur & Teeri, 12984 (f). Canal zone, Liesner 1378 (A + GH, F). Chiriqui, S. Puerto Armuelles, Gunaabano, Busey 492 (F, MO). Chiriqui, Burica Penen Sula, Busey 766 (MO, NY). Veraguas, Rio Concepcion, Liesner 2846 (F, MO, NY). Same locality, Liesner 13178 (MO). Colon, Laolzo (F, MO). Quebrada Manzanillo, Busey 744 (F, MO). San Jose Island, Johnston 291 (MO, US). Chiriqui Lagon, Wedel 1950, 2917 (A + GH, BM, US). San Jose Island, Archipilago, Erlanson 524. (US). Not localized, Rowlee 355 (US). Isla Colon, Wedel 497 (A + GH, BM). Balboa, Canal Zone, Standley 26971, 28567 (US). Panama City, Harkins 1197 (A + GH). Balboa, Canal Zone, Nee 11495 (MO). Colon, Kennedy 2992 (MO). Daiven, Flozom 4611 (MO). Canal Zone, Gentry 6435 (MO). Bocas del Toro, Blum 1352 (MO). Canal Zone, Greenman & Greenman 5211 (MO). Canal Zone, Pina, Lewis et al s.n. (MO). Colon, Croat 9836 (MO). San Blas, Edwards 11 (MO). Panama, Saboga Isl., Edwin et al 5139 (MO). Mataechui to las Cuseauas, Cowell 3477 (NY). San Jose Island, Erlanson 524 (NY). Isla de Coibu, near Maria River, 22/10/79, Antonio 2298 (LTR).

COSTA RICA: Aguiares, Scarpenter 569 (US, WIS). Guanacaste, Durkee 76-394 (F). Limon, Baker & Burger 35 (F). Puntarenas, Burger & Liesner 6559 (F, MO, NY). Not localized, Pittier & Ton 13805 (P). Isla de Coco, Valerio 1093 (F). Guanacaste, Wilbur & Stone 9942 (F). Not localized, Solis 182 (F, MO). Puntarenas, Biolley 17310 (A + GH, US). Puntarenas, Lems s.n. (NY, US). Nicaya, Jonduz 13805 (A + GH, MO, US). Limon, Mossbach 3638 (A + GH). La Liorona, Jansen 11096 (MO). Guanacaste, Jansen 11514 (MO). San Jose, 1914, Matthews, s.n. (MO). Guancaste, Croat 304 (MO). Guancaste, Stone 1977 (MO). Isla del Coco, Jimenez 3196 (NY). Arbu de la placede Nieoya, Conduk 13805 (K).

NICARAGUA: Chinandega, near rio Chiguito, Elviejo, fl. 27/12/1969, Atwood 2641 (A + GH, F, K, MO). Zelaya, Siuna, Seymour 5023 (A + GH, BM, F, K, MO, NY). Zelaya, Puerto Cabezas, Robbins 5928 (A + GH, BM, F, MO, NY). Chinandeya, Aserradores Is., Baker 2084 (A + GH, G, K, MO, US). Managua (com. name Almendro), Caldera 13 (MO). Managua, elv. 150 m., 6/12/1979

(Com. name Almendro), Castro 54 (MO). Mata galpa, Rio Tuma at El Tuma 40 km E. of Matagalpa, alt. 400 m, premontane wet forest, gallery forest, 2nd- growth on hillside, tree 5 m. 25/5/1977, Neill 2002 (MO), Zelaya, Casa La Salle, Puerto Cabezas, 14° 1 N 83° 23 W, 3/10/1978, Kurkoff 10545 (MO). Departmento de Mangua, Reparto Bosque dee Alfamira, Managua, Elev. 150-190 m (Arbolito de 3 m, flores verde amarillas aromaticas, nombre comun Almendro), 11/9/1979, Grijalva 552 (LTR).

HONDURAS: Near La Ceiba, Atlantida, Yuncker et al 8424 (A + GH, BM, G, K, MO, NY, US), 8849 (A + GH, BM, K, MO, S, US). El Zamorano, Molina 21916 (F, NY). Tela, Atlantida, Standley 54789 (A + GH, F). Comayagua, Standley & Chacon 5782 (F). Cay Glovers Reef, Cosentine 179 (F). Puerto Sieria, Wilson s.n. (NY), 135 (US). Ceiba, on sea beach, Dyer A42 (US). San Pedro Sala, Thieme 5610 (US). Puerto Cortes, Hernandez & Barkley 40472 (A + GH). Corest, Garcia 106 (MO).

EL SALVADOR: One mile E. of Caco Beach, Case et al 166 (MEXU). San Migual, Jucker 918 (K, F, G). San Salvador, Carlson 508 (F). San Migual, Standley 21151 (A + GH, US). San Salvador, Renson 276 (NY, US). El Salvador, West 3548 (MO, US).

GUATEMALA: Alfriede de Poll 20/9/1980 (US 32342, 32344, 32345, 32346). Peten, Ortiz 1944 (BM, F, US). San José, Dept. Escuintla, Smith 2517 (A + GH, G, K, NY, US). Same locality, Spellman 6366 (F, MO). La Libertad, Lundell 3268 (A + GH, BM, F, NY). Zacapa, Zacapa, Steyermark 29005 (F). Zacapa, Zacapa, Standley 74164 (F). Finca Cuntān, Dept. Suchitepequez (F, US). Izabal, Le Doux et al 2111 (MO, NY). Izabal, Harmon & Fuentes 5699 (MO). Suchitepequez, Harmon 2392 (MO).

BELIZE: Belize, Hedger 273 (BM). East Snake Cay, Stoddser 96 (BM). Stann Creek, Schipp 498 (A + GH, BM, F, G, M, MO, NY, S). Belize, Egler 42-44 (F). Belize Lundell 4250 (F, S). San Antonio, Crozal, Gentle 4936 (MO, NY). S.W. Cay II, Fosberg & Stoddart 53882 (US). Glover's Reef, Middle Cay, Sachet &

Stoddart 1629 (B, MO, US). Hatchet Cay, Fosberg & Spellman 54387 (NY, US). Little Water Cay, Fosberg & Spellman 54332, 54215 (US). N.E. Cay, Fosberg & Sachet 53809 (BM, MO, NY, US). S. Water Cay, Spellman & Stoddart 2204 (MO, US). Hunting Cay, Spellman & Stoddart 2421 (MO, US). Ranguana Cay, Spellman & Stoddart 2259 (US). Lime Cay, Spellman & Stoddart 2359 (MO, US). Frank's Cay, Spellman & Stoddart 2394 (MO, US). N.E. Sapodilla Cay, Spellman & Stoddart 2301 (MO, US).

MEXICO: Tabasco, Nevelo et al 66 (MO, MEXU). Tabasco, Ortega & Marquez s.n. (MEXU 549). Tabasco, Calzada 2309 (MEXU). Veracruz, Cox-Vasque 75, 76 (MEXU). Veracruz, Isusael s/n (MEXU). Veracrus, Large 129 (MEXU). Not localized, Matuday 16534 (NY, MEXU). Veracruz, Jones 22729 (MEXO). Vera Cruz, Sousa 4303 (MEXU). Puerto Morelos, Sousa 10875 (BM). Baja California, Ames et al s.n. (MEXU 243272). Tabasco, Maldonado s.n. (MEXU 262514). Veracruz, Lot 1369 (A + GH, MEXU). Veracruz, Isla de Lopas, Lot 1313 (A + GH, BM, MEXU). Veracruz, Lot 281 (A + GH, F, MEXU). Oaxaca, Zizambo & Colunga 123 (MEXU). Oaxaca, Schultez & Pablo Recko 959 (MEXU). Veracruz, Echavez s.n. (MEXU 105798). Veracruz, Rosas 653 (MEXU, U). Pochulta, Oxaxa, Conzatti et al 3239 (MEXU). Veracruz, Martinez 486 (MEXU). Not localized, Bruff 1503 (MEXU). Veracruz, Williams 9104 (F). Acapulco, Palmer 72 (F, K, MO, NY, US). Yucatanne, Izamal, Gaumer & Sons 23917 (A + GH, F, MO, US). Xucatanac, Gaumer 470 (A + GH, F, MO, NY, US). Yucatan, Merida, G. Rivas 22 (F). Yucatan, Emrick 155 (F). Not localized, Congatti 3239 (US); Rose 1816 (US); Seler 3879 (A + GH). Pochutla, Oaxaca, Markvinius 681 (US). San Marcos, Nelson 2277 (NY, US). San Blas, Tapic, Nelson 4325 (US). Candelaria, Reko 3239 (US). San Blas, Nayarit, Ferris 5424 (A + GH, US). Temascaltepec, Guayabal, 22/8/33), Hinton 4566 (A + GH, K, NY). Sinaloa, Dun et al 21830 (MO, NY). Guerrero, Acapulco Bay, Clark 7194 (MO, NY). Oaxaca, San Mateo de Mar, Zizumbo & Colunga 123 (MO). Chilpancing, Andrews 568 (NY).

CUBA: Havana: Hermann 249 (F), Shafer 222 (F, NY), Curtiss 689 (A + GH, BM, F, G, K, M, MO, P), Hermann 144 (F, NY, Morton 10685 (US), Ekman 549 (S). Santa Clara: Rob Combs 232 (A + GH, F, K, MO, NY, P, US), Howard 4896 (A + GH, BM, NY, P, S, US), Rutten 338 (U). Las Villas, Gonzalez 680 (BM, F, NY, S). Oriente, Holguin to Calcum, Shafer 1554 (F, NY, US). Pinar del Rio, Stenenso 1789 (US). Soledad, Orcas Limones (US). Baracoa, Underwood & Earle 584 (NY). Not localized: Rutten & Rutten s.n. Mar-Apr. 1920 (U), Rutten & Rutten 79 Mar-Apr. 1921 (U).

JAMAICA: Orcutt 4295 (K), Yuncker 18412 (BM, F), Wight 158 (F, NY), Harris 10824 (F, K, NY, P, US), Maxon 10514 (S, US), Harsherger 91 (US), Sargent s.n. (A + GH). Navy Island, Millspaugh 1836 (F). Montego Bay, Sauer 1829 (F). St. Elizabeth, Barkley (38682). Barahona, Fuertes 181 (A + GH). St. Ann., Unnewell 14354 (A + GH). Navy Island, Axnedhalue 2002 (NY).

HAITI: Nash 901 (NY), Leonard 9960 (US), Leonard & Leonard 14049 (US), Leonard 9585 (F, MO, NY, US), Bartlett 17451 (US), Ekman 9668 (K, NY, S, US). Desert s.n. (WIS 3568).

DOMINICAN REP.: Scarff 23A (WIS), Sauer 2042 (F), Suaer 2155 (F), Allard 14775 (US), Allard 15911 (S, US), Abbott 176 (US), Liogier 20216 (NY). Fuertes 181 (BAF, BM, F, G, GOET, HBG, K, M, MO, NY, P, U, US), Poiteau s.n. in 1802 (G, P), Ekman 12526 (A + GH, G, S), Ekmman 12541 (S, US), Krukoff 219 (S), Eggers 1535 (GOET), Wright et al 177 (US), Faris 499 (A + GH).

PUERTO RICO: Yale School of Forestry 3551 (WIS), Heller & Heller 1226 (F, K, NY, US), Little 13114 (F, US), Little 13087 (F, NY, US), Sintenis 6695 (G, P, S), Sintenis 735 (GOET, M, US), Krukoff 16911 (U), Krukoff 187 (MO), No collector 329 (US), Underwood & Griggs 357 (US), Pery 33 (US), Little & Wadsworth 16502 (NY, US), J. A. Duke 7267 (US), Shafer 2681 (NY, US), Goll et al 100, 915 (US), Sargent 509 (US), Howard et al 15945 (A + GH), Britton et al 1762 (NY).

LESSER ANTILLES: Trinidad: Broadway 6066 (BM, K), Fenderl 368 (BM, P), Raynal 1555 (K), Philcox 7797, 7800 (K), Britton et al 403 (US), Marshall 12348 (K). Granada: Sauer 2232 (F), Broadway s.n. (F175956, K, NY). St. Croix: Ricksecker 172 (F, MO, NY, US). Dominica: Stern & Wasshausen 2432 (WIS), Lloyd 612 (K, NY), Hodge 660 (NY), 531 (BM, MO), 2694, 3065 (A + GH). Grand Cayman: Burnt 1759 (BM), Procter 15116 (BM), Leuro G.C.30 (BM, NY), Stoddart 7036 (BM), Allison et al 1316 (F). Guadeloupe: Sauer 2123 (F), Duss 3100 (US), Perrottet in 1824 (G), M' et M Steule s.n. (P), Rodriquez 3885 (P). Martinique: Duss 1800 (F), Hahn 485 (P), Belanger 98 (P), Egler 34-256 (NY). Virgin Islands: Woodworth 188 (F), Fishlock 102 (NY). Island of St. Croix: Ricksecker 218 (F, MO, P, US), 242 (F). St. Thomas: Eggers 496 (GOET, JE, M, P). St Bay: Dulic 492 (P). Tabago: Broadway 13 (G). Bonaire: Arnoldo 460 (U), Stoffers 1092 (U). Arube: Arnoldo 324 (U). St. Eustatius: Gross-Meyer s.n. (U). Saba: Boldingh 299 (U), Stoffers 3308 (U). Island of Raiatea; Moore 305 (U). Cocos Is.: Klawe 1486 (US), Sevenson 316 (A + GH). Barbados: Goeduis 346 (BM), Miller 44 (US, Rorell 146 (NY). Antigua: Box 1064 (BM, US). Kingstown, St. Vincent: Morton 5429 (US). Virgin Gorda: Britton & Fishlock 1077 (NY, US). Bermuda Islands: Collins 239 (A + GH, F, NY, P, US), Brown & Britton 1121 (NY). Little Gayman: Wkingo 55 (BM, NY).

BAHAMA: Hitchcock (F 175438), Correll & Hill 45271 (F, NY). Howard 10202 (A + GH, NY, US), Gillis 11985 (A + GH), Danbar 387 (A + GH, Nash & Taylor 1365 (NY), Earle 59 (NY), S.R. Hill 2410 (NY).

2. TERMINALIA LATIFOLIA

JAMAICA: Swartz (Lectotype, S; isolectotype, BM, S). Wright (BM). Manchester, Shooters Hill to Mizaph, Adams 12383 (BM, M). Cockpit Country. N. of Appleton, Norman 36 (BM). Moneaque, Alexander 891 (K). Moneaque

Jan. 1850, Alexander s.n. (K, G, P), Distin (K). 1944, Purdie (K). Moneaque, 1850, identified as <u>Bucida</u> <u>buceras</u> (K), Moneaque, 890 (K). Wullschlagel 1293 (M). 1827, Murray 78-84 (G, FI). Westmoreland, Clark's Wood district, Kramer 1712 (U). Parish St. Elizabeth, 4.7 miles by road north of black river, sea level, Proctor 36256 (MO, U). Britton & Hollick 1992 (NY). Parish St. Ann., Howard & Proctor 14042 (A + GH). St. Ann, 1 m.S. of center of Inverness, Goodriend s.n. June 1977 (F). Westmoreland, Clark's wood district, S.E. of Woodstock, Proctor 22209 (A + GH), Catadupa, St. James, Proctor 6537 (US). Manchester, Miller 1281 (US). no collector, no. 47+ (S). Jamaica March no collector 1563 (LE). Jamaica, Bown 124 (NY), Britton 475 (NY), Honeage in 1850 (NY). Jamaica, Much (A + GH), Purdie (A + GH).

GUATEMALA: Tomas 317 (W).

3. <u>TERMINALIA</u> <u>ARBUSCULA</u>

JAMAICA: Haover: Summit of Bubby Hill, one mile S.E. of Hillsbrook, <u>Proctor</u> <u>31312</u> (F). Summit area of Dolphin Head, <u>Proctor</u> <u>28638</u> (BM). Manchester: near auchtembeddie, <u>Proctor</u> <u>26436</u> (A + GH, NY). Trolawny: Miss Laura's Hill, Willson Valley district, about one mile north of Warsop, 1964, <u>Proctor</u> <u>24780</u> (A + GH, BM, MO, NY, U, US), Proctor 48554 (NY); Proctor 36268, 31812 (MO). Ramgoat Cave distict, Cockpit Country, July 1955, Howard & Proctor 14417 (A + GH, BM, US). Not localized Swartz (lectotype S, isolectotype BM).

4. <u>TERMINALIA</u> <u>ACUMINATA</u>

BRAZIL: Rio de Janeiro: Constantenio 8326 (U, S), Ducke 8326 (K, US), Freire Allemáo 1846 (BK), Freire Allemaõ, without locality and date, written on the lable "Guarajuba" (BR), Glazio 6521 (BR, C, K, LE), Glazio 11947 (A + GH, BR, C, K, LE, MO), Glazio 6143 (BM, C), Sellow 1160 (BM, K), without number (C, FI, US), Whitford 23, Cultivated (A + GH, K, S, US, WIS 3523).

5. TERMINALIA LUCIDA

BRAZIL: Pará: Hoffmannsegg s.n. (BM, in 1812; BR, lectotype). Rio Araguaia, Rio Inaja 13/8/1978, Silva 4824 (LTR). Jacunda, margin of R. Tocantins 20/10/1977, Silva et al AS77 (LTR). Itupiranga, along R. Tocantis, 22/10/1977, Berg & Anderson 682 (LTR). R. Tocantis, Alcobaca, Ducke 15563 (BM, RB). In vicinibus Pará, Caripi, Jul.-Aug. 1849, Spruce 166, s.n. (K). Marajó Pacoval, Huber 371 (BM, G, R, RB). Serra de Araacoara ad fluvium Japura, 1820, Martius (M). Mosqueiro ad nipes fluvii, fl. 18/10/1940, Ducke 609 (F, MO, NY, R). Ilha do Marajó, Black 48-3516 (NY). Maraba, Capoeira do Campo, 4/6/1949, Black 49-7944 (IAN). Ueriana, Guedes 247 (G). R. Tocantis, 1 km E. of Bren Branco, 44 km S. of Ticurui on old BR 422 in Sandy Soil, 17/11/1981, Daly et al 1390, 1391 (LTR). Breu Branco, 27/9/1945, Froes 23536 (BM, IAN). Ilha do Marajó, Soure, Siqueira 6881 (R). Bananal, Sta. Isabel, Andrade 434 (R). Rio Xingu, frente Souzel mun., 17/11/1955, Froes 32316, 32323 (BM, IAN). Ilha do Marajo Faz. Ribanciara, 16/11/1969, Oliveira 5091 (IAN). Ilha do Marajo, R. Paracauri, 30/8/1969), Oliveira 4903 (IAN). Maranhão: Margem do R. Grajun 15/12/1978, Rosa & Silva 3005 (LTR). Sao Raimundo das Mangabeiras, Eiten & Eiten 5412 (K, US). Lorêto, R. Balsas, Eiten & Eiten 5461 (G, K, SP, US). Maranhao, Carvalho 2 (RB). Road from São Luiz Gonzaga to Santo Antonio 53 to 55 km from Bocabal, 1/10/1980, Daly et al 396 (LTR), Rio Mearim - Lapela, 15/1/1976, Silva 4187 (IAN). Maranhão, Fróes 24087 (BM). Piauí: Netto 33 (R). Amarante, Lisboa 2364 (BM, G, RB, US). Terezinha, Falco 5168 (RB). Goias: Rio Araguaia, 14/8/1978, Silva 4822 (LTR). Porto Real, Pohl 2358 (A + GH, F, W). Tocantius, Macedo

3937 (K). Tropical Brazil, Burchell 8132, 8467 (A + GH, K, P, US).

FRENCH GUIANA: Maroni les Hattes, Lemee 1901 (P). Maroni, 1858, Sagot 1007 (BM, K, P). No locality, Leprieur in 1833 (G). Cayenne, Van Robr 158 (BM).

SURINAM: Wiawia Reserve, 3 km E. of Motkreek, Sterring 12480 (NY, UO. Same locality, Sterring 12527 (U). Marowigne inferior, Christiankondre, Hekking 1077 (U). Marowyne R. (Franch side), Wullschlaegel 1445 (BR), Foot of Voltzberg, Lanjouw 931 (BM, RB), this specimen differs slightly from T. lucida by having rather obovate leaves with less number of secondary veins.

GUYANA: Suddie, Essequibo Coast, Forest Dept., F.N. 2688, R.N. 5481 (FDG). Suddie beach near D.C.'s house, Forest Dept. R.N. 6388 (FDG).

VENEZUELA: Estadio D.A., Tobejuba, Gines 5233 (US). Estadio D.A., Burojoioba, Gines 5179 (US).

TRINIDAD: Top of beach, Blandar Bay, near Toco Bay, Cowan & Forster 1387 (A + GH, NY, P, US). Iuascas Bay, Broadway 6067 (A + GH, BM, F, K, S, US). Cedias - Cbattam, Broadway 8846 (K, NY). Grin Bay, Swabey 12561 (K, NY). Salybia Bay, Philcox 7801 (K, NY). Galeota Point, Carrick 1203 (K). Coastal woods, Manzanilla, Britton & Britton 2177 (A + GH, K, NY, US). Manzanilla, near the Depot mouth of the Branche river, Broadway 2364 (BM, G). Broadway 7466 (US). Raynal 15558 (K).

COLOMBIA: Antioquia, between punta Las Barcas & Turbo, Duke 9747 (NY, US). Antioquia, swampy area on peninsula. 1 km W. or Turbo, Feddema 1994 (NY, S, US). Turbo, Haught 4542 (COL, NY). Antioquia - Turbo, Zona de Playa Cerca al Campo de aterrizaje, Isidoro Cabrera - R. 1171 (COL).

PANAMA: Canal zone: Coco Solo (Mangrove swamp several trunked tree, 10 m tall, 15 inches diam, bark rough) Al Gentry 6058 (F, MO), Panama, S. Hayes (US 202835).

NICARAGUA: Salas 12 in 1966 (not seen, taken from the check list of the vascular plants of Nicaragua by F. C. Seymour 1980).

HONDURAS: Dept.de Gracias A Dios: Nivel del Mar, Clima Ilvioso tropical, Nelson & Hernandez 949 (MO).

GUATEMALA: Dept. Izabel: Seashore around Punta Palma, a cross bay from Puerto Barrios, Steyermark 39814 (F).

6. TERMINALIA DICHOTOMA

BRAZIL: Para, 1849, Spruce 308 (A + GH, BM, F, FI, G, LE, M, NY, P, R), 167 (R). Amazonas, Kurkoff 8472 (BM, F, G, LE, MO, NY, P, R, S, U, US), 4881 (A + GH, BM, F, LE, M, MO, NY, R, S, SP, U, US), 6353 (BM, MO, NY, R, S, US, WIS), 6141 (A + GH, BM, BR, F, LE, MO, NY, R, S, U, US. Para, Belem, Ducke, 17691 (G, RB, U, US), 15468 (RB, US). Para, Black 48-3025 (IAN, U, US), Amapa, Pires et al 50335 (LTR, NY, R, US). Amapa, Amapa, Ribeiro 1572 (LTR, NY). Para, Prance et al 1566 (LTR, R). Rio Puras, between Born intento & Boa Fe, Prance et al 16376 (INPA, LTR, NY, R). Para, Ducke 5195 (BR). Amapa, Rio Oiapoque, Irwin et al 48079 (F, NY, R, S, US). Para, Belem, Archer 7916 (F, MO, NY, R, S, US). Amazonas, Froes 26413 (BM, R, UB). Para, Froes 32743 (BM). Amapa, Black 49-842) (BM). Para, Pires 7123 (BM). Para, Ducke 15468 (BM). Belem, Pires & Black 406 (A + GH). Amapa, Irwin et al 47154 (MAN, LTR, NY, R). Para, Belem, Silva 25 (IAN, NY, R, US), 353 (US). Para, Huber 371 (US). Para, Belem, Pires 51843 (NY, US). Careiro Propridade do sr., Rodriques & Melo 4971 (INPA). Munic. de Limaero rio Japura, Damiao 271 (INPA). Para, Belem, Pires 4836 (IAN). Belem, Silva 226 (IAN). Belem, Pires & Silva 11850, 11856, 11857 (IAN). Belem, Pires & Silva 10711 (IAN). Maranhao, Froes 34929 (IAN). Brazil, 1865, Burchell 8578 (R). Brazil, Baldzukoff 6141 (R). Amapa, Irwin et al 47845 (R).

FRENCH GUIANA: Saul Monts La Fumée, Boom & Mori 2507, 2118 (LTR). Bords de la Riviere du Maroni, Melinon 134 (P). Karauany, Sagot 795 (BM, BR, P, S).

Karuanany, Sagot s.n. (BM, BR, S). Cayenne, 1775, Fusee Aublet s.n. (BM). St-Laurent-du Maroni, Forester 4047 (CAY). Saut Canori, Oldeman 282 (CAY). Fleuve Approuague, au petit Saut Couota, Oldemann B-1926 (CAY). Richard Herb. (P). Cayenne, loc. in Lond 1863, Aublet 281 (Sterile) (BR). Poiteau in 1819-1821 (A + GH, F, G). Cayenne, Granveille 4691 (NY.) Poiteau in 1826 (FI, P).

SURINAM: Marowyne, Kappler 1962 (FI, P). Hostmann 744 (A + GH, BM, FI, G, GOET, M, NY, P, R, U). Lanjouw 815 (NY, R, S, U). Tapanahoni R., Versteeg 697 (P). Tihiti Savanne, Lanjouw & Lindeman (NY, R, U). Saramacea, Teunissen/LBB 15484 (U). Wayombo, Stable 363 (A + GH, CAY, NY, R, VEN). School of Forest. 363-a (R, WIS), 363 (WIS). Wullschlaegel 878 (BR, G, GOET, W). Bosbeheer 158 (MO). Bokopondo dist., Donselaar 1522 (NY). Broadway 3110 (BM).

GUYANA: Roraima, Schonburk 846 (BM, F, FI, G, NY, P, R), 246 (G). Mazaruni Station, Forest. Dept. 2705 (R, U). Pomersoon, Cruz 2979 (A + GH, F, MO, US). Moruka R,, Cruz 4578 (A + GH, F, MO, NY, US). Kartaleo 141 (A + GH). N.W. District, Cruz 1333 (A + GH, NY, US). In silivis insulae Arowabish Essequebo, Herb. Meyer no 113 (GOET, holotype) Near Dadanawa, Cruz 1440 (A + GH, F, MO, NY, US). Kamakusa U. Mazaroni R., La Cruz 4156 (A + GH, F, MO, NY, US). Kaituma R., Adenson 26 (NY), 98 (R). Mazaroni - Potaro dist., Mori et al 8153 (LTR, NY, VEN). Coomaka, Persaud 187 (NY, R, US). Essequibo R. Moraballi Creek, Sandwith 475 (NY, R). Wabawak, Forest Dept. 411 (NY, R). Anderson 39 (R). Jenman 6592 (R).

VENEZUELA: Delta Amacuro: Swampy Marucaria saccifera forest along lower section of river, upstream from Casa Cuyubini, inundated forest Rio Cuyubini, alt 90 m. 12/11/1960, Steyermark 87513 (MO, NY, U, VEN 60471); occasional along Rio Acure 1-10 km above mouth, 13/4/1955 (Tree 15-25 m. Fruit green. "Cafacillo". Wood heavy, used locally for rafters.), Wurdack 335 (NY, VEN 38725); Tucupita, Depto Antonio Diaz, riverine forest along Cano Araguao, 9/10/1977, Steyermark et al 114417 (LTR, MO, US, VEN); Depto Pedemales (boundary with Depto Tucupita), Cano Simoina, alt 50 (mixed evergreen forest of low to medium sized trees), Steyermark et al 114357 (VEN); Antonio Diaz: riverine forest along Cano Araguao, bet. mouth of Cano Jajene and Isla Mono Burojo, Steyermark et al 114783 (VEN); Wiuiguiua, Gines 5108 (US).

COLOMBIA: Puerto Narino and vicinity along lower Rio Loretoyacu, Zarucchi & Schultes 1076 (COL). Bolivar, Sahagun, Pennell 4113 (US).

PERU: Dept. Loreto: Vicinity of Iguitos, Hacienda Soledad on Rio Itaya rivershore, Asplund 14498 (S). Near mouth of Rio Itaya, Croat 19616 (C, F, MO, NY). Lavictoria on the Amazon River, Williams, 2723 (F). Maynas, Las Amazonas, Rio Napo, Rimachi 4377 (F).

7. TERMINALIA ERIOSTACHYA

Distribution:

CUBA: Not localized, Herbarium Richard, R. de la Sagra (holotype, P). Ramon de la Sagra (Pl. Ins Caba) 285 (BM). Ramon de la Sagra 281 (K). Oriente: Banks of Maise river, Leon 17734 (A + GH, NY). Soetea hills, Grosby & Matthews 22 (NY, WIS). Litus meridionalis Baracoae, R. Tacre, Borhidi 4374 (BP). Cupey in sulvor, Ekman 6327. Prope Corjo in ripa fluminis, Bayamo, Ekman 5081 (S). E. Cuba, Gill & Whitford III (WIS). From junction of Camino Road and San Gregorio Norte Trail, Corua, Grosby & Matthews 51 (WIS). Habana: Lowas de Cawoa, in forest at the hillside, Ekman 13505 (S). Havane, 1833, Ramon de la Sagra 624 (G). Pinar del Rio: Peninsula de Guanaha Caleibes in limestone forests S. of La Grifa, Ekman 18157 (G, K, S). Near Cortes, Roig 1727 (NY). Rio del Medio: southern foot of Sierra de Jamias, Southern Baracoa Region, Leon 12132 (NY).

8. <u>TERMINALIA</u> <u>CHICHARRONIA</u>

A. Subspecies <u>chicharronia</u>

CUBA: Cuba, Wright 2570 (A + GH, BM, G, GOET, K, MO, P, S). Cuba, Guanabo Marzo 1829, Herbarium Richard n. 185, Ramon de la Sagra s.n. (F, G, P, lectotype); same details, n. 28 (fr.) (G, P). Cuba, Sagra 164 (P). Oriente, Ekman 2815 (G, P, S). Havana, Loma de lapita, San Miguel de Padron, Roig 6 (P). Same locality, Leon et al 9106 (P). Havana, Leon 11633 (NY). Rangel, Pinar del Rio, Leon 12582 (NY). Havana, Ekman 6309 (S). Oriente, Ekman 6309 (S). Prov. Oriente, Ekman 7480 (F, G, K, NY, S). Cuba, Ramon de la Sagra "286 Terminalia" (G). Oriente, Sierra Maestra, Bisse & Lippold 14343 (JE).

B. <u>Subspecies</u> <u>neglecta</u>

CUBA: Loma del Tibi Sail, Leon & Clement 6642 (NY). Pinar de Rio, Shafer 13412 (F, NY), 13478 (BM, F, NY). Santa Clara, Jack 8258 (NY). Pinar de Rio, Sierra de Anate Leon 11491 (A + GH, NY, P). Wright 2569 (A + GH, BM, G, GOET, K, MO, NY, P, S, US, W). Wright 352 (MO). Pinar del Rio, on top of Pico Tey, Cerra de Rosario, Alain 2739 (A + GH). P. R., Ensenada de la Bandera, Vinales, Alain 2886 (A + GH). P. R., Ensenada, in El Ancon valley, Vinales, Alain 441 (A + GH). Pinar del Rio, Ekman 10516, 16601, 16639 (S). Pinar del Rio, Ekman 11546 (NY, S). Pinar del Rio, Ekman 11546 (NY, S). Pinar del Rio, Roig & Arcuy 2539 (NY). P. R., Loma pelada de Cuyajabs, Leon 13833, 13834 (A + GH, NY); same locality, Leon 13831, 12581 (NY); same locality, Ekman 17325 (G, S). Pinar del Rio, Leon & Roig, 13457, 709 (NY). Santa Clara, Howard 6512 (A + GH, NY), 5703 (NY, P, S). Habana, Sierra de Anfae, Ekman 16920 (G, NY, S). Same locality, Leon 13148 (A + GH, NY). Sierra de Anfe, Leon 13457 (A + GH). Prov. Las Villas, Mina Cardita, Tirinidad Mount., Howard 5703 (A + GH). San Blas, Howard 6512 (A + GH). Banco mount., Leon 6642 (A + GH). Pinar del Rio, Bahia Honda, Loma Pelada de Cajalbana. Bisse & Lippold 18254 (JE, isotype of

T. neglecta). Prov. Habana, Isla de Pinos, 4/3/1967, Bisse 1728 (JE). Prov. Pinar del Rio, Bahia Honda, Las Pozas, Bisse & Rojas 4940 (JE). Las Pozas, Arroyl del Medio, Bisse & Rojas 4913 (JE). Prov. P. R., Bahia Honda, charrascos al oeste de la loma de Cajalbana Julio 1968, Bisse 9566 (JE). Prov. Las Villas, Sierra del Escambray, 6/11/1968, Bisse & Lippold 9824 (JE). Prov. pinar del Rio, Vinales, 16/11/1968, Bisse & Lippold 10742 (JE). Prov. P. R., Sierra de la Güira, 28/12/1970, Bisse & Lippold 18401 (JE). Prov. Habana, Isla de Pinos, Bisse 19845 (JE). Prov. P. R. Sierra Faustino, Sur Diego de los Banos, Borhidi & Capote s.n. (BP). Isla de Pinos, in silv. calc. stat. inundatis, NW a punta del Este, Borhidi et al s.n. (BP). Pinar del Rio, Sra de los Organos, Sierra de Guasasa, Borhidi s.n. (BP).

C. Subspecies domingensis

HAITI: Massif de la Salle, N. Slope of Montagne Noire c. 75 m in rocks, Ekman 1957 (K, S). Massif du Nord, Ekman 4419, 4420 (S). Massif de la Hotte, Ekman 5353 (S). Hispaniola, Civ. Haiti, Massif des Cahos, Ekman 3429 (S).

REPUBLIC OF DOMINICA: Santo Domingo, Prov. Azua in Arroyo Guayabal ad las Lagunos, Jul. 1912, Fuertes 1941 (isotypes of T. domingensis, G, NY, P, S, U, W). Santo Domingo, Ekman 14695 (S). Isabel do Torres. Alain & Liogier 23105, 24278 (NY), 19372 (F, NY). Rincon de Uboa, Alain & Liogier 19026 (F, K, NY).

D. Subspecies orientensis

CUBA: Prov. Oriente: Dry ridges east of Arroyo Blanco Valley, April 7 1926, Grosby & Matthews 64 (NY, holotype of T. orientensis). Moa Cayo Coco, Acuna 12587 (US). Woods, Moa, Leon & Clemente 23266 (A + GH). Pinelands, Moa, near the Saw-mill, Clemente 4952 (A + GH, NY). Banks of a stream, near the Saw-mill, Moa, (Leon et al) Howard 20232 (A + GH, NY, US). Mayari, Sierra del Cristal, Woods at Los Mulos April 2-7 1956, Alain et al 5368 (A + GH, isotype of T. pachystyla). Cerro Weraflores, Figueiras 1306 (US). Nicaro Rio Ceife, Bucher 531 (US). In Pinetis Serpentinoso Montis ML. Montecristo, Borhidi et al s.n. (BP). Montanis and Aserrio de Mina Delta Supra la Melba, Boridi et al s.n. (BP). Moa in fructicat. serpent. ad Rivum Yamanigiiey Borhidi et al s.n. (BP). La Casimba, Sierra de Nipe, Mayari, Leon & Alain 19237 (NY, isotype of T. nipensis). Thickets, Pena Prieta, alt 600 m, Alain 3155 (NY). Woods, southern slopes of Sierra de Cristal, Alain & Figueiras 4737 (NY). Cayo la Plancha, near airstrip, Nipe, Leon & Alain 19204 (NY). Valley of Arroyo Blanco, Corua Farm, Grosby & Matthews 62, ser. no. 9216 (C, F, MO, WIS). Guarao river, Grosby & Matthews 53 (F, WIS). Sierra de Nipe, Ekman 2543, 5734, 10082 (S), 3098 (F, S). E. Cuba, Gill & Whiford 102 (WIS). Prope Villa in Monte Verde dictam, June-Jul-1859, Wright 1239 (G, K). Sierra de Nipe, Montenis de Loma de la Torre, Borhidi et al s.n. (BP). Serra de Nipe, Borhidi & Muniz s.n. (BP). Cupeyal, Borhidi et al s.n. (BP). Sierra de Nipe, montanis Salto del Rio Guayabo, Pinares de Mayari, Borhidi et al s.n. (BP).

9. TERMINALIA OBLONGA

BRAZIL: Para: Rio Itacaiunas, afl. do R. Tocantins, Aug. 1970, Pires & Belem 12774 (IAN). Same locality, September 1970, Pires & Belem 13075 (IAN). Monte Alegre, Froes 30476 (BM, UB). Matto do Cacoal Imperial, Obidos, 23.6.1912, Ducke 17676 (RB, S, U, US). Rio Jucoesdina, affl. do Rio Branco de Obidos, Ducke 17675 (K, RB). Uponte Alegre, Froes 30466 (IAN). Amazonas: Rio Purus, Ducke 25020 (G, K, P, S, U, US). Esperanca, mata da terra firme, 1942, Ducke 880 (F). Local Calreira Muzungu, 8-7-1974, Ribeiro 533 (IAN). Near mouth of Rio Embira, Kurkoff 4860 (F, MO, US). Acre:

Near mouth of Rio Macauhan, on terra firme, basin of Rio Purus, Kurkoff 5641 (A + GH, BM, G, K, LE, M, MO, NY, S, U, US). Porangaba, Rio Jurua-Mirim, 21/5/1971, Maas et al 13206 (LTR). Seringal Boa Agua, July 1972, Pires & Rosa 13663 (IAN). Same locality, 31/7/1972, Silva 3535 (IAN). Pernambuco: Nazare da Mata, 13/1/1959 (fl.), 20/3/1956 (fr.), Coelho & Moraes 1338 (SP, holotype of T. mameluco).

PERU: Peru, Herb. - Webbianum Ex Herb. Pavon (F, FI, isotypes). San Martin, west of Nueva Aspusana, Mathias 6121 (F). Huanuco, distrito Padre Luyando, Pcia, Gutierrez 65 (F, G, NY, W, WIS), 38 (G, NY, W, WIS). Satipo Reserva Forestral, Depto Junin, Prov. Jauja, Vasquez 15, 32 (F, NY, US, WIS). Dept Huanuco, Prov. Pachitea, Dist Honoria, Aspajo 9 (F, NY, US). Dept. Huanuco, Prov. Leoncio Prado, Dist. Jose Crescpo, Rafael s.n. (COL, F, G). Lower Rio Nany, Dept. Loreto, Williams 596 (F, K, US). Dept. Loreto, Prov. Coronel Portillo, Gomez 3 (F, P, US). Same locality, Salas 7 (F, NY, P, US, WIS). Prope Tarapoto, Preuviae orientulis, 1855-6. Spruce 4507 (A + GH, BM, F, G, K, P, W). Tarapoto, Spruce 4587 (A + GH, BM, BP, BR, F, G, GOET, K, LE, NY, P, S, W). Pongo de Manseriche, Maranon, Tessmann 3573 (G, S). Pozozo, Loreto, Munos 3 (WIS). Huánuco, Prov. Huánuco, Tingo Maria, Asplund 12159 (G, S, US). Amazonas, Quebrada Wampusik, Kayab 927 (A + GH, MO). Huanuco, Coronel Portillo, Shunke 5261 (A + GH, NY, US). Loreto, Lower Rio Huallaga, Williams 3969 (US). San Isidro, Tessmann 4993 (NY). Loreto, Pucallpa, Loidith 12 (MO). Loreto, Pucallpa, Jose 51 (MO). San Martin, Klug 4183 (BM).

BOLIVIA: Bosque Rio Suruti, Buella Vista, Sara, Santa Cruz, Steinbach 5574 (A + GH, F, MO). Sara, Santa Cruz, Steinbach 6779 (A + GH, BM, GOET, K, U). La Paz, Prov. Sud Yngas, Puerto Linares, 27 km. hacia Paos Blancos (LTR). Urber des Serracia Ricardo Franco, Schmidt 29 (M).

ECUADOR: Limoncocha, Nupo Province, Mowbray 705 (MO, NY). Borbon, Esmeraldas, Little & Dixon 21018 (NY, US). Equateur, Benoist 1931 (S).

COLOMBIA: Depto del Magdalena, Mpio de Fundacion 3 leguas al norte de Santa Rosa, Romero-Castaneda 11167 (F, MO). San Jose del Guaviare, Cuatrecasas 7465 (F, NY, US). Comisaria del Caquetá, Venecia, Rio Ortequeza, Cuatrecasas 8952 (COL). Estrella, Curran 293 (A + GH, WIS). Dept. de Chocó, Rio Sucio, Orilla del Rio Traando, en Teresita, Arciria 98 (COL). Dept. Choco, upper Rio Truandó, La Terestia, Al Gentry 9417 (COL). River Valley, Boyaca, Whitford 21 (A + GH). Magdalena, Romero 1402 (US). Chocó, de Acandi, Romero-Castañeda 6444 (MO, NY). Choco, Rio Truando, bet. La Nueva & La Esperanza, Duke 9893 (NY).

VENEZUELA: Estado Barinas, Reserva Forestral Caparo: Bosque tropofito, unidad 1, parte sur entre pica 7 & 9, 16-18 km sureste de Campamento cachicamo, este de El Canton, 9/4/1968, Steyermark et al 101958 (A + GH, VEN 79997). Same locality, 10/4/1968, Steyermark et al 102066 (M, NY, US, VEN 79994). Cano Hondo del fundo "Los indies" Mun Sta Rosa, Dtto Rozas del Edo Barinas, 16/1/1965, Romirezz s.n. (VEN). En Potreros, Cercanias de Machiques, Zulia, 20/3/1964, Ijjasz-Mardiz 84 (VEN 64836). Fundo La Guaquira, 10 km al S. de San Felipe, Distrito San Felipe, Estado Yaracuy, 9-2-1972, Chavez 17 (VEN). Edo Cojedes, Feb. 1969, Aristequita & Zabala 6902 (VEN 75522). Aiame El Portuguesa, Delgado 517 (VEN 79489). Edo Barinas, El Caimital (Barrancas), 20/11/1972, Veillon 141 (VEN 92386). Estado Yaracuy, 35 km N. de San Felipe hacia Aroa, 19/2/1954, Little 16246 (VEN 81809). Zulia, primary forest along the road (in construction) Machiques - Colon near the Rio Catatumbo, 83 km W.N.W. of Santa Barbara - San Carols del Zulia, Bruijn 1420 (K, M, MO, NY, S, U, US, VEN 76310). Estado Zulia, (N. V. Guayabon) 20/11/1968, Aristequieta et al 6774 (VEN 76312). Edo Yaracuy - Falcon, Reserva Forestral "Rio Tocugo", en los alrededores de la quebrada Elcharal, August 1970 (fl.), Blanco 933 (NY, VEN 8470), 932 (U). Zulia, 26/8/1957 (fl), Medina 822 (VEN 42354). Zulia, 20 km S. de Selva Humeda, 5/1/1954, Little 16132 (VEN 79492).

Merida, Santa Elena - Carretera Panamericana, Selva Pluvial, 27/1/1954, Little 16206 (VEN 81808). Edo Cojedes, Agua Blanca, Nov. 1948, Standen 121 (VEN 79490). Edo Apure, Reserva Forestral San Camilo, Selva siemprererde, trechos planos, vecindades del chiricoa, 9-10 kms el este del easerio San Camilo (El Nula),Steyermark et al 101696 (NY, S, US, VEN 79987). Parque Nacional El Avila, Selva de Galeria, Quebrade Chacuito, Marana s.n. (VEN 113059). Edo Portuguesa, viveros de Aravre, 8/3/1950, Delgado 640 (VEN 81807). Estado Barinas, 20 km al No. de Barrancas, municipo Cruz Paredes, 30/3/1972, Marcano Berti 73 (VEN 89390). Edo Barinas, May 1953, Aristequieta 1698 (VEN 33816). Selvas de Yumare, Estado Yaracuy, Bernardi 7024 (F, FL, G, K). Barinas, 1/2/1971 Jimenez Saa 1257 (LTR). Zulia, Sierra de Perija, 24/8/1967, Steyermark & Fernandez 99632 (LTR, MO, NY, US). Zulia, Mara, virgin semi-evergreen forested slopes at Pozo de la Danta, along Quebrada de la Danta, 29/5/1980, Steyermark et al 122856 (LTR). Zulia, Perija, rio Aricuaisa, 3/3/1982, Bunting 11102 & Lobo (LTR). Zulia, Mara, Cuenca de los rios Socuy - Guasare, al rededores del Campamento Carichuano de Carbozulia, via Caño Colorado, 3/8/1981, Bunting 10141 (LTR). Zulia, Mara, via Las Cuatro Bocas - Rio Cachiri - Hola, El Dibujado, 29/7/1981, Bunting 10098 (LTR). Mara, Alrededores de Campamento Carichuano, en la via entre el Caño Puso de Diablo y el Caño Vaqueta, 10/6/1981, Bunting 9998 (LTR). Zulia, Burro Negro, 23/2 1980, Bunting 9183 (LTR). Zulia, Bolivar, entre Las Tres Marias, 14/2/1980, Bunting 9026 (LTR). Zulia, Colon, alrededores de Tres Boas, 6/2/1979, Bunting 6984 (LTR). Same locality, 2/8/1979, Bunting 7828 & Fucci (LTR). Puerto Cruz, F. District, Whitford 35 (A + GH), 445 (WIS). Steyermark 127 ser. no. 45659 (WIS). Curran & Marshall 151, 149 (WIS).

PANAMA: Guayabo de Montana, Changuinola Valley, Cooper & Slater 10153 (A + GH, F, WIS). Region of Almiante, Prov. of Bocas Del Toro, Cooper 55 (BM, F, K, LE, NY, US). Barrow Colorado Island, Canal Zone, Aviles 873 (F).

Remedios and vicinity, eastern Chiriqui alt. 0;100 m, Dec. 1911 & Jan. 1912 (A), Pitter 5467 (US, holotype of T. chiriquensis). Barro Collorado Island, Canal Zone, Robin 2211 (A + GH, F). Chiriqui, Burica Peninsula, Liesner 130 (A + GH, BR, K, MO, NY, P, US). Colon, Al Gentry 6698 (MEXU, MO, XAL). Canal zone, Croat 13922 (K, MEXO, MO). Changuinola Valley, Cooper & Slater 55 (WIS). Bocas del Toro, Stern & Chambers 115 (MO, US, WIS). Bocas Del Toro, Ghanguinola Valley, Dunlap 290 (K, US). Prov. Darien, Train from Pucuro to Cerromali, mouth of Tapalisa River, Gentry & Mori 13544 (COL, MO). Barro Colorado Island, Canal Zone, Foster 1490 (A + GH). Del Darien, Campamento Buena Vista, Stern et al 937 (A + GH, MO). Barro Colorado Island, Foster 2211 (A + GH, NY). Panama, almnante, Seibert 1534 (US). Potrero, Changuinola Valley, Dunlap 261 (US). Marrogunti, Williams 994 (NY, US). Barro Colorado Is., Foster 1453 (MO). Los Santos, Tyson et al 3128 (MO). El Llano confluence of Rio Terable & Rio Bayano, Duke 5835 (MO). Puerto Armuelles, Croat 22649 (MO). One km W. of El Llano, Edwin & Tyson 6844 (MO). Darien, Duke & Nickerson 14918 (MO). Darien, Between Rio Punusa & R. Pucro, Duke 14644 (MO). Canal Zone, Croat s.n. (MO). Darien, Pinas, Duke 10658 (MO). Darien, Gentry & Mori 13860 (MO). Maria Chiquita, Colon, Holdridge & Maasola 6530 (MO). Vill Alondra, Colon, Lea & Holdridge 15 (MO).

COSTA RICA: Finca Laselva, Puerto Viejo, Sarapiqui, Heredia Prov., Hartshorn 1167, 1078 (F). Palmer Norte de Osa, prov. of Pantarenas, Allen 5876 (A + GH, F, US). In the Golfo Dulce region on the Pacific coast, (C.N. Guayabo de Montana) Munoz 3 (F, WIS). Bebedero, Provincia de Guanacoste, Standley & Valerio 46711 (F). Along river road trail east of Q. El Surá bridge, Finca La Selva, Hartshorn 1334 (F). Vecindad de los Aguilares, Tilaran, Prov. Guanacoste, Jimenez 358 (F). San Mateo, Ambrenes 2685 (F). 28 miles due west of Puerto Limon, Prov. Limon, Shank 15889 (F). About 5 km east of Tilaran, Williams & Williams 24606 (F, NY, US). Vic. El

General, Prov. San Jose, Skutch 3990 (A + GH, K, MO, NY, S), 4252 (A + GH, MO, NY, S, US). San Ramon, Alajuela, Brener 22685 (A + GH, NY). Alajuela, Guatuso de San Rafael, Holm & Iltis 886 (A + GH). Lost Ayotes, near Tilaran, Standley & Valerio 45259 (US). El Arenal, Standley & Valerio 45145 (US). Capulin, Rio Grande de Tor Coles, Prov. Alajuela, Standley 40116 (US). Santa Cruz, Liesner 4940 (MO). Guanacoste, Bawa 241 (MO) Puerto Viejo, Frankie 339 (MO). Finca La Selva, Hartshorn 1003 (MO). Puntarenas, Liesner 1951 (MO). Forested hills near Golfito de Golfo Dulce, Prov. Puntarenas, July 27, 1951, Allen 6282 (F, US, holotype of T. bucidoides). 8 km. on the Pacific Trail from Rincon, Peninsula de Osa, Godfrey 66873 (MO). 8 km del Sur de Rincon, Peninsular de Osa, Peia, Puntarenas, Jimenez 3017 (NY). Colon, Holdridge & Maasola 6530 (MO). Puntarenas, Allen 30 (BM).

NICARAGUA: Dept. Zelaya, dreaje del Rio Alemán, Nov. 27-29, 1951, Shank & Molina 4839 (F). Granada, Volcan Mo_bachon SE Side, Finca Cutirve 600 m, 4/3/1977 (MO). Guamil, Rio Grande, Dept. Zelaya 23/4/1949, Molina 2345, (A + GH, BM, F, US), 2355 (F, US). Dept. Managua, between El Crucero and house of Finca Santa, "Guayabillo", Standley 8359 (F). Dept. Managua, ca. 2.3 km from Hwy 12 on road along ridge of Sierra de Managua from Hwy 12 at km 17 to Hwy 2, Stevens & Krakoff 5305 (LTR).

HONDURAS: Lancetilla, Dept. Atlantida, Williams & Molina 13055 (F, MEXU). Near Progreso, Dept. Yoro, Hottle 34 (F). Dept. Atlantida, Vicinity of San Alejo, near Rio San Alejo, Standley 7785 (F). Lancetilla valley, near Tela, Dept. Atlantida (A + GH, US). Vicinity of Tela, Standley 54490 (A + GH). Dept. de Colon, Saunders 189 (BM).

GUATEMALA: Dept. Santa Rosa, Plains north of Los Cerritos, Standley 79590 (F, G, NY). Dept. Suchitepequez, near Santo Domingo S. of Mazatenago, Standley 88883, 88890 (F). Dept. Retalhuleu, between Retalhuleu & Nuevalinda, Standley 88514 (F), 88515 (F, US), 88503 (US). Dept.

Retalhuleu, Vicinity Retalhuleu, Standley 88801 (F). Dept. Santa Rosa, near Oraterio, Standley 60653 (F). Dept. Escuintla, Standley 63603 (F). Dept. San Marcos, Standley 68766 (F). Dept. Escuintla, near San Jose, Standley 64093 (F). Dept. Suchitepequez vicinity Tiquisate, Steyermark 47648 (F). Finca San Francisco, Dept. Quezaltenango, Steyermark 52126 (F, US). Colomba, Skutch 1979 (A + GH, BM, F, G, NY, US). El Estor, Izabal, Contreras 11194 (MEXU, MO, S, US). Magatenaugo, Bernolli & Cario 2978 (GOET), 2983 (GOET, K), 3345 (LE). Quezaltenango, Colomba, Skutch 2026 (NY, US). In silvis Maza Tenanso, Bernolli 925 (K, NY). No locality, Kuylen 56 8887 (WIS).

EL SALVADOR: Coastal highway west of La Libertad, Dept. La Libertad, Allen 7205 (A + GH, F, NY, US). Dept. Ahuachapan, near Salto de Atochuecia, Standley & Padilla 2871 (F). San Jacinto, Salvador Calderon 1433 (MO, NY, US). San Salvador, Calderon 2199 (A + GH, NY, US). Sonsonate, Dept. Sonsonate, Standley 22342 (NY, US).

BELIZE: Mullins Riv., B. Hond. "Nargusta", Hummel 718 (K).

MEXICO: Chis, Matuda 16447 (BR, F, MEXU). Escuintla -Chiapas, Matuda 580 (MEXU, US). Chiapas, Miranda 6754 (MEXU, U). Esperanza, Escuintla, Chis, Matuda s.n. (K, MEXU 5393, NY). Chiapas, Acapetahua, Miranda 1803 (MEXU). Chiapas, Gonzales 11340 (MEXU, NY). Esperanza, Escuintla, Chis, Matuda 17461 (MEXU, NY).

10. TERMINALIA VALVERDEAE

Distribution:

ECUADOR: Guayas: Cerro Azul, entrado por Casas Viejas, Cordillera de Chonzon, Aug. 1978, Valverde 301 (MO, holotype). Loja: Valle Seco de e Playas, Catacocha, Acosta Salis 7997 (F).

11. TERMINALIA PHAEOCARPA:

Minas Gerais, S. Terezinha, Ituiutaba, Macedo 1150 (BM, NY, RB, S, SP), 1196 (BM, MO, US). In silvis primavis montosisque prope S. Luzia, Minas Gerais, Riedel 2521 (A + GH; G; K; LE, lectotype; P). Brazilia, Fercal, Rizzini s.n. (RB). MG., Horto Florestal de Paraopeba, (fls) 22-8-1959, Heringer 4050 (SP, UB). Zona do Calcareo, Corrego Maranhao, Mata de encosta, Pires et al 9477 (UB). Brasilia, DF. Margem do lago, Heringer 14846 (UB). Minas Gerais, Capto do Mato, Lagoa Santa, 4/9/1864 (fl), Warming s.n. (C, lectotype of T. hylobates; F; P). Minas Gerais, 1870, Warming s.n. (BM, NY). Federal Dist., 20 km E. Brasilia 6/7/1966, Irwin et al 18036 (BM, LTR, NY, SP, UB). D.F., 28/4/1966 Irwin et al 15427 (BM, C, LTR, MO, NY, U, UB). D.F., 5 km W. Formoza, 8/10/1965, Irwin et al 9058 (C, LTR, NY, U, UB). D.F., Brasilia, 27/9/1965, Irwin et al 8705 (BM, C, K, LTR, MO, NY, UB, US). Bahia, Rio Corrents, 2/7/1964, Pires 58128 (BM, K, LTR, NY, S, UB, US). Coias, 66 km. N. Jatai 22/10/1964, Prance & Silva 59560 (A + GH, K, LTR, NY, S, U, UB, US). Goias, 35 km N. Brasilia 8/5/1966, Irwin et al 15710 (BM, LTR, NY, U, UB, W). Bello Horizonte, Samp 7443 (F, R). Bello Horizonte, Mello Barreto 2250 (F). Not localized, Bruchell 6376 (K). "Bapitoo do matto", Kuhlmann 112 (RB).

12. TERMINALIA ARGENTEA

BRAZIL: Pelixlandia, 25 km do Sul, Minas Gerais, 22/2/1975, Hatschbach et al 36400 (LTR). Rod. BR 462, Goias, 17/11/1973, Hatschabach & Koczicki 33359 (C, LTR, MO). 55 km E. of Brasilia on road to Planaltina 13/9/1964, Irwin & Soderstrom 6169 (K, LTR, MO, NY, UB, US). Rod Rapouso Tavares, S. Paulo, 17/9/1974, Hatschabach & Kummrow 34813 (LTR). 20 km N.E. Catalao, Goias, 23/1/1970, Irwin et al 25193 (LTR, NY, U, UB). Swamp forest, near

Lagóa Mestre d'Armas, about 5 km N.W. of Planaltina, 23/7/1960, Irwin et al 18333 (BM, K, LTR, NY, MO, UB, US). Goias, 26-31 km S. of Goiãnia along highway BR-153, 10.4.1976, Davidse et al 12262 (LTR). Mt. Serra da Bodoquena, 16.11.1967, Stranga 1210 & Castellano 26794 (LTR). Goias 4/3/1978, Magnaso 87 (LTR). M.G., Estrada de Capinopolis Monte alegre Mun e Capinopolis 28/5/1963, Magalhães 14267 (LTR). Mato Grosso, Camaiuras, 1965, Fitticau & Coelho s.n. (LTR). Mt., Garapú, 3/10/1964, Irwin & Soderstrom 6639 (INPA, LTR). Bahia, Serra da Agua de Rega, 28/2"1971, Irwin et al 31259 (LTR). Goias, Road from highway BR-153 t Itaporá, 12 km W. of village of Presidente Kennedy, 2/2/1980, Plowman et al 8301 (LTR). Mt. Xavantina, 26/9/1964, Irwin & Soderstrom 6375 (LTR). 3 km. S. de Corrego do Jacu, 25/9/1975, Hatschabach 37146 & Kummrow (LTR). Piauhy, Gardner 2566 (BM, F, FI, G, K, NY, P, US, W). Minas, Glaziou 20294 (K, P). Goyas, 1896 Glaziou 21123 (BR, G, K, P, R). Goias, Irwin et al 24531 (BM, F, NY, P, US). Minas Gerais, St. Hil. in 1877 (P, type of T. sericea). Minas Gerais, Claussen 72, 76 (P). Mato Grosso, Argent in Richards 6754 (K, NY, P, U). Mt., Cerrado, Xavantina, Argent et al 6523 (K, P, U). Goias, Aragarcas, Argent et al 6391 (K, NY, P, U). Central Brazil, Weddle 2751 (P). Goyas, Sierra do Pyrenees, Agost 162 (P). Brasilia, Riedel 24 (P). Sao Paulo, Eiten & Eiten 2213 (A + GH, F, NY, SP, US). Minas Gerais, near Contagem, Betim, Williams & Assis 7426 (A + GH, BR, K, MO, NY, R, SP, US). Minas, Pitangui, Netto 11224 (BR). M.G., W. of Montes Claros, Irwin et al 23722 (BM, C, F, K, NY, SP, US). Goias in valley of Rio Maranho, Irwin et al 18916 (BM, F, MO, NY, US). Santa Luzia, Lagoa Santa, Barreto 2248 (F), 2249 (F, R). Minas, Macedo 1116 (MO, US). Bahia, Martius 1714 (M, holotype & isotype). Bahia, Lutzelburg 3078 (M). Mato Grosso, Xavantina, Lima 58-3126 (K). Sao Paulo, Mogy Mirim, Kuhlmann 3519 (SP). Goyas, St. Hil. 2576 (P). Ghiquitas, Dorbigny 784 (BR, G). No locality, Ule 2932 (HBG). Paraopeba, Minas Gerais, Magalháe 18896 (NY). Minas Gerais, Glaussen 1839, 190 (G), 1840 (BM, K). Riedel 2641 (G). Brasilia, Riedel s.n. (A + GH, G, FI). Mt., Xavantina Rd., Ratter

& Ramos 222 (K, NY), 537 (K). Vaccaria, Jaboticatubas, Barreto 10717 (R). M.G., Netto 224 (R). M. Gerais, Meia Ponte, Ule 161 (R). Goias, Serra dos Pyrenēos, Ule 162 (R). Mt., Guiabā, Coxipō da Ponte, Hoehne 4170 (R). Mt. Caceres, Hohne 4520, 4168 (R). Minas Gerais, R. Cipo, Duarte 7581 27239 (NY). Bahia, Zehntner 585 (R). D.F., Cerrad, Brasilia, Heringer 9031/1225 (UB). Sao Paulo, Ituverava, Gibbs et al 2868 (NY, UB). Mato Grosso, Gibbs et al 5439 (F). Goias, Rodovia, Itumbiata Goiania, Gibbs et al 2642 (F, NY, UB). 75 km N. of Cormba de Goias, Irwin et al 19027 (BM, NY, U, UB, US). Minas Gerais, Regnell 524 (US). Sao Paulo, Regnell 1575 (P, S, US), 5244 (S). M.G., Hatschbach 30009 (US). Parana, Senges, Rio do Funil, Hatschabach 6271 (US). Parā, Serra do Cachimbo, Pires et al 6437 (BM, NY). Mt., Kuntze s.n. (identified Myrobalanus brasiliensis OK) (NY, US). Mt., Garapa, 1/10/1964, Irwin & Soderstrom 6505 (BM, INPA, LTR, NY, W). Mt.,Garapa, Prace et al 59230 (LTR, M, NY, S, UB, US). Mato Grosso, Harley et al 10408, 10532 (IAN, K, MO, NY, RB, UB). M.G., 8/2/1970 Irwin et al 26342 (G, LTR, NY, SP, UB). Goias, S. Paraiso, Irwin et al 21695 (BM, C, F, K, NY, SP, UB, US). Mirand-Mato Grosso, Hatschabach & Cherer 30425 (C, MBM, MO, NY, US). Mt., Weddell 3338 (P). M.G., Glaziou161 (P). Mt., Ratter et al 2148 (IAN, I, MO, NY, S), 1117 (NY). Goias, Heringer 23499 (NY). S. Paulo, Sello 5560 (K, P). In silvis ripae fluvii Parana et ad fl. Pardo, Aug. 1826, Riedel 429 (A + GH; LE, lectotype of T. modesta Eichler). In campis near S. Carlos, S. Paulo, Jan 1834, Riedel 1956 (K, LE, P). Mt. Estrada Camp Grande - Rochedo, Hatschabach 21857 (BM, C, F). Mt. Krapovickas & Schinini 32831 (F). Goias, 25 km N. Itumbiara, BR153, Cristohal & Arbo 33108 (F). Goias, Aragarcas (C, MBM). S. Paulo, Mogi-Guacu, Perto de Padua Sales, Mattos & Mattos 13132 (SP). S. Paulo, Mattos 15058 (SP). Minas Gerais, Watsches & Gchrt 36347 (SP). S. Paulo, Itarare, Mattos s.n. (SP). Mt., Capad Bouito, Watsches & Gohrt 84 (SP). Goias, S. of Caiapo, 22/10/1964, Irwin & Soderstrom 7204 (LTR, NY, SP). S. Paulo, Mogi-Guaçú, Kuhlmann 4174 (SP). Minas Gerais, Beri-Biri, Hatschbach 30187

(MBM). Mt., Paxixi, Hatschbach 24599 (MBM). Mt., Fda Sta. Cruz., Hatschbach & Oquinaraes 21913 (MBM). M.G., 23/8/1964 Irwin & Soderstrom 5489 (K, LTR, UB). Goias, Ratter et al 3411 (K). Federal District, Ratter et al 3531 (K, UB). Mato Grosso, Ratter et al 4101 (K, UB). Mt., Macedo et al 434 (INPA), Para Rodivia Belēm - Brasilia km 92, Kuhlmann & Jimbe 318 (INPA, K). Goias, F. Lagoa Santa, Ratter et al 2437 (K, NY, U, UB). Mt., Ratter et al 2285 (K, UB). Mt. Onishi & Fonsêca, 219/986 (K). M.G., Oliveira 172 (IAN). Belem, Bosque Municipal, Black 1622 (IAN). Iasoa-Santa 1953, Mazalbaes s.n. (IAN). Minas, Gerais, 28/10/64, Heringer 9900 (IAN). Rodovia Brasilia - Fortaleza, Formos, Belēm & Mendes 1649 (C, IAN, K, NY, UBO. Região do Vale Rio Paranaiba, Frões 33443 (IAN). Bahia, Cancel a 89 km do Sul de Barreiras, Black 54-17886 (IAN). Zona S. Jorge, Belterra BR 65 km 94 E., Santarēm 20/11/74, Santose s.n. (IAN). Same locality, 22/11/74, Santose s.n. (IAN). Serra do Cachimbo 17-Das 1956, Pires et al 6457 (IAN). M.G., Heringer 9032, 9900 (UB). Goias, Sindy 986 & Onishi (UB). Mato Grosso, Sindy 1219 & Onishi (UB). M.G. Valio 322 (SP). S. Paulo, Moji-Guaçú, Itandro 513 (SP). Santa Riba do Passa Quatro, S.P., Pinho 19 (SP). Ituietaba, Macido 828 (SP). Capão do Campo, S. Martinho, Hofgen 5774 (SP). M.G., Santos & Castellanos 24035, 28462 (NY). In campis ad Paractata, Sept. 1834, Warming s.n. (BM, C). Sierra de Patangui, Sello s.n. (A + GH, FI). Bruchell 5226, 6940, 5583, 5341, 6170-2, 7719, 7955 (K), 56A & 7719 (A + GH). M.G., Duarte 2876 (MO). M.G., Hatschbach 3000 (NY). Prope Cuyaba, Aug. 1872, Riedel 1095 (A + GH; G; K; LE, lectotype of T. biscutella; P). Mt. Santa Anna, Chapada, Mealme 2468, (G, S, US). Mt., Cuyaba, Mealme 2293 (G, R, S). Santa Cruz, Moore 450 (BM, holotype of T. festinata). Minas, Shepherd et al 1238 (MBM).

BOLIVIA: Santa Cruze, Buena Vista, Peia del Sara, Steinbach 7160, 6413 (A + GH, BM, F, G, GOET, K, MO, NY, S, U, US), 6611 (A + GH, BM, K), 1578 (BM). West Valaro, July 1892, Kuntze s.n. (F, NY). D'Orbigny 709 (P). Santa Cruz, Krapovickas & Schinini 31928 (F). San Ignacio, Santa Cruz, Schmidt 135 (M).

PARAGUY: Concepcion, Hassler 7243 (A + GH, BM, C, G, K, MO, NY, P, S, US). Villa Concepcion dans les bois, Balansa 2234 (G, K, P). N. Paraguay, between Rio Apa & Rio Aquidaban, Fiebrig 4788 (A + GH, G, K, M). Concepcion, Rojas ex coll. pl. n. 56 (BAF). Rio Paraguay, Muello s.n. (BAF). Concepcion, Saws & Vogt 5236 (US). Serra de Amambay, Punta Paca, Hassler 11175 (G).

13. TERMINALIA KUHLMANNII

Known only from the type (see the text).

14. TERMINALIA JANUARIENSIS

Minas Gerais, at gate of eatern boundary, Ynes Mexia 5348 (A + GH, BM, F, G, K, S, U, US). Brazil Meridional 1839, Guillemin 849 (F, G, K, P). Brasilia, Raddi (FI; G, lectotype). Brasilia, Riedel s.n. (A + GH, C, G, W), 609 (LE), 1331 (FI, K, LE). Rio Janeiro, 1886, Glaziou 8668 (BM, C, G, K, LE, PX. Minas Gerais, Glaziou 20 295 (BR, K, LE, P, S). R. Janeiro, Magdalena, Costantino 2650 (S, U). R. Janeiro, Corcorado, Glaziou 2492 (S), 2991 (C, BR, P), 1303 (BR, C). Jangue, Prov. Phinarum, Phol s.n. (BR, M). Rio de Janeiro, 1842, Houllet (BR). Glazio 831 (BR). Minas Gerais, Gomez 2824 (UB). Schott (W). S. Paulo, Capital, Hoehn s.n. (US), Rio Janeiro, Widgren s.n., (identified as T. lucida (T. macrostemon Sprengel)) (S). M.G., Heringer 1490 (SP). In silvis Serra das Orgãos, Luschanth, October 1834, (BR, holotype of T. grandialata; G; LE; M; P). Brasilia, Riedel 16897 (BM). Pernambuco, de Moraes 1336 (SP, holotype of T. camuxa).

15. TERMINALIA GUYANENSIS

VENEZUELA: Edo Lara, Egua Salada, 3/11/1968, Smith 5056 (VEN 111923). Caracas,Dto Fedral, 17/5/1943, Delgado 328 (VEN 9851). State of Bolivar, N.E. Upata, 21/3/1966, Breteler 5087 (U, VEN 71304). Between Bolivar and Delta Amacuro, near the border, 10/3/1966, Breteler 4960 (U, VEN 71311). Edo Bolivar, La Isabel a Rio Grande, El Palmer, Dto Pair, Aug. 1961, Conejos 44 (VEN 73217). Monogas, Montana de Aguacate, between Caripe and Caripito, 19/4/1945, Steyermark 62174 (F, VEN 36211). Bolivar, N.E. of Upata, 21/3/1966, Breteler 5085 (U, VEN 71300). Delta Amacuro, Bosque Pluvial, Este de Rio Grande. E.N. de El Palmer, 13-29 Jun. 1964 Marcono Berti 187 (F, US, VEN 105915), 187 (A + GH, BM, VEN 63146). Delta Amacuro, same locality as above, Enero-April 1965, Zabala 29 (VEN 65890), 29 (VEN 65921). East of El Pichacho, N. Las Nieves and Las Chicharras, 5-8/2/1961, Steyermark 89070 (A + GH, S, VEN 60470). Near the border (= Rio Grande o Toro), between Bolivar and Delta Amacuro, 10/3/1966, (fl.) Breteler 4952 (U, US).

GUYANA: Wahuwak, Kanuku, Forest Dept., F. No 207, R No 5690 (FDG, K). Takutu Ck. to Puruni R., Mazaruni River, Forest Dept., F. No. 2075, 12 No 4811 (FDG, K, U).

FRENCH GUIANA: Poiteau s.n. (A + GH, U, isotype). Cayenne, Richard Herbarium (fr) (P). Plateau de la Douane, environ 3 km de Saül, Olderman 3190 (CAY). Saül, Monts La Fumée, 15/Oct. 1982, Boom & Mori 2134 (LTR). Same locality, 21/Oct. 1982, Boom & Mori 2237 (LTR). Same locality, 21/Oct. 1982, Mori & Boom 15121 (LTR). Guyane, Jul. 1824, Poiteau s.n., (type collec.) (K).

SURINAM: In montibus, qui dicuntur Nassau, in bos bij km 9, 9, Lanjouw & Lindeman 2853 (U).

16. TERMINALIA EICHLERIANA

BRAZIL: State of Bahia: Serra d'Acurra, Prov. Bahiensis, Blanchet 2794 (lectotype BR; isolectotypes BM, BP, BR, F, FI, G, K, LE, P, RB)(The specimen in FI bears the following extra information Certão do R. S. Francesco 1838); Enter jiguy e Brejao, regiao da Serra de Sincora, Carrasco, Feb. 6, 1943, Lomos Froes 20213 (F, K); Caetate, Lutzelburg 4091 (M); Queimada Nova (Mun. Seabra), 3/1/1977, Hatschbach 39530 (MBM 59855); Joaziero, a Camindo de Carasaja, 19-9-1912, Zehnter 585 (R 91392); Xique-Xique, Serra do Tiririca Grota do Pequenino, Zehnter 87-980 (R 91476).

17. TERMINALIA FAGIFOLIA

BRAZIL: "Brasilia", Riedel s.n. (Fl), Maranhão: 35 km S. Loreto, Eiten & Eiten 10588 (K, SP, UB);between Balsas & Parnaiba, Eiten & Eiten 10467 (K, SP), 5447 (K, U, US); Grajahu, Lisbôa 2508 (BM, RB); Caxias, Ducke 724 (RB); Caxias, Campo, Black et al 54-16716 (BM). Piaki: Not localized, Lutzelburg 159 (M), 1646 (M); Pira Curuca, M.A.L. 2395 (RB); Jabaleiro Grande, Lisbôa 2395 (G); Piracuruca, Salim Joedy 41 (RB); Sao eiamundo Monato, Jose Santino 225 (RB); Auta Sol, Lutzelburg, 1768 (RB); between Campo Major & Therezina, Dahlgren 975 (F, K); Serra Branca, Ule 7459 (K); Prov. Piauhy 1841, Gardner 2567, (lectoparatypes, var.parvifolia, BM, F, FI, G, K, NY, P, US, W). Ceara: not localized, Allemão 574 (P); Arapaha, Allemão & Cysneiros 574 (R). Bahia: Barra to Boqueirão, Zehntner 35 4 (R, RB); S. Anna, Zehntner 3089 (M); Barreiras to Santa Anna, Zehntner 499 (R, RB); 30 km o de Barreiras, Hatschabach 42080 (MBM); Barreiras, Black 54 - 17783 (BM), Sta Maria, Boqueirão, Zehntner 2081 (M); Cerrado 4/7/1946, Pires 58157 (BM, LTR, NY, US); inter Malhada et Caitete oppiduium, 1714, Martius (N); Espigão Mestre 2/3/72, Anderson, Stiber & Kirbride 36428 (BR, MO, NY,U, UB); Serra do Rio do Contas, Harley et al 15222, 15034 (K, M, MO, NY, U); near Utinga, Fazenda in Cerato de S. Fransisco, 1839, Blanchet 2773 (BM, BR, G, K, LE, P, W). Serra Geral de Caitite, 1.5 km S. of Brejinhes das Ametistas, 11/4/1980, Harley 21220 LTR; Chapadào Ocidental da Bahia ca. 10 km S.W. of Correntina, on the road to Goiaz 26/4/1980, Harley 21787 LTR. Goias: Serra do Rio Preto 19/11/1965, Irwin et al 10564 (BM, LTR, NY, U, UB); same locality Lutzelburg, 1778 (U), 1767 (RB), 5931 (S); Rio de Parata, Vicinity of Posse 9/4/1965, Irwin et al 14572 (BM, INPA, LTR, NY, UB); Serra do Cristais, 2 km N. Cristalina 5/11/1965, Irwin et al 9928 (C, K, LTR, MO, NY, UB, US); same locality, Irwin et al 13473 (NY, UB); Sersa Geral do Paraná, Sao Joa 22/3/73, Anderson 7678 (LTR, NY); Cachoeira do Pipiripau, Maia & Eunice s.n. (UB); Formosa, Duarte 9391 (RB); Goyas Central, Glaziou 21124 (BR, C, G, K); Goias - Brasilia 20/7/1963, M. Silho & Rizzini 406 (LTR). Distirito Fedral: Paranõa 20/9/1965, Irwin et al 8481 (BM, K, LTR, MO, NY, UB, US); Planopiloto, Ala Norte, Brasilia 3/1/1963, Heringer 24509 (LTR); same locality, 9086 (UB); Brasilia , Heringer 6697 (UB); same locality, Cobra & Oliveira 185 (RB, US); not localized, Valio & Moraes 415 (RB, US). Mato Grasso: Rio Verde 11/11/75, Hatschabach 37411 LTR Piraputanga, Hatschabach 23801 (MBM); Poconé, Cosia 84 (RB); not localized, no collector, (R 91511). Minas Gerais: Diamantina, Cafundó, Barreso 9856 (F, R); Serra do Espinhaco, 18 km E. Diamantina, 14/1/1970, Irwin et al 27469 (G, LTR, NY, P, SP, UB); Same locality, Irwin et al 23470 (BM, C, K, NY, US); Mendanha 16/11/1971, Hatschabach 28046 (LTR, US) Rio das Almas, Hatschabach 41668 (MBM); near R. São Francisco, Warming w.n. (C, P); Grão Mogol, Mukgraf 3405 (F); same locality, Kukgraf et al 28646 (MBM); same locality, Hatschabach 41470 (MBM); in Campis S. Philippi, Prov. Minarum, 1818, Martius s.n. (Lectotype, M); not localized, Pohl s.n. (BM); Januaria, Heringer 9828 (UB); Minas-João Pinheiro-Cerradão, Rizzini s.n. (RB); Alegres, Riedel 2639 (A + GH, LE, P); Alegres, Serra da Chapada, Riedel 972 (K, LE), 1144 (G, LE); Fando, in dos Bois, Pohl 3427 (A + GH, F, LE, W);

not localized, Glazio 10712 (C, P), Saint-Hiaire 1947 (P); Caxapora do Gentio Incolis, Martius s.n. (lectoparatype, M). Espirito Santo: Espirito Santo-Sete Cidades, Porque Nacional, Boqueirao, Barroso 16 (F, K, KB). BOLIVIA: St. Cruz, Robore of Chiquitos, Cardenas 2959 (F, G).

18. TERMINALIA ACTINOPHYLLA

BRAZIL: Maranhão: Sao Francisco, Savanne, in der Vane von Sturzbachen, Snethlage 600 (F); Municipio de Caxia, margem Igarapé dos Galdei Rões, 1976, Elias de Paula 799 (UB). Piaui: Picos-Oeiras, beira da estrada, 30/7/1964, Castellanos & L. Duarte 33544 (HB, LTR); not localized, 1840, Gardner 2068 (NY); Municipio de Pedro II, Farmaçao de Chada, Sucre 9294 (LTR); Serra Branca, Jan. 1907, Ule 7469 (G, K). Ceará: not localized, Alemão & Cysneriros 577 (K) (Mixed with Buchenavia tetraphylla). Bahia: in Silvis Catingas in mediterraneae Prov. Bahiensis, Brazil, 1818, Martius s.n. (lectotype, M; 2 isolectotypes, M); same locality, 1819, Martius s.n. (lectoparatype, M). Minas Gerais: campos ābidos, Sellow 3071 (R).Goias: Chapada dos veadeiros, 16/3/73, Anderson 7257 (LTR); not localized, 1914, Luetzelburg 425 (M); Chade Formos-Paraná, 8/3/1978, Alberto 41 (LTR).

19. TERMINALIA AUSTRALIS

ARGENTINA: Buenos Aires, Hudson, Krapovickas 2816 (A + GH, NY, SP). Conchitas, Buenos Aires, Castellanos 17042 (BM). Punta Lava, Black & Ragonesi 51/11439 (BM). Misiones, Santa Ana, Rodrigues 602 (BM, BAF, F). San Agnacio, Santo Pipo, Schwarz 4854 (A + GH, F). Isla Martin, Garcia, Moreau 7169 (BM). Entre Rios, Colon, Castellanos 31/1191 (BM). Entre Rios, Pedersen 474 (BR, C, G, US). Corrientes, Santo Tome, Pedersen 2917 (A + GH, BK, C, G, U, US). Santo Tome, Venturi 438 (BAF). Corrientes, San Martin, Krapovickas & Cristobal 28991 (A + GH, G). Corv., Ituzaingo, Cristobal & Krapovickas 1729 (A + GH, F, G). Punta Lava, B. Aires, Cabrera 1575 (NY, SP). La Plata, B. Aires, Amedia 1098 (C). Punta Lara, B. Aires, n.c. 36417 (F). Concordia, Entre Rios, Cabrera & Sagastaqui 14304 (C). Eldorado, Misiones, Burkart 14674 (A + GH, K), 14143 (K). Bosque de Punta Lara, Dawson 864 (A + GH, F, NY). San Isidro, B. Aires, Fosberg 47744 (US). Isla Lautiogo, B.A., Abbiatti 1071 (US). Arroyo Leiso, Missones, Bertoni 2162 (A + GH). Duranona, Scwarz 4239 (A + GH). Entre Rios, Cordini 35 (k). La Plata, B.A., Sparre 355 (K). Entre Rios, Meyer 10656 (W). Missiones, Schevay 1283 (W). Santa Tome, Corr., Jbarrola 1474 (W).

URUGUAY: San Javier, Rio Negro, Herter 1013 (A + GH, F, G, LE, M, N, Y, US), 82822 (BM, F, G, GOET, HBG, M, U). Salto, Salto Chico, Herter 1013a (A + GH) 95290 (A / GH, G), 4008 (F, HBG, MO). Ribera isquierda del Uruguay, Verano 17038 (BM. Concepcion del Uruguay, 1877, Lorentz s.n. (BM, W). Concepcion del Uruguay, 1878, Lorentz 1700 (A / GH, BAF, F, FI, G, HBG, JE, K, PI), 640, 4781 (M), 421, 152 (GOET). No locality "Uruguay" Berro 8265 (F). Salto, Berro 4008 (F). J. Bot. Montevideo, Nov. 1935 n.c. (G). Paysandu, Rossengurtt B-4915 (A + GH, SP, U), B-4225 (A + GH, U). Mesta de Artigas, Rio Uruguay, Paysandu (F, US). Colonia, Riochuelo, Rocas, Cabrera 3905 (F, US). Toropaso, near Colonia do Sacramento, Prov. Missionum, St. Hilaire 2591, 2382 (P, types).

BRAZIL: Rio Grande Do Sul, Rambo 46403 (P, W), 44055 (BR, F, P, W), 49224, (NY, US, W), 38008 (C, P, US), 44335 (US). St. Catarina, Dusen 17805 (A + GH, F, NY, P). Paran, Hatschabach & Guimataes 20575 (A + GH, BM, C, F, K, M, NY, P, SP, US). Sello 962 (BR), 817 (C, NY, US). Enens Marques, Parana, Hatschbach 35171 (C). R. G. Do Sul, Costasacco 712 (US). Rio Pelotas, Barra Grande, S. Catarina, Reitz & Klein 14448 (BM, US). Sello in 1815-17 (BM). Itapiranga, S. Catarina, Smith & Klein 13160 (G, NY, P, R, S, US). Mun. Riqueza, Riverbed, Bank of Rio Iracema, Smith & Klein 13117

(C, G, NY, F, R). Itapiranga, St. Cat., Smith & Klein 11815 (NY, R, US). Sao Miguel d'Oeste, Smith & Klein 13246 (A + GH, F, P, R, US). Itapinanga, woods bank of R. Urugai, Smith & Reitz 12644 (NY, P, R, US). Requeza, R. Iracema, Smith & Reitz 12602 (A + GH, F, P, R, US). Villarica, Rio do Peixe, S. Cat., Smith & Reitz 12935 (A + GH, F, P, R, US). Passo do Ricardo, Pabst 6591 (R). Passo da Olaria, R. G. do Sul, Vidal 1599 (R). I.A.S. Pelotas- R. G. do Sul, Sacco 712 (NY, R). Otto Alegra, R. G. do Sul, Mealme 344, 7 (R). R. G. Sul, Santos 2775 et al (R). R. G. do Sul, Ihering 32 (R). S. Leopold, R. G. do Sul, Rambo 35821 (A + GH, NY). Rio Piquiri, Lindeman et al 8732 (U). Barrado quarai, Lindeman et al 8443 (U). Pareci Novo, Henz 37641 (F). S. Feo de Paulo, Rangbo 31268 (F).

20. TERMINALIA TRIFLORA

ARGENTINA: Chaco, Pederson 3981 (BR, G, MO, NY,MO, S, U). Empedrado, Corrients, Pederson 4675 (BR, G, NY). Rio Huacra, Catamarca, C. A. O'Donell 18/11947 (G, US). Tucuman, Lillo 7156 (G, P). Salta, Oran, Eyerdam & Beetle 22810 (A + GH, G). Corrientes, Schinini 13618 (G). Corrientes, Schinini & Cristobal 13649 (F, G, MO). Corr., Capital, Krapovickas & Cristobal 26478 (G). Oran, X 1873, Lorentz & Hieronymus (BAF, BR, F, G, GOET, lectotype, LE, P, PRC, S). Tucuman 22-93/XII/1872, Hieronymus & Lorentz 103 (BAF, BM, G, NY). Tucuman, Tafi, Sleumer s.sn. (W). Tucuman, Vervoorst 9280 (W). Forosa, Morel 1273 (G, W). Salta, Oran, Rodriguez 1029 (BAF, BM, NY), Salta, Oran, Schreiter 3437 (BM), 3379 (BM, F, W), Santa Victoria, Meyer 17669 (W). Oran, Rio Piedras, Rodrigues 83 (BAF, F), 135 (BAF, F). Oran, Santa Victoria, Logname & Cuezzo 9603 (W). Salta, Riopescado, Vervoorst & Cuezzo 7728 (W). Jujuy, Ynto, Venturi 365 (BAF, BM). Jujuy, San Pedro, Venturi 5316 (A + GH, MO, US) Jujuy, Ledesma, Venturi 5215 (A + GH, BM, F, MO, US). San Pedro, Venturi 5023 (US). Chico, Venturi

240 (BAF). Resistencia, Meyer 16401 (US, W). Las Palas, Jorgensen 2102 (BM, US). Corrientes, Santo Tome, Venturi 1313 (BAF, BM). Misiones, Santa Ana, Rodrigues 601 (A + GH, BAF, BM, F). Mis., Gaudelaria, Belgrano 1811 (BAF). Mis., San Ignacio, Schwarz 3404 (S), 3310 (S). San Ignacio, Mumiet 103 (BM). Mis., Puerto Sirsopeu, Rojas 460 (A + GH). Misiones, Ekman 1933, 1934 (S). Corrientes, Empedrado, Pedersen 1157 (BR, S, US). Mis. Ignazu, Schwarz 7159 (S). Mis. Capital, Schwarz 6561 (W). Candelaria, Salta Venturi 9505 (A + GH, BM, MO, US, S). Tucuman, Tafi, Caotillor 2076 (BM, F). Tucuman, Rio Chico, Wonetti s.n. (BM). Tafi, Schreiter 458 (BM). Tucuman, Venturi 266 (BM). Tucuman, Rio Pali, Schreiter s.n. (BM). Tucuman, Capital, Lillo 10749 (BM, F). Tucuman. Ramada, Schreiter 795 (BM). Tucuman, Capital, Venturi 5350 (A + GH, BM, MO, S, US). Tucuman, Al Potrerillo, Wonetti 1514 (BM). Tuc. Saladillo, Lillo 7149 (BM). Tucuman, Tucuman, Lillo 8605, 1712 (BM). Oran, Rodrigues 9139, 1351 (BM) Tucuman, Cerro del Campo, Monetti 2110 (BM) Tucuman, Venturi 2222 (A + GH, BM, F, US). Formosa, Jorgensen 2378 (BM). Tucuman, Lillo 2140, 3207, 1464 (BM). Tucuman, Schreiter 1536 (BM). Tucuman, Castillou 2975 (BM). Tucuman, Venturi 956 (BM, F, MO). Jujuy, Lillo, 5100, 5003 (BM, F). Jujuy. Cerro de San Pedro, Schreiter 100 (BM). Jujuy, Tinelli 5149 (BM). Oran Lillo 10935 (BM). Formoza, Morel 8935 (K, MO, NY). Foromoza, Morel 4032 (F, MO). Tucuman, Legname 3939 (NY). Tucuman, Digilio & Legname 4403 (C). Tucuman, Digilio et al 4299 (NY). Misiones, Schwarz 6562 (NY). Correintes, Schinini 301 (G). Tucuman, Schreiter 6466 (U). Resistensia, Chaco, Rojas 12341 (A + GH). Quebrada, Salta, Oran, Legname & Cuezzo 5784 (A + GH). Salta, Santa Victoria, Nusser 47 (A + GH). Salta, Marmel et al 9251, 8688.(A + GH). Tucuman, Peinand 35183 (A + GH, NY). Salta, Oran, Willni 349 (A + GH). Tucuman, Schreiter 6476 (A + GH). Chaco, San Fernando, Isla Soto, Schinini 16142 (F, MO). Corietnes, Capital, Shinini 13618 (F). Tucuman, Venturi 1895 (F, US). Tucuman, Capital, Venturi 8421 (F). Tucuman, Burruyaui, Bulettr 169 (F).

Tafi, Villa 601 (MO). Tucuman, Capital, Meyer 12636 (MO).

PARAGUAY: Paraguaria Centralis, Prope Sapucay, Hassler 11830(A) (A + GH, BAF, BM, C, F, G, K, MO, NY, S, US), 11830a (fr.) (A + GH, BAF, F, G, K, NY, US). (The 2 specimens at G are identified var. glabrata Hassler). Altos via Aeoe, Chodat 87 (G). Corientes, Cordillera de Altos, Fiebrig 97 (A + GH, BM, F, G, HBG, K), 181 (A + GH, BAF, BM, F, T, GOET, HBG, K, PRC). Orillas Montes San Bernardillo, Hassler 1329, 1329a (G). Bardsdu Mebay, Pres de Paraguari, Balansa 4570 (G). Sierra de Amambay in alta planitic, Hassler 3471 (F, NY), 11333 (A + GH, BAF, G). Paraguaria centralis, Prope Sapucay & Hassler 11746, 11746a (A + GH, BAF, BM, G, G, K, MO, NY, S, US). In dumets near Ilacurebi, Hassler 3125 (A + GH, G, K, P). Prope Concepcion, Hassler 7170 (BM, G), 750 (BM, F, G, K, P), 750a (G, lectotype of T. hassleriana; NY, P). Concepcion, au les bois 1877, Balansa 2233a (F, G, P, lectotype of M. balansae), 2233 dated 1875 (BR, G, K, P, S), 2233b (G, K, P), 2233c dated 1874 (GOET, P). In camp prope San Bernardino, Hassler 866 (G, K, P). Hassler 11774, 770 (K), 3471 (BM, F, NY, S, US). Villa Elisa, Dept Central, Pederson 4233 (BR, G, NY, P, S). Missiones, Pedersen 5211 (K, S). San Bernandino, Osten 8127 (BM, S), Rojas 1239a (S). San Pedro, Alto Paraguay, Primaria Woolston 296 (C, K, NY, S), 1318 (C, K, NY, S), 1319 (C, K, NY, S, U), 288 (C, K, NY, S, SP, U), 289 (K, NY, S, SP, U). Capital, Shinini 15373, 15368 (F, MO), Shinini & Bordas 13351 (MO).

BOLIVIA: Dept. Santa Cruz, Cerra La Negra, Steinbach 8176 (A + GH, BM, K, F, S). No locality, Steinbach s.n. (F 637074). Dept. Tarija, Motovi, Troll 193 (JE, M). Santa Cruz, Cardenas 2837 (F, G).

BRAZIL: Rio Vacaria (Mun. Rio Brilhante) Matto Grosso, 24/10/1970 Hatschbach 25172 (LTR, MBM). Joaquim Tavora, Arredos, Paraná, 30/11/1976, Hatschbach 39279 (LTR). S. Paulo, Baywundo s.n. (R91368). S. Catarina, Tapera 14/10/1969 (fl), Klein & Bersolin 8349 (BM, LTR), from the same tree, 18/11/1969 (young fls), Klein & Bersolin 8428 (BM, LTR). Same locality and from the same tree, 16/12/1969 (Mature fr.), Klein & Bersolin (BM, LTR). S. Catarina, Conas Vieras, 19/11/1969, Klein 8467 (BM, LTR). Joanopolis-Serra da Fazenda do Sr. Caio. Matias, Kuhlmann & Goncalvos 1336 (SP). S. Paulo, Amparo, Monte Negre, Kuhlmann 503 (HB, SP, US). S. Paulo, Tatui, 18/10/1957, Kuhlmann 4234 (HB, SP, US). S. Paulo, Araraquara, 4-11.1966, Medina s.n. (SP 1050650.

21. TERMINALIA ULEANA

Known only from the type specimens (see under the species).

22. TERMINALIA REITZII

BRAZIL: Santa Catarina: Serra do Matodor, Rio do Sul, 11/1/1958 (fl.), Reitz & Klein 7076 (A + GH, BM, BR, K, U, US). Same locality and from the same tree. 21/11/1972 (fr.), "Garajuvinha" Reitz & Klein 12194 (BM, holotype, NY). Same locality, 11/11/1963 (fl.) Reitz & Klein 16138 (BM, BR, G, M, NY).

23. TERMINALIA AMAZONIA

BOLIVIA: Santa Cruz, Sara, Steinbach 6617 (A + GH, BM, F, G, GOET, K, MO, U), 6397 (A + GH, BM, K). Sata Cruz, Cerro del Auibaró, Pcia del Sara, Steinbach 2947 (BM). Lapaz, S. Yngas, Rio Bopi, Krukoff 10446 (F, K, MO). Santa Cruz, Sara, Bosquedel R. Suentei, Steinbach 6557, 3523 (A + GH, BM, F, G). Santa Cruz, Rio Blanco, Steinbach 3442 (BM, F, G, K), 345 (BM). Peia del Sara, Steinbach 2527 (BM).

BRAZIL: Santa Isabel, Belem, Para, Ducke 17678 (G, K, MO, NY, P, RB, U, US, VEN), 2042 (A + GH, MO, NY, P, R, RB, U, US, VEN). Belem, Mata da terra firme, Ducke 206 (HB, IAN, R, SP, U). Amapa, Monti Douvado, Moore 5, 55, 56 (NY). Belem, Para, Pires, 51885 (NY, US). State of Acre, near R. Macauhan, Krukoff 5712 (BM, F, G, K, M, NY, P), Acre, Sena Madureira, Prance et al 7717 (F, INPA, K, NY, U, US). Amapa, Riojari, Olieira 4062, 3948 (IAN, NY). Pará, near Jobrica, Ducke 17683 (G, K, P, RB, US). Belem Pará, Pires & Black 1232 (P). S. Luiz do Maranhão, Ducke 355 (HB, RB). Sal Luiz, Granja Barreto, Maranhão, Ducke 2187 (COL, G, P). Estrada Santarem

-Guiabá, BR-165, Para, Nilson s.n. (INPA), same locality, Hamberto s.n. (INPA). Maranhão, Itapicuru, Black et al 54-16640 (IAN). R. Jari, Mone Dourado, Pará, Oliveira 3782 (IAN). Pará, Pires 7396 (IAN).

GUYANA: Mazaruni & Cuyuny Rivers, Graham 355 (NY, US). Lower Demerara River, Jenman 4347 (F, K, NY), 4359 (BM, F, K, NY), 5076 (K). Malofoe, Cuyuni R., Meutyn 247 (F, K). Atkinson field, Irwin BG-39 (US). Hohenkerk 136B (K). Siruni Creek, Forest Dept. 161 (K). Davis 1062 (K). S. side of Kanaku Mount., Forest Dept. 261 (K). Morahalli Ck., Essequibo, Forest Dept. 1282 (K).

FRENCH GUIANA: Cayenne, Patris (F 679073) S. Camopi, Grenad 1293 (CAY, P). Balate-St. Jean, Petrov 234 (CAY). Cayenne, n.c. 107, 321 (CAY, M, P), 224 (M), 241 (M, P); not localized, Bois 7585 (CAY, P). Aubreville 222 (P). Bureau Agricole & Forestier 1953-1954 (P). Cayenne, n.c., no number (BM, P). Trois Sants Forest Primaries, 23/8/1977, Grenand 1401 (LTR).

SURINAM: Broko Pondo, Lim Sang 16250 (NY). Lely Mts., Lindeman et al 430 (K, NY). Zanderij 1, Toekadie & Kwai 57, 93 (IAN, K, NY, U, WIS). Suriname River, Lindeman 9820 (NY, VEN). Browusbay 6594 (F, U). Hostmann 1305 (A + GH, BM, K, P). Suraname R., Lindemann 3812 (U). Zanderij - Grounds of Land's Bosbeheer, Lems 5100 (U). Maratakka R., Snake Creek, Maas 10834 (U). Jodensavanne - Mapane Creek area, Schulz 7221 7983 (U), Lindeman 3885 (U). Mapanegebied, Elburg 9820, 13533 (U). Blakawatra, Boerhoom 9140 (U). Saramacca R., W. of Poika rain forest, Schulz 7628 (U). Watra Miri For. Res., B. W. n 2026 (U). Zandery I, B.W. n 374, 1488 (U). Stahel & Gonggrÿp 6594 (U). BAFOF Ser. For. No 321M, St. Laurent (U). Route de l'Acarouany, no 7585, 2/11/1956, no 107 M 9/11/1953 (U). Gonggrÿp 30 (U). Near Jodensavanne, Heyligers 441 (U). Zanderij I, Stahel 93 (A + GH).

COLOMBIA: Tumaco, Romero Casteaneda 5349 (NY). Santa Marta, Smith 1772 (NY). Mutis 3392 (US). Cordillera Oriental, Norte de Santander, Hoya, Cuatrecasas et al 12389 (A + GH, BM, F, MO, U, US). Santa Marta, Smith 2726

(A + GH, BM, K, MO, P). Choco, Municipo do Rio Sucio, Forero et al 1671 (COL). Bolivar, Pennell 4113 (NY).

ECUADOR: Grubb, 8 km S.E. of Tena, Pennington & Whitmore 1958 (NY). Rio Blanco, Little 6256 (F, NY). Esmeraldas, Little 6267 (K, US, WIS), 6268 (F, K, US, WIS), Quininde, Little 6256 (K, WIS).

PERU: Near Tarapoto, Spruce 4909 (A / GH, BM, BR, F, G, GOET, K, NY, P, W). Huanco Dept., Tingo Maria, Vasquez 101 (F, NY, P, US), 90 (F, P, US, WIS). San Martin - Juan jui Alto Rio Huallaga, Klug 3792 (A + GH, BM, F, K, MO, NY, US). Coronel Portillo Prov. Loreto, Magin 74, 85 (F, NY, US, WIS). Balsapuerto, Loreto Dept., Klug 3107 (A + GH, BM, G, F, K, MO, NY, US). Junin, Mazaroni, Woytkowski, 5999 (A + GH, MO), 6017 (MO) Huanuco, Coronel, Dept. Calleria, Schanke 6251 6224 (G, LTR, NY). Amazonas, Brent Berlin 342 (A + GH, MO, XAL). Dept. San Mart, Shunke, 7645 (XAL). Stromgehict des Marawn, Ost-Peru, Tessman 4014 (G). Tingo Maria, Huãnuco, Schunke 6159 (F, US). Lamaso San Martin, Williams 6441 (F). Lower R. Huallaga, Loreto Dept., Williams 3968 (F). San Martin, Mariscal Cacēres, Shunke 7654 (MO). Pacallpa, Loreto Dept., Angulo 10 (MO).

VENEZUELA: A Este de El Palmar, Carretera La Tigra, Estado Bolivar, 11/7/1964 Marcano Berti 296 (K, VEN 73461). Paēz, Qda Chaguaramas, 10° 6'N 65° 55' W, 7/6/1977, Gonzalez, & Davidse 944 (LTR, MO, VEN). State of Scure, 140-220 m alt., Steyermark 62831 (F, VEN 31953). Distrito Jimenez, Paso de Angostura, Sitio de represa de Yacamba, en la confluencia de la Quebrada Honda con el Rio Yacambu, Lara, alt. 500 m, 27/12/1973, Steyermark et al 108793 (MO, NY, VEN 99021). Mongas, Guarapiche forest reserve, primary forest, Campo Colorado, alt 0-100, 7/5/1966, Breteler 5148, 5138 (MO, NY, US, VEN). Estado Apure, Reserva Forestral San Camilo, Solva siempreverde a lo largo de la Quebrada La Azulita, alt. 280, 30/3/1968, Steyermark et al 101597 (US, VEN 79986). Miranda, Paēz, drainage of the Rio Guapo and Rio Chiequito, 44.5 km directly (in a straight line) SE of Caucagua, 66° 01' W 10° 05' N, alt. 200-400 m, 1/6/1977, Davidse & Gonzalez

13605 (VEN 127368). Bolivar, Sierra Imataca, alt. 3000 m ("Pata de danta"), 7/2/1959, Bernardi 7096 (VEN 64194), 7561 (K, US). Delta Amacuro, Selva Humeda, 15 km SE de Los Castillos (alt 30 m), 12/7/1980, Little 17670 (F, VEN 53208). Selvas de Ymare, Estado Yaracuy (100-150 m alt.), 7/2/1959, Bernardi 6937 (K, VEN). Reserva Forestal de Guarapiche, Maturin, Edo Monagas (n.v. Guacharaco), July 1969, Aristeguieta et al 7252 (NY, VEN 77276). 115 km South of El Darado, N.E. of Luepa, Edo Bolivar (alt 800-1200), Mar. 1962, Steyermark & Aristequieta 8 (K, NY, US, VEN 58489). Territorio Delta Amacuro, Bosque Pluvial, Este de Rio Grande. Este Noreste de El Palmar, Cerca de los limites del Estado Bolivar, (Arhol 32 m. tall 43 cm. diam. N.V.: Pata de data blanco), Marcano Berti 503 (BM, NY, VEN 63147). Along Rio Reforma $\frac{1}{4}$-1 km. above junction with Rio Toro, Sierra Imataca, Estado Bolivar, (Tree 25 m. tall; leaves subcoriaceous, deep green above, dull green below), alt. 200-250, 11/12/1960, Steyermark 87916 (A + GH, MO, VEN 60473). Bosque de bajio a mās o menos 5 km. al Este de Turiba, Distritio, Cedeno, Estado Bolivar, (Tree 18 m. tall, 40 cm diam.), Marcano Berti 2576 (VEN). Selva buméda, Altiplanicie de Nuria, 50 km. VE. de Guasipati, Edo Bolivar, alt. 600 m., 6/7/1960, Little 17603 (VEN 53222). Rio Toro (Rio Grande), between Rio La Reforme and Puerto Rico, north of El Palmar, alt. 200-250 m. (Common tree 20 m. tall, leaves subcoriaceous, dark green above, paler below.), 7/12/1960, Steyermark 87840 (VEN 60470). Sehras de Juetojro. St. Jeresa, Edo Miranda, Bernardi 5647 (NY, VEN 39927). Distrito Sucre, Selva siempreverde al 10 largo de la Quebrada Zurita, Paso Hondo, sur de Limonal y Santa Fé, alt. 40 m, Steyermark et al 17826 (VEN 94731). Atures, valle del Rio Manapiare, (N.V.: Mezcla), 18-19 June 1976, Berry 2228 (LTR, MO, VEN 127367). Near the border between Estaolo Bolivar and Territorio Delta Amacuro. (Tree with straight angular bole and buttresses up to 2m. height, 27 m. tall. Diam. at 2 m. 54 cm. Bark brown, fissured peeling off in flakes, with pinkish slash-wood pale brown, leaves thinly coriaceous, glossy, smooth and medium green above, pale green beneath), 14/3/1966, Breteler 5016 (NY, U, VEN 71322, W). Altiplanicie de Nuria, moreor less level forest on trail between

El Cruzero and slightly beyond pica lol, ESE of Villa Lola, alt. 315 m. (Tree 30 m. tall; leaves firmly membranous, rich green above; used for house construction, and railroad ties), Steyermark 86354 (NY, VEN 51208). Cerro "El Encantado", Selva densa, Primaria. Orilla rio Caripito, Estado Monogas, (Tree 30 m. tall 35 cm. diam, N.V: Guire) April 1959, Buza 6706 (K, NY, VEN 406). Sierra de Perija, Zulia, 1050 m. alt, tree 10m. tall, 22/3/1964, Ijjasz-Madriz 63 (VEN 64837). Las Caracas-Coba Codera. Edo Miranda, (Arbal 6 m. tall.) June 1962, Aristeguieta 4853 (NY, VEN). Edo Miranda, 1200 m. alt. (Arbal 6 m. tall), June 1957, Aristeguieta 2815 (NY, US, VEN 41295). Edo Bolivar, Campamento "El Paraiso" a 48 km. N.E. del Cuserio los Rosas, este ultimo a 17 km. de Upata, (N.V.: Pata de danta), April 29-June 4 1965 Blanco 90 (US, VEN 65376). Venezuela. Near the border (Rio Grande o Toro) between Estado Bolivar and Territorio Delta Amacuro, 14/4/1964 (fl.), Breteler 3811, (F, M, MO, NY, P, U, US, VEN 60787). Pie de Monte, Sierra del Norte o de la Culata, Edo Miranda (200m. alt.), Chacon 1 (VEN). Small riverine tree along the Orinoco, 30 km below La Urbana, March 14-15/1949 (fl.), Maguire 29017 (NY, US, VEN 31341). Edo Bolivar, Campamento "El Paraiso" a 48 km, N.E. del Caserio Los Rosos, este ultimo a 17 km de Upatal, April 29-Jun. 4 1965 (fl.), Blanco 105 (NY, VEN 73912). Las osillas racosas del Oredio Caura El Chaptro, Bolivar, 17/3/1939. Williams 11532 (F, US, VEN 9854). Near the border (= Rio Grande ó Toro) between Estado Bolivar and Territoria Delta Amacuro, 14.4.1964, Breteler 3812 (NY, P, U, US, VEN 60788),4990 (U). Arbol de Unos 4 m. alto. Cerca de los rapidos, Pto. Ordaz - San Félix, Edo. Bolivar, April 1964, Aristeguieta 5316 (MO, NY, VEN 79493). Territorio Federal Delta Amacuro, Bosque Pluvial, Este de Rio Grande. Este-Noreste de El Palmor, cerca de los limites del Estado Bolivar, 1964, Marcano Berti 141 (A + GH, BM, BR, F, K, M, MO, NY, P, RB, US, VEN), 171 (BM, F, K, MO, VEN). Altiplanicie de Nuria, Woods along trail between end of savanna east of Hato de Nuria and Quebrada Agua Linda (Tree 20 m.tall, leaves subcoriaceous, deep rich green and shining above, paler green below.

alt. 540 m.), 18/7/1960, Steyermark 86477 (NY, VEN 51207). "Copito de Cerro" Arbol 25-30 m. tall. en la sierra alta de Figre, Bajo Caura, Bolivar, 17/4/1939, Williams 11842 (A + GH, F, NY, US, VEN 9855). Selva no inundada, la Puchima, Palmar (N.V.: Pardillo negro), 30/4/40, Williams 12948 (A + GH, F, K, US, VEN 9856). Yuamitas P.N. Aragua, 16/9/1938, Estado Anzoatequi, Williams 10337 (A + GH, F, NY, US, VEN 9852). Arbol torcido de 12-15 m. tall, en La Playa del Salto de Para Anedio Caura, Bolivar, alt 250-300 m, (fl.), 10/3/1939 (fl), Williams 11454 (A + GH, F, US, VEN 9853). Campamento orocoima, orilla del Rio El Toro, a pie de la sierra Imataca. Selva rala, conrocas de manganeso (Tree 25m. tall. 30 cm. diam. N.V.: Guaracacha), Buza 7561 (NY, VEN 361). State of Bolivar. N.E. of Upata, El Paraiso Camp, Breteler 5090 (U, VEN 71316). Delta Amacuro, Departmento Tucupita, 5-14 km ESE of Los Castillos de Guayana, 50-200 alt., 28/3-2/4/1979, Davidse & Gonzalez 16353 (LTR, VEN). 2 kms. SE, of Los Patos, north of Rio Hacha about 15 kms. North of Rio Supamo, 30 kms S. of El Manteco, alt 365, Steyermark 87006 (NY, VEN 58644). Anzoatequi, Cerro la danta, Steyermark 61096 (F,), 62831 (F, NY). Bolivar, El Trigre - la Soledad, Marcono Berti 741 (US). Sucre, Steyermark et al 107826 (MO). Miranda, Paéz, Gonzalez & Davise 858 (VEN). Puerto Cruz, Fedral Dist. Whitford 23 (A + GH). Delta Amacuro, Otiila del rio El Toro, 13/4/1959, Bernardi & Ruza 7571 (K, US). Edo Tachira, On Rio San Buena, 13-15 Mar. 1980, Liesner et al 9496 (LTR, MO). Bolivar, Represa Guri, ca. 0.5 km SSW of dam, 31 Mar. 1981, Liesner & Gonzalez 11031 (LTR, MO). Miranda, Dto Paéz, Fila El Guapo, 1-2 Jun. 1977, Gonzalez & Davidse 858 (LTR, MO, VEN). Edo Sulia; Colón, alrededores de Casiqua El Cubo, 6/2/1976, Bunting 6960 & Al Fonzo (LTR). Same locality, Bunting et al 7361 (LTR). TRINIDAD: Toco Road, Britton et al 1809 (A + GH, NY, US) Mt. Iarris, Cautial Range, Broadway 7567 (BM, F, G, K, NY, US). Trinidad, Savannah, Kostemans 15014 (U). Saig Stiertch, Broadway 9400 (A + GH, K, U). Botanic Garden, Lookarthill, Broadway 5691 (F, K). Fendler 284 (BM, K). Kuntze

1110 (NY). Swen's Park, June 1894, n.c. 5498 (NY). Trinidad & Tobago, used for general constructional work, Brook 12134, 12135 (K)..Arena Reserve, Marshall 12138, 12370 (K). Trinidad.

PANAMA: Panama, Rocky Slope on interamericana highway 4 miles NW of Bejuco, Duke 4581 (MO). Canal Zone, Victoria Fill, Allen 1754 (A + GH, F, MO, NY, US). Aneon Hill, Canal Zone, Piper 5553 (NY, US). Barro Colorado Island, C. Zone, Croat 5093, 8194 (F, MO, NY), 7858 (F, MO). Panama Prov., Correa & Dressler 698 (A + GH, MO, NY, RB, US). Cerro Jefe, Panama Prov., Allen 3436 (FI, G, K, MO, NY, P, US). Darien, Canal Zone, Duke 10658 (MO, NY), 13551 (MO). Near Chepo, Panama, Kluge 21 (F, US, WIS). Between Clayton & Corozal, Standley, 29071, 26389, 26574, 27552, 30279, 28678 (US). Darien, Rio Causi, Kirkbride & Bristan 1433 (MO, NY). Duke 5821 (MO). Canal Zone, Nee 11019 (A + GH, MO, XAL), Nee & Tyson 10889 (A + GH, MO, XAL). Rio Mamoni, Panama, Gomez et al 2933 (F, MO, XAL), Correa & Dressler 698 (Cabra, Pacora, Navy Project 431, 432 (WIS). In woods, Panama, April 1862, Hayes 718 (BM, KO. Panama, n.c. 10 (GOET). Colon, Holdrige 6396 (MO). Dariem, D'Arcy & Sysma 14573 (MO). Cerro Azul, Porter et al 4065 (C, F, MO, NY). West of Limon Bay, C. Zone, Johnston 17240 (A + GH). B. C. Island, C. Zone, Woodworth & Vestal 742 (A + GH, F, MO), Foster 2183 (A + GH, NY). Canal Zone, Nee 7366 (MO). B. C. Island, C. Zone, Carpenter 49 (F). Canal Zone region, Kirchner 713 (F). B. C. Island, Shattuck 713 (F, MO), 837 (MO). N. of Balboa, Gillespie P-27 (US). Canal Zone, Standley 31296 (US), 27388 (MO). Corozal, C. Zone, Kenoyer 658 (US). Juan Dias, Panam, Standley 30619 (US). Capra, Pacora, Yale Sch Forestry 430 (US, WIS). C. S. Christopherson 151 (US). Cerro Azul, Panama, Gomez et al 5053, 3433 (MO). Canal Zone, Al Gentry 3312 (MO). B. C. Island, Croat 4924, 5558, 5570, 8750, 5562, 5407, 4775, 5563, 56060 (MO). Darien, Cohn 1 (MO). Colon, Howen 234 (MO). Canal Zone, Duke 10593, 15190 (MO).

COSTA RICA: Basin of El General, San José, Skutch 4899 (A + GH, F, MO, NY, US). S.E. Buenos Aires, Barbour 1002 (MO, NY, US). E. of Palmar sur de Osa, prov. Puntarenus, Allen 5874 (A + GH, BM, US). Heredia, Puerto Viejo 10° 26 N 84° 01 W, Hartshorn 1064, 1168 (F). Puntarenus, Barbour 1002 (WIS).

NICARAGUA: Tast asli 3 km S.W. of Jalapaa, (alt. 700 m, dry lsope, also along stream. Tree 15 m), 8/4/1977, Neill 1693 (LTR). 1.8-1.9 km N. of base camp, S.E. of Cerna San Isidro, Rio Kama, Rio Escondido (Tree 35 m. 28 cm. d.b.H "Guayba negro"), Proctor et al 27133 (NY). Between Siuna & Limbaika, Zelaya, Seymour 4983 (A + GH, MO). 3 km E. of El Empalme, 42 km E. of Siuna, Zelaya, 14/8/1977, Danin 77-5-8, 77-5-5 (MO). E. Nicaragua, Shank, 15, 59 (WIS). Selaya,C. 248 km W. of Rio Wawa Ferry on Road from Puerto Cabezas to Rosita, ca. 1.4 km W of Cano Truslaya 14° 06 N 83° 44 W (elev. 90 m; steep slope of crumbling metamorphic rock; low evergreen forest tree 15 m. tall), Stevens & Krukoff 8686 (LTR). Zelaya, between 0.3 & 1.9 km N. of Lambaika 13° 29' N 84° 13' W (elev. 8-10 m, swamps and dense swamp forest near Rio Prinzapolka, large tree, 26/4/1978, Stevens & Krukoff 8291 (LTR).

HONDURAS: Colon, Hagen & Hagen 1351 (F, NY). Rodezno, Dept. Copan, Whitford & Stadtmiller 11,28(US, WIS). Tela, Atlandida, Standley 54490 (F, US). Camayagua, Williams 18056 (A + GH, F, US). Cortes, Yojoa, Allen 6165 (A + GH, F). Atlantida, Standley 56778 (F). Olancho, N. Catacamas, Standley 18692 (F).

BELIZE: Sibun River, Gentle 1613 (K, MO, NY, US). El Cayo district, near Vaca, Gentle 2515 (MO), 254 (A + GH, MO), 8648 (US), 9685 (F). Toledo between Orange Point & Moho River, Gentle 7630 (A + GH, F). Toledo, Temash R,, Gentle 5215 (A + GH, F, K, MO). Creek Valley, Gentle 3268 (A + GH, MO, NY). Stann Creek, Middlesex, Gentle 2854 (A + GH). Toledo dist., Big Creek, Monkey River, Gentle 4027 (A + GH, F, MO). Winzerting 111. 11 (US). Santa Maria, Cohune 18 (US). British Honduras, Kluge (WIS 7567). Belize, Project 42, ser. 45568; project no 54, ser. 45608 (WIS); project 55 ser. 45609 (US, WIS). Schipp 769 (A / GH, BM, F, K, MO, NY), 8470 (F). Belize, Bons & Yorests s.n. (BM, BP). Pine ridge, Siffee R., Peck 771, 939 (A + GH, K).

Bartlett 12870, 5. Mar. 1931 (F). Sibun R., Lamb 17, 18 (K). Concervater of forest (B.H.2) April 1947 (F). El Cayo and vicinity, Chanek 194 (F, K). Kluge 12 (US).

GUATEMALA: Peten, Saxactum to Clemente, Bartlett 12792 (A + GH, BM, F, NY, US), 12106 (US). Near Puerto Barrias, Isabal, Standley 73131 (F), 23763 (A + GH, NY, US), 24893 (US). Between Ixcan & R. Ixcan, Steyermark 49300 (F, US). Izabal, around Punta Palma, Steyermark 39799 (F). Izabal, Whitford & Staddtmiller 46 ([1]MAD, US), 28 (MAD). Peten, Lundell 2916 (A + GH, F, K, US, XAL), 2512 (A + GH, BM, F, K, MO). East of Izabal, Jones & Facey 3224 (XAL). Fao-Fydep 17 (MAD). El Peten, Lundell 16731 (A + GH). Izabaal, Rio Dulce, Steyermark 39392 (A + GH, F), 39540 (F). Izabal, in Montan de Mico, Steyermark 39081, 38081, 38281 (F). Izabal, along Rio Frio, Steyermark 41540 (F). Alta Verapar, along Rio Icvolary, N.W. of Finca, Steyermark 44771 (F). Hueheutenango S.E. of Borillas, Steyermark 49505 (F). Petén, Ortiz 960 (F). Izabal, 6 m E of Quirigua, Barbour (F, MO). Petěn, Carmelita, Egler 42-247 (F). Machaquila, Contleras 9785 (F). Near the Finca Sepacuite, Cook & Griggs 563, 625 (US).

MEXICO: Tenosique, Pennington & Sarukhan 9151 (K, NY). Oaxaca, Choapam, Mexia 9246 (A + GH, F, G, K, MO, NY, US), 9295 (F, MO). Vera Cruz, Zacuapan, Purus 3800 (A + GH, BM, MO, NY, US). Ejido Benito Juarez, Pennington & Sarukhan 9068, 9537 (K, NY). Oaxaca, Sousa 3662 (US). Liebm. 3400 (C, US, W). Vera Cruz, Roos 156 (US). Chiapas, Gomez 1287 (MO). Vera Cruz, Valdivia 1589, 462, 1484 (XAL). Vera Cruz: Glazada 4t al 2938 ([2]XAL), Vazquez 477 (XAL), Vazquez 530 (MO, XAL), Vazquez 54 (XAL), Orozco 237 (F, XAL), Calzada & Jic 2938 (XAL). Oaxaca, Rzedowski 34072 (MO, XAL). Palenque, Chis, Fuentes s.n. (XAL) Tabasca, Calzada & Aprellano 2222 (BM & XAL). Vera Cruz (N.N. Canshan), Calzada & Jic 3118 (XAL). Marada, Liebmann s.n. (K, holotype of T. excelsa). District de Txutepec, Oaxaca, no collector and number (K). Selva Lacundona, Chis, n. c., no number (K). Vera Cruz; Dorantes 3446 (XAL), Gomez s.n., 93215 (XAL), Chavelas & Zamera ES 4880, ES 4990 (XAL),

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1 Herbarium, Forest Products Laboratory, Center for Wood Anatomy Research, Madison, USA

2 Herbario, Instituto Nacional de Investigaciones sobre Recursos, Bioticos,

Leon s.n. (XAL). Oaxaca; Calderon 1356 (MO, XAL), Ezedowski 34072 (XAL), Sousa 2454 (XAL), 3662 (F), Williams (F, MAD). Chipaas, Miralnda 6223, 6348 (XAL). Balancan, Tabasco, Calazada 2349 (F, MO, XAL). Vera Cruz, Nevling & Gomez 783 (A + GH). Vera Cruz, Palo Dulce, Mell 681 (F). Chiapas, Gonzales 3500 (MO).

24. TERMINALIA GLABRESCENS

BRAZIL: Not localized: Riedel s.n. (A + GH, F, FI, G, K, W), 17072 (BM). Bowie & Cunningham 301 (BM). Burchell 5184, 5524, 7360 (K). Pará: Regiáo Garotire, Campos Gerais, Silva 730 (IAN). Maranháo: Sao Luiz do Maranháo, Ducke 355 (R, RB), Lisboa 2267(BM, G, US). Sao Luiz, Granga Barreto, Froes 28538 (BM, UB), 25628 (BM), Ducke 2187 (IAN). Barra do Corda, M.A.L. 2465 (RB). Cearai Araripe, Allemão & Cysneiros 575 (R). Herto Florestae de Pifajára, Kuhlmann 4 (RB). Pernambuco: Páre Ferro Lado, 18/12/1951, Ducke & Lima 77 (IAN, R, SO?. Grana, Zehntner 287, 297 (R). Bahia: Paraiba, Pohl s.n. (W), 3379 (F, LE, W). Fas do Carro Quebrado, Heringer 4026 (UB). Fazenda do Cipo, Santa Luzia, Standley 22776 (R), Barreto 9247 (F). Grinna, Lutzelbarg 2066 (M). Saldanha, Glaziou 9 (P). Fazenda Fluresta, Lutzelbarg 1905 (M). In Catingas Maracas, 1818, Martius (M, RB). 5 km SE of Maraú at the junction with new road N. to Ponta do Mutá, 2/2/1977, Harley 18514 (LTR). Goias: Jaragua, Heringer 14831 (UB). Road to Tocantinopolis, 10/8/1964, Prance and Silva 58638 (A + GH, K, LTR, NY, U, UB, US). 50 km. South Caiapônia, road to Jata;, Irwin et al 10007 (UB). Serra do Caiapo 29/6/66, Irwin et al 18007 (A + GH, C, K, LTR, NY, US). in Chapadões bei Ueioc-Ponte, Ule (73) 2930 (HBG, R). Sitio de Francisco Alves, St. Hilaire 875 (P). Chapada dos Veadeiros, Daurte 10755 (RB). Mato Grosso: 2 km. past Alto Garca to Goiania, 30/9/63, Maguire et al 55955 (BM, LTR, NY). 6 km. S.W. Xavantina, Ratter and Ramos 278 (K, NY, UB). Valede Sonhos, Ratter, Fonsêca

& Castro 2213 (K, NY, UB). Xavantina, South bank of Rio do Mortes, Ratter, Castro & Ramos 305 (K, NY, UB, RB). Mato Grosso: Santa Anna, da Chapadao, Malme 2365 (G), Malme 2249 (S). Smith 283 (R). Minas Gerais: Carmo de Rio Claro, Santa Rosa, Andrade 985 (R). Caeté, Hoehne 6093 (R). Ituiutaba, Fundão, Macedo 1147, (K, MO, US), 408 (MO, SP). Paraopeba, Heringer 3566 (A + GH, UB). Lagoa Santa, Glaussen 18437 (BM), 96 (F, G), 72 (K). Glaussen 73, 1593 (P), 305 (BM, BR, G), without number (BR, F, G, K). Cerato, St. Hilaire without number (P). Biribirg, Glaziou 19145 (BM). Fazenda, S. Jose, Varjao, Santos & Castellanes 24130 (NY). Patos, Duarte 3032 (NY, RB). Montes Claros, Kuhlmann 57 (RB). Granjas Reunidas, Nanes 407 (RB). Baneto 160 (RB). Fas. do Raggao, Heringer 3600 (RB). Parcopel, Heringer without number (RB). Guiaba, Schwacke 4487 (RB). Ouro Preto, Schwacke without number (RB). Serra da Piedade, Caeté, Reidel 38 (LE, W), 58, 65 (LE), 610 (LE, K). Rio de S. Francisco, Reidel 2640 (BM, LE). Rio Pardo, Reidel 437 (LE). Without locality, Reidel 34, 45 (LE). Região do Vale do Rio Paranaiba, 7/9/1957, Froes 33432 (IAN). Distrito Fedral: Gallery forest at Cateinho, 15 km. S.W. Brasilia 12/9/1964, Irwin & Soderstrom 6147 (A + GH, C, LTR, NY, U, UB). Low gallery forest, 50 km. E. Brasilia, 20/8 11964 Irwin & Soderstrm 5349 (A + GH, C, K, LTR, NY, UB, US). 10 km. N. Palanaltina, 2/10/65, Irwin, Sousa, & Santso 8879 (BM, K, LTR, NY, R, UB, US). Glaziou 1074 (BM). Rio de Janeiro: Ule 5814 (G, HBG, K) Near Urbem, Kuhlmann 533 (U). Villa Hona, Glaziou 11946 (A + GH, BR, F, G, K, LE, NY), 11947 (LE). Queimado, Glaziou, 10726 (A + GH, BM, BR, F, G, K, LE, NY, P, S). Ouro Preto, Glaziou 14686 (K, LE). Glaziou 12660 (BR, F, G, K, LE), 12661 (K, LE), 10711 (K). Sao Paulo: Santa Rita do Passa Quatro, Hemmendroff, 177, 186 (W), Kuhlmann 1579 (SP). Araraguara, Lofgren 8827 (SP). Casmorama, Tanabi, Gehrt s/n. (SP). Moji-Mirim, Hoehne s/n. (K, SP, US), 28337 (A + GH). Cabreva, Hoehne s/n (US). Itirapina, 11-11-1943 Lima s/n, (SP). Rod Rapouso Tavares, 17/9/74, Hatschabach 34811 (A + GH, LTR, NY, US), 21/10/70 24974 (C, LTR). Ipanema, Jreñe & Azevedo 103 (R). Fazenda Santa Genebra, Filho 10380 (RB). São Simão, Fazendo Bo Caiana (SP). Parana: Cianrte, Hatschabach 16702 16986 (C, F). Rio Grande Do Sul: St. Hilaire 873, 875 (P).

PARAGUAY: In Alta Planitie, Sierra de Amambay, Hassler 11364 (A + GH, BAF, BM, C, G, K, MO, NY, P, RB, S, US, W). Arillas Montes, Nuvera, Hassler 1364 (G).

25. TERMINALIA QUINTALATA

VENEZUELA: Estado Bolivar: Mesta del Jaua, Cerro Sarisarinam, alt 1320, 13/2/1974 (fl.), Steyermark et al 108911 (LTR, VEN 100080), 108860 (LTR, K, NY, VEN 100079). Verro Guanacoco, 3/3/1974, Steyermark et al 109739 (LTR, VEN 100078). Cumbre de Cerro Guaiquinima, a 10 largo del Rio Szczerbanari, alt 750 m, 23/5/1978, Tree 12 m tall, Steyermark et al 17225 (F, VEN 126918, 117401 (VEN 126508). Orillas del Caroni, Cerro del Salto Frepuchi, alt. 410, arbol 20 m, Mar. 1947, Cardona 2365 (LTR, VEN 55463), junto a lost randales karukuja in 9/10/1946 (fls) 1791 & 1793 (VEN 26831). Cumbre de Cerro Guaiquinima, Salto Szczerbanari y alrededores del Rio Szczerbanari, parte central del cerro, 22/2/1977 (fl.), Steyermark et al 11430 (LTR, VEN 120688). Cerro Auyan-Tepui, alt. 100 m, tree 8 m, Tanero 1949 (fl), Caradona 2612 (VEN). Rio Aveeii-Cilldail alt 350-400, 4/9/1954 (fl) (N.V.: Vonta-Yek), Bernardi 1689 (FI, K, NY, VEN). Rio Icabaru-Sabana Y Watas, Bernardi 6686 (G, NY). North Valley, Cerro Guaiquinima, Rio Paraguay, 10-12/1/1952 (Paratype of T. guaiquinimae), Maguire 33094 (BM, NY, VEN 41061). Along Rio Sarven, near Camp 9, alt. 1200 (N.V.: Churi-tepui), Wurdack 34328 (NY). Amazonas: Punta Baxia ou pe da Serra Araca, Rosa & Cordeire 1565.

GUYANA: Potaro River Gorge, below Amatuk Portage, May 19/1944, Maguire & Fanshawe 23551 (BM, BR, F, FDG, G, K, MO, NY holotype, P, U, US). Upper Mazaruni River, Kataima, alt 550, Tree 20 m, Maguire & Fanshawe 32640 (BM, NY, RB). Potaro River Gorge, Kaieteur Plateau, May-June (fls), Maguire &

Fanshawe 23459 (A + GH, BM, K, NY, P, U). Upper Mazarumi River Basin, Tree 8 m, 25/10/1960, Tillett & Tillett (F, LTR, NY). Kaieteur Savanna, Tree 5 m high, Maguire & Fanshawe 23313 (NY). Pakaraima Mts, Mt. Ayanganna, between Chenowieng & Chi-Chic alt. 1000 m, Maguire et al 40656 (BM, NY). Kaietuer Plateau, Forest Dept. F 1934, R 4670 (FDG). Marabelle Creek, Essq. R. Forest Dept. F 777, R 3513 (K). Sagaraimadai, Mazaruni R., Forest Dept. F 3314, R 6723 (FDG). Pakatũk, Palh, Potaro River, Jenman 1455 (K, U). BRAZIL: Ter. de Rondônia, Igarapẽ Preto, RADAM, Ponto 61-Q. XB-SC-20. (Arvore de 10 m. Fl. creme, Campo Cerrado), 4/7/1975, Ribeiro 1.099 (IAN).

26. TERMINALIA YAPACAN

VENEZUELA: Amazonas: Yapacana Savanna III, Cerro Yapacana, Rio Orinico, (Tree 8 m high, fruit brownish-red, dominant savanna & marginal tree) 1/11/1951, Maguire et al 30590 (BM, NY holotype, US, VEN 31340). Same locality, 20/11/1953, Maguire et al 36582 (A + GH, F, MO, NY, US, VEN 37739, W, 30480 (F, K, NY, US). 1 km E. of Maroa, Sabana de arena blanca & bosque enano, 125 m alt. (tree 3-4 m tall), 20/4/1970, Steyermark & Bunting 102847 (LTR, NY, VEN 84709). Yapacana savannas, NW base of Cerro Yapacana, elev. 125 m (Bushy tree 2-5 m), 16/9/1957, Maguire et al 41512 (F, LTR, NY, VEN 97504). Dept. Atabapo, Cabecera del Caño Cotua, Cerro Yapacana, 14/2/1978, Huber 1630 (VEN), 1689)LTR). 1 km E. of Moroa, Rio Guainia, Tree 2-7 m, Maguire & Wurdack 35686 (A + GH, G, NY, S), 35716 (BM, MO, NY, US). Canó Yapacana, 15/1/1958, U.V. & K.M. 6602 (VEN 42984). Alto Rio Orinico, Yapacana Savanna, at 125 m alt., Maguire & Wurdack 34525 (NY, P, U, BM, F, MO, NY, W). Atabapo, extensas sabanas al NE y E del Cerro Cucurito ribera SE del Medio Caño Yagua, 17 ENE 1979, Huber 3099 (VEN). Atabapo, Sabanas y bosques entre las cabeceras del Caño Cotúa, 3° 38' N 66° 52' W, Huber & Tillett

2994 (VEN). Dept. Atures, Sabana Ubicada a prox. 2 km al N del rio Guayapo, 27/7/1980, Huber 5543 (LTR). Same locality, 20/2/1979, Huber 3181 (LTR). Atures, 12 km al WSW del Cerro Autana, 16/7/1980, Huber 5567 (LTR). Sabanas de arena blanca a Unos 10 km al N del sector NE del Cerro Yapacana 3° 44 N 66° 48 W, 28/2/1980 (fl), Huber 4798 (LTR). Dept. Casiquiare, extensas sabanas ubicadas a uns 20 km al NW de Yvita, en las Cabeceras del Caño Pimichin, 11/2/1981, Huber & Medina 5669 (LTR). Depto Atabapo, Sabanas y bosques al E del Caño Perro de Agua derecho del rio Orinoco, 3 Nov.-10 Dec/ 1978, Huber & Tillett 288 (LTR). Same locality, 6/12/1978, Huber & Tillett 2890 (LTR). Atabapo, sabanita a unos 15' al Sur de Chipital, ribera izquierda (S) del bajo Caño Yagua, 16/6/1979, Huber 3094 (LTR). Atures, Sabana de arena blanca en la ribera N del rio Venturi, frente al caserio de Canaripo, 22/8/1978, Huber 2433 (LTR).

27. TERMINALIA GUAIQUINIMAE

VENEZUELA: Cerro Guaiquinima, Rio Paragua, Bolivar, alt. 1600-1700 m, 7/1/1952, Maguire 33008 (BM, NY, holotype, VEN 41059), 33008-A (VEN 41539). Same locality, Jan 10-12/1952, Maguire 33056 (BM, NY). Cerro Guaiquinima, Bolivar, 7/1/1952 Maguire 33000 (BM, NY, holotype of *T. virgata*, VEN 41058). North valley, 4/1/1952, Maguire 32952 (BM, NY, US). North valley, 1/4/1952, Maguire 32951 (BM, NY, holotype of *T. opacifolia*, S, US, VEN 41057).

38. TERMINALIA STEYERMARKII

VENEZUELA: Known only by the type specimens (see under the species).

29. TERMINALIA RAMATUELLA

COLOMBIA: Vaupés, Rio Atabapo, drowned river margin, frequent on the Colombian bank between San Fernando and Cacqual, 130 m, (bushy tree 7 m high, fruit tan), 18 Nov. 1953, Maguire et al 36264 (BM, LE, NY, S, VEN 37736). Same locality, flowering material, Maguire et al 36260 (A + GH, NY·). Confluencia de los rios Casiquiare & Guainia, lower R. Guainia, 13/3/1942: Williams 19791 (A + GH, MO, NY, VEN 9846). Vaupés, Rio Negro at Confluence of Rios Guainia and Casiquiare, Caño Ducuruapo, Schultes & Lopéz 9392 (A + GH, NY). Dept. Guainia, 1-2 km W of Rio Guaimia along Cano, 5 km N of Boca de Casiquiare, 5 Feb. 1980, Liesner & Clark 9120 (LTR, MO).

COLOMBIA or VENEZUELA: Rio guainia above its confluence with Rio Casiquiare, May 1854, Spruce 3498 (BM, GOET, K, LE, NY, W). Rio Guainia between Rio Negro and Comunidad, (bushy tree 5-10 m), 12 April 1953, Maguire & Wurdack s.n. (M, NY, RB, VEN 35542, W), 35549 (P, NY, VEN 37734).

VENEZUELA: Amazonas: Rio Guainia, on right bank of Caño San Miguel, just below Limoncito, (Riverine tree to 10 m high), Maguire et al 41879 (LTR, S). Dept. Atabapo, upper portion of Caño Caname (tree 5 m, low inundated forest), 3 May 1979, Davidse et al 17149 (LTR, MO). Dept. Casiquiare, Saban arbustiva temporalment secada, en la ribera s del medio Caño San Miguel, 23 Feb 1979, Huber 3374 (LTR.

BRAZIL: Amazonas: Içana bank of Rio Cubato, 19 Nov. 1945 Fróes 21421 (K). Basin of R. Negro Rio Cubata, 5 June 1942, Frões 12455/198 (A + GH). Rio Negro, São Felipe, Lago Acuene, Igapõ, 22/9/1952 (fls.), Fróes 28648 (IAN). R. Negro Içana Uacaná river, lowland restinga, 22 Apr. 1974 (IAN). Ca. 150 km above Barcelos, R. Negro, 1978, Madison et al 6215 (F).

30. TERMINALIA VIRENS

VENEZUELA: Rio Atabapo, San Fernando, Feb. 1971, Medina 544 (VEN 84016). R. Atabapo, San Fernando, Feb. 1971, Medina 544 (VEN 84016). R. Atabapo, Cerca Isla Zapo, 18 Aug. 1964, Vareschi & Jaffe 8000 (VEN 49789). Savanna I, NW base of Cerro Yapacan, 10 Sept; 1957, Maguire et al 41501 (VEN 97500). Same locality, Maguire et al 41493 (LTR, VEN 97505). Occasional along Cano Yapacana, Maguire et al 30764 (BM, IAN, K, VEN 31339). Margen de una laguna, Cerca de Yarita, 30 Jan. 1942, Williams 14078 (VEN 9847). Same locality, 31 Jan. 1942, Williams 14127 (VEN 9848). Cano de Moyo, 22 May 1975, Berry 580 (MO, VEN). Cano Yapacana, (small or medium riverine tree, occasional in low bush around laguna) 9 Nov. 1953, Maguire et al 36556 (F, MO, P, RB, VEN 37738, W). Cano Yapacana from laguna to mouth at 125 m alt., 17 Mar. 1953, Maguire & Wurdack 34606 (BM, holotype of Ramatuella maguriei, S, VEN 37730). 15 km above San Fernando, Rio Atabapo, 17 Oct. 1950, Maguire 29258 (NY, holotype of Ramatuella latifolia, VEN 31338). Cerro Yapacana, Savanna, N.W. base of Cerro Yapacana, Maguire et al 41493 (LTR, VEN 97505). Atabapo, S.E. bank of the middle part of Cano Yagua, Davidse et al 17442 (VEN). Caño Caname, Dept. Atabapo, Huber et al 3689 (VEN). Atabapo, white sand savannas on the northern bank of the lower part of Caño Caname, 2 May 1979, Davidse et al 17075 (LTR, MO). Atabapo area between the western base of Cerro Yapacana and the headwaters of Caño Cotúa, 6 May 1979, Davidse et al 17220 (LTR, MO). Cano Yapacana, 1953, Maguire & Wurdack 34569 (A + GH). Dept. Atabapo and Casiquiare, 10-24 Nov 1980, Pinate & Mondlfi 1028, 1013 (LTR). Atabapo, 18 Ene 1979, Huber 3126 (LTR). Atabapo, saban entre el Caño co Cotua y el Cerro Yapacana, 25 May 1978, Huber 1785, 1797 (LTR). Cano Caname, Atabapo, 29 Apr. -4 May 1979, Huber et al s.n. (LTR). Atabapo, 14-28 Feb. 1978, Huber 1555 (LTR). Amazonas A lo largo del rio Temi, alrede dores de Yavita, 22 Apr. 1970 Steyermark & Bunting 102965 (LTR).

VENEZUELA or COLOMBIA: Rio Guainia above its confluence with Rio Casiquiare, Nov. 1854, Spruce 3758 (BM, GOET, K, LE, W, lectotype); from type locality, Schultes & Lopez 9359 (A + GH, IAN).

BRAZIL: Amazonas: Rio Curicuriary, tributary of Rio Negro, 23 Nov. 1936, Ducke 34638 (K, S); Same locality, 20 Nov. 1936, Ducke 34639 (K, S); Same locality, 22 Feb. 1936, Ducke 34640 (INPA, K, S). Rio Negro, Enuixy, Matezinho, 18 May 1947, Froes 22340 (BM). Cuadricula, SA-20-X-Aporto 02A Rio Xeriuini, Zona de Igapóa Lagos, 17 Apr. 1974, Pires & Leite 14025 (LTR). R. Xeriuini, Caatinga Seca, Pires et al 13992 (IAN, LTR).

31. TERMINALIA CRISPIALATA

BRAZIL: Amazonas: Caatinga ad Igarape Juraxare affl. Rio Vaupes, 2 Nov. 1932, Ducke 25024 (K, isotype); from type locality, 29 Sept, 1935, Ducke 34637 (INPA, RB, S), Ducke 221 ser no 31948 (NY). R. Negro, R. Tea 40 km above mouth, village Bacuri, Kubitzki et al 79-238, 79-239, 79-242 (INPA). Rio Içana, Urumuturu mata de caatinga, 26 Mar. 1952, Froes 28040 (BM, LTR, UB). Rio Aracá, subtributary of Rio Negro, Campinarana, 24 Oct. 1952, Fróes & Addison 29040 (BM, LTR, UB). R. Xeriuini Caatinga Seca, Pires et al 14025 (INPA, RB). Basin of Rio Negro, R. Ueiuxi, 100-200 km above mouth, black water flooded savanna forest on sand, 21 Oct. 1970, Prance et al 15471, 15504 (INPA, LTR); Same locality, 8 Nov. 1971, Prance et al 16168 (INPA, LTR).

VENEZUELA: Amazonas: In Caatinga about Yapacana Savanna I, Rio Orinoco, 7 Jan. 1951, Maguire et al 30796 (NY, holotype of Ramatuella obtusa, VEN 31337). Savanna, right bank Rio Pacimoni 50 km above hoca, 7 Feb. 1954, Maguire et al 37562 (NY, VEN 37742). Deto Atabapo, Caño Caname, 29 Apr.-4 May 1979, Huber et al 3744 (LTR), Same locality, 3 May 1979, Davidse et al 17146 (LTR, MO). Rio Içana, Tunui, Pé da Serra, 24 Oct 1947, Murca & Pires 764 (IAN.

COLOMBIA: Dept. Guainia, Ca. 5 km N. of Boca de Casiquiare (where Rios Negro, Guainia and Casiquiare join), 5 Feb. 1980, Liesner & Clark 9079, 9082 (LTR, MO).

B. BUCIDA

1. BUCIDA MOLINETI

BAHAMAS: Andros Is., Red Bays (April 17) and Frech Creek (June 12), 1890, John & Northrop 502 (BM, F holotype of T. spinosa, G, K, NY). Arndros, June. 28-31 1910, Small & Carter 8770 (K). Bahamas, local name "Parks doush-boy", 13/5/1952, Baker s.n. (K). Great Bahama, Eight Mile Rocks, Feb. 5-13 1950, Britton & Millspaugh 2566 (A + GH).

CUBA: 1860-1864, Wright 2573 (BP, G, K, W). Las Pailas, 5 m high, Eggers 5438 (GOET, K). Palm Barren, Santa Clara, Britton & Cowell 133332 (K). Isla de Poinos, Borhidi et al s.n. (BP). Wright 2773 (BP). Prov. Mantanzas, Canasi, Lomas de Galindo, Sept. 1969, Bisse et al 18373 (JE, isotype of Bucida ophiticola); same locality, May 1974, Borhidi & Risco s.n. (BP). Oriente: Santiago, in litore ad Santiago bay, 12/6/1918, Ekman 9211 (G). Santiago, W. shore of Santiago bay on the very beach, rare, (arbor parva), 22/6/1914, Ekman 1424 (G). Santa Clara: in coastal thickets in sandy salty ground, 28.3.1924, Ekman 18867 (G).

BELIZE: 1.5 miles NW of Belize, Northern Highway Marshy Savanna, 24 May 1973, shrub to 5 ft., Dwyer 10703 (MO).

2. BUCIDA BUCERAS

MEXECO: Zona Comprendida entre los rios Chancalah, Chocol-Jahito & Tulija, Chis, Pennington & Sarukhan 9178 (K). Camp. Cerca De Champán, Pennington & Sarukhan 9350 (K). Camp Experimental Forestal "El tormento", Escár Cega, Pennington & Sarukhan 9383 (K).

GUATEMALA: Santa Teresa, Subin River, Lundell 2785 (K). Tikal dist. Peten, Cook & Martin 187 (C).

BELIZE: Botanic Station, Hummel s.n. (K). Belize, June 1898, Camptell s.n.

(K). El Cayo vicinity, Chanek 147 (K). El Cayo vicinity, Gentel 2324 (K). Coro Zal district, Gentel 991 (K). B. Honduras, Peck 390. Jacinto hills, Schipp 1226 (G, K). Medium sized tree growing at edge of mangroves known locally as Bullet tree "Rare", Schipp 759 (G, K). Mullens River, 19/3/21 Hummel s.n. (K).

CUBA: Isla de Poins, Curtiss 479 (G, K). In Savanna Mascariges et Matenzae 1824 Martius s.n. (G, K). Sierra de Nipe, Oreiente, Ekman 6006 (K). Santiga bay, Oriente, Ekman 9210 (K), Santa Clara, Comps 109 (K). Matangas, Rugel 55 (K). Oriente, Bayate ad Rio Jagua, Ekman 7371, 8574 (G, K). Havan, 1831, Sagra 172 (G). 1860-1864 Wright 2572 (G, K). Bayate ad Rio Piedra, Ekman 6258 (G, K). Bayate ad Rio Ripam, Ekman 2436 (G, K). Soledad, Santa Clara, Jack 7009 (G, K). Santa Clara, Urban 4975 (C). Cuba, Benzon 263-6074, 263-60436 (C). Habana, Borhidi & Muniz s.n. (BP). Oriente, Borhidi et al s.n. (BP).

JAMAICA: St. Catherine, Skelding 3581 (K). Jamaica, Hooker 1843, 1886 (K). Jamaica, 1850, Alexander s.n. (K). Jamaica, Harris 1909, 10816 (K). Edge of heart Moraes, Negiri, Harris 10244 (K). Jamaica, Wright s.n. (K). St. Catherine 1957, Yuncker 17347 (G).

HAITI: Presquiledu Nord, Ekman 4020 (G, K). Vicinity or Port de Poix, Leonard & Leonard 11191 (K).

DOMINICAN REPUBLIC: Sobre rocas, Orilla del rio Chavon, La Roman Liogier 20728 (K). Samana vic., Abbot 2224 (C). Santo Domingo, Ekman 14587 (C, S). Fuerter 116 (G). Poiteau in 1802 (G).

PUERTO RICO: Yayco, 1880, Carber 58 (K). Puerto Rico, Mr & Mrs Lteller 1270 (K). Prope Barre Ionesa, Sintenis 6720 (C, G, K). Jajarto, Fajando fruticetis litoralibas, Sintenis 1652 (BP, G, K). Prope Mayaguez ad Guanajibo, Sintenis 731 (BP, G, K). Portorico, Sintenis 2857 (K). Portorico, Eggers 1326 (W). Rincon, Sintenis 5805 (G). Grigri, Herb. de Ventenant (G). Nov. 1902, Heller.

LESSER ANTILLES: St. Thomas; Eggers 132 (BP, G, W). 16.5.1906, Lovenlund s.n. (C). Plant of Ind. Occid., 1905-06, Raunkiaer s.n. (C, G). St. Thomas, 10.2.1906, Sydrideu, s.n. (C). Barbados, April to Jun. 1895, n.c. (K). Virgin Is., Beard s.n. (K). St. Croix, May 29-1871, Eggers s.n. (C). St. Croix, 31/3/1875, Eggers s.n. (C). St. Croix, Liebmann s.n. (C). St. Croix, Jun. 1871, Eggers s.n. (C). St. Thomas, 3 and 5 Jan. 1896, Cuepaulacu 147, 124 (C). St. Croix, Ilansen 73 (C). St. Thomas, Ostenfeld 120, 479 (C). St. Thomas, 11.12. 1905, Raunkiaer 2274 (C). St. Jan, Coralbas s.n. (C). St. Croix, D'Arcy 4723 (C, MO). St. Thomas May 1932, Fugerrahaub (C). St. Croix, Joerh s.n. (C).

3. BUCIDA MACROSTACHYA

GUATEMALA: El Rancho, 28 Dec. 1907, Kellerman 7744 (F, holotyoe; G).

MEXICO: Chacalpa Estate, Liebman S401 (BM, C, holotype of Bucida megaphylla).

BELIZE: SW of Cayo, summit of ruins, tree 60 ft. tall, Dwyer 120 (MO).

C. BUCHENAVIA

1. BUCHENAVIA OCHROPRUMNA

BRAZIL: Amazonas: Maues, Limão-Limeeiro, Rodrigues & Coelho 7706 (INPA). Baixo dio Negro, Ilha do Gauião, Byron 67-80 (INPA). Rio Cuieiras, Igarapé da Cachoeira, Rodrigues 6037 (INPA). Manãos, Igarapé da Cachoeira Grande, "igapó profunde inundato, arbor parva", 28 Mar. 1937, Ducke 445 (INA, INPA, K, NY, R, S, US). 28 Mar. 1937, Ducke 35172 (K, RB). Rio Negro, Baia, Elias et al 486 (INPA, UB). Igapó-Rio Negro, Arara, Loureiro et al s.n. (INPA). S. bank of R. Negr., Baia de Bueussu, 15 km. above Manaos. Sandy river beach, tree 4 m., Prance et al 10440 (INPA, S). Manaos "igapo ad faucem fluminis Tarumá Grande", 7 Apr. 1932, Ducke 25019 (K, RB). Rio Negro, in the vicinity of Barcelos, 19 Apr. 1952, Fróes 28438 (BM, IAN). Region of Parintins, Lago do Jurutí, 18 Jan. 1957, Fróes 33069 (BM, IAN). Maues, vio Parauari, Igapo, Colho & Lima 392 (INPA). R. Taruma mirim, upstream Manaus, Kubitzki 74-28 (INPA). R. Univini, Iago de água Pret, 22/4/1974, Pires et al 14114 (INPA, LTR). 14117 (LTR); 23/4/1974, Pires et al 14163 (IAN). Manaus, r. Negr. rio Ariau ., Cavalcante 3246 (INPA). Rio Preto, Rodrigues & Coelho 5849 (INPA). R. Uatumá, Ivo et al 3383 (INPA). Borba, Margem do rio Aari, Rodrigues 1572 (INPA). Manaus, Margem do rio Taruma, Rodrigues & Caelho 2423 (INPA). Manaus, rio Cuieiras, Rodrigues & Caelho 4029 (INPA). mouth of R. Gueiros, Anderson, ABA 90 (INPA). Rio Uatuma, ilha Itaqui, Cid et al 192 (INPA, LTR). Manaus-Itacoatiara Highway, Rio Urubu. Prance et al 4731 (INPA, M, R, S). Barcelos margem de Fgarapé, Duarte 7060 (M, RB). Aramanahy, Rio Tapajoz inter. (ovr pará) ad ripes. Kuhlmann 21473 (RB, S). Mana Road. Flooded river margin, shrub, growing in water, Manaus, Prance et al 11545 (INPA, S). Manés, Campbell et al P22012 (M, S). Manaus, Porta Negro, Prance et al 4664 (INPA, LTR, R, S). Manaus, Igarape da Cachoeira Grande, Igapó, Ducke 1977 (A + GH, NY, R). Rio Acari (Acary), varzea restinga, Cooper III (UB, US). Camanaus, Rio miua mata alta, Nascimento

829 (US). Pará: Municipia de Oriximiná vio Trombetos, 16/7/1980 Cid et al 1525 (LTR; 23/7/1980, Cid et al 1745 (LTR). T. F. de Roraima, Rio Xoriuini, Ponto, Santos 196 (LTR). Lago de Taro, Ducke 13586 (RB, S). Lago de Jurenty Velho ribro, Ducke 21350 (S). Near Santarém, Jan. 1850, Spruce 309 (M, lectotype) and without n. (BM, FI, G, K, W). Santarém, by river, "bush of 10 feet", Jan. 1850, Spruce 619 (K). Lago Cucari, plateau of Santarém, 15 Apr. 1955, Froes 31671 (BM, LTR). Igarapé Cucari, Plateau of Santarém, 15 Apr. 1955, Froes 31773 (BM, LTR). Mata da Pirelli, Ananindeua, 8 Jan. 1958, Silva 501 (BM). Rio Aramun, Almeirim, 2 Sept. 1918, Ducke 17287 (BM). R. Trombetas, Pena s/n (IAN).

COLOMBIA: Rio Negro, El Castillo, Schultes & Lopez 9302 (US).

2. BUCHENAVIA PARVIFOLIA

BRAZIL: Rondonia, Basin of Rio Madeira, Prance et al 8798 (A + GH, F, INPA, NY, P, R, S, U, US). 10 km above Fortaleza, Prance et al 8551 (A + GH, F, NY, P, R, S, U, US). Serra de Dedal, Pará, Ducke 17693 (RB). Breves, Pará, Ducke 12386 (RB). Manaus, Reserva Forestral Ducke, Aluizio 273 (INPA). Manaus - Caracari, Mello et al 21 (INPA). Manaus, Amazonas, Rodrigues 5464, 5466 (INPA). Manaus, Amazonas, Rodrigues & Osmarino 5697 (INPA). Manaus, Rodrigues & Loureiro 5736 (INPA). Manaus, Reserva Florestal Ducke, Rodrigues & Osmarino 8317 (LTR). Belém, Parà, 8/1/1950 Gnedes 239 (BM, IAN). Bosque Rodrigues Alves, Belem, Guedes 239 (BM, IAN). Bosque Rodrigues Alves, Belem, Guedes 233 (BM). Manáos,in non flooded forest, 14, June 1933, Ducke 25016 (INPA, K, R, RB, S). Cachoeira Grande, Manaós, in non-flooded forest, 3 Jan. 1937, Ducke 374 (K, MO, NY, R, S). Sapo Paulo: Salesopolis, Estacao Biologica de Boraceia, Perto do Rio Claro, 27/4/1966, Mattos 13570 (IRRN, isotype of B. rabelloana); Same locality, 15/3/1958, Kuhlmann 4335 (SP); Same locality, 26 Sept (April in original description) 1966, Mattos 13855 (SP).

Paranzpiacaba, 23/5/1946, Kuhlmann 3182 (SP74124); 19/8/1946, Kuhlmann s/n (SP 157742); 26/10/1946, Kuhlmann 2840 (LTR). Manaós, Rio Tarumá, Fróes 26580 (BM). Pará, Vila Braga, Rio Tapajoz, 23 Sept, 1922 and 24 May 1923, Ducke 17686 (K, S, isolectotypes).

FRENCH GUIANA: Saül, Monts La Fumee, 1 Dec. 1982, Mori & Boom 15300 (LTR).

GUYANA: Basin of Essequibo River, near mouth of Black Water Creek, Smith (F). On way to 2nd. Plot., Forestry Dept. No 5, Field No G255, Rec. No 7231 (NY).

VENEZUELA: T. F. Amazonas, Estacion Experimental de Sta. Barbara del Orinoco, Berry & Chesney 2061 (MO, VEN). Amazonas, Cerro Sipapo, 24 Nov. 1948, Maguire & Politi 27370 (BM, IAN). Southeastern base of Cerro Duida, Amazonas, Steyermark 57794 (NY). Atures, Virin rain forest along Rio Cataniapo, 7/5/1980, Steyermark et al 122124 (LTR). Atabupo, Rio Cancucuncima 28-30/Jan. 6-8 Feb. 1982, Steyermark et al 125858 (LTR).

COLOMBIA: Comesaria del Vaupes, Gutierrez & Schultes 774 (US). Amazonas, R. Vaupés, Cerea de Mifaflores, en Trocha Miraflores - Lago del Dorado an bosque de tierra firme. Roa 265 (INPA).

3. BUCHENAVIA TETRAPHYLLA

BRAZIL: Bahia, 3/3/1972, Anderson et al 36518 (G, LTR), 7/3/1972, Anderson et al 36767 (LTR). Mato Grosso, 10/9/1972, Rater et al 2405 (LTR). Goias, 18/3/1973, Anderson 7448 (LTR). Amazonas, 25/3/1978. Anderson 12249 (LTR). Amapa, 17/9/1960, Irwin et al 48328 (LTR). Piaui, 30/7/1964, Castellanos & Duarte 576 (LTR). Amazonas, 11/9/1973, Prance et al 17736 (LTR, M). North Goias, Prance & Silva 58639 (LTR,M). Prope Barra, Prov. R. Negro, Spruce 1112 (M), 1662 (IAN, A + GH, BP, /), 1661 (W). Amapa, Pires et al 50501 (LTR). Elta Suclia videtur, Herb. Sohreberianum (M). Amazonas, Fores 25068 (IAN). Rio Negro Prov., Spruce 1652 (P). Rio Janeiro, Glaziou

13803 (C, P), 10721 (P), 10719, 10722, 10723, 10725 (C). Maranhão, Frões 25691 (INA, PN, NY). Amazonas, Froes 25183 (INA). Piauhy, Gardener 2838 (NY, W). Between Parana da floresta and the mouth of R. Branco, 26/6/1979, Alacar 35 (LTR). Prope Panure ad R. Vaupēs, Oct. 1852-Jan. 1853 (BP, W). Manaus, Amaz., 12/7/1882 Herb. Schwacke III 613 (GOET). Providenoia, M. Gerais, 12/7/1951 Bootos s.n. (RB). Pará, Mosqueiro , 20/6/1943, Ducke 1262 (A + GH, IAN, NY, R, US), 17684 (RB) Serra de Bateuite, Guaramirango, Pará, Ducke 17681 (RB). Braganca, Pará, Ducke 17685 (INPA, RB). Ceará, Guedes 499 (RB). Jacobina, Bahia, Martielli 5214 (RB). Ceara, Allemão & Cyseiros 578, 579, 580 (R). M. Grosso, Mealme 2456 (R). Bahia, Anderson et al 36767. Midddle R. Negro, Schultes & Lopez 8933 (US). Ceará, Tose 1175 (RB). Minas Gerais, J. G. K. 2440 (RB). No locality, Xavier 1299 (RB). Manaos, Schwacke 3779 (RB). Rondonia, Cordeiro 936 (IAN,LTR). Faz. Modelo, Tigipio, Lima 49-389 (IAN).

BOLIVIA: Santa Cruz, Steinbach 6406 (GOET, MO). Lapas, Larecaja, Krukoff 11074 (A + GH, MO, NY). Beni, Prov. Ballivian, R. Yacama, Beck 5615 (LTR).

FRENCH GUIANA: Cayenne, Le Blond 403, 437, (P). Cayenne 1792, Le Blond (P). Cayenne, Benoist 2 (P). Herb. Tircher (LE). Cayenne, 1839, Le Prieur (F). G. Francaise, 1821, Perrotteo s.n. (F). Grant's Road, Matabon, Broadway 536 (US). Cayenne, 15/12 1978, Grenand 1734 (LTR).

SURINAM: Suriname, Hostmann & Kappler 1151 (W). For. Res. Sectie O, tree no 30, B.W. 4661 (MO, RB), 6261 (NY, RB); 6000 (RB).

COLOMBIA: Amazonas, Feb. 1977, Roa 665. Vaupes near mouth of Rio Kudayari, Zarucci 1925 (US).

VENEZUELA: Salia, Miranda, entre la via El Consejo El Pensado y el limite con el Edo Falcōn, 21-22/5/1980, Bunting 9302 & Stoddart (LTR). Dto Fedral, Regio forestral de Bejarano, Delgado 508 (VEN 49388). Bolivar, along R. Karuai, W. of La Laja, Steyermark 60780 (VEN). Cerro de la Mesa, Aragua, Pittier 15718 (VEN 49387). Lara, 4 km from Sanare road from Quiber, Wrieiier 79 (VEN). 2 km autes de Sanare, Lara, Smith 3081 (VEN). Cruz Parades, Obispos, Barinas, Berti & Lezama 2960, 2982 (VEN). Caserio Imataca, via Campamento R. Grande, Blanco 216 (VEN 73913). Bolivar, 24-48 km N.E. del Carerio Los Rosas, Blanco 231 (VEN 73908). Miranda, Bosque de los Guayabitos, Aristeguieta 2757 (VEN 41036, W), 3038 (VEN 42695). Bolivar, entre San Felix y Puerto Ordaz, Steyermark 94265 (VEN 59590). Amazonas, Orinoco R., S. Isla del Raton, Breteler 1966 (MO), 4735 (F, U, US). Entrada Caserio de Pica-Pica, Aristeguieta et al 6853 (NY, US). Aragua, Steyermark 89736 (US). Cerro Cotarral (El Vigra), forested slopes along S. side of R. Paragua, Steyermark 86895 (NY). Miranda, Alto Hatillo, Steyermark & Berry 111998 (NY). Tucupita, D. Amacuro, Davidse & Gonzalez 16346 (LTR). Anzoategui, Liberated, 27/11/1981, Davidse & Gonzalez 19488 (LTR, MO). Est. Tachira, 10 km of La Fundacion, Liesner & Gonzalez 10349 (LTR). Atures, 17/4/1978, Davidse & Huber 15245 (LTR). Bolivar (N.V. Pala de danto redondo), Berti 771 (IAN).

PANAMA: Rio La Meastra, 0-25 m alt, tree 8 m, Allen 35 (A + GH).

COSTA RICA: El General valley, Finca vol can Angel, Schubert & Rogerson 750 (F).

CUBA: E. Cuba, Gill & Whitford 91 (MAD). Pinar del Rio, Leon 13477 (P), 14717 (A + GH, US). Santa Clara, Jack 6793 (A + GH), 7009 (P). Isla de Pines, Curtiss 376 (A + GH, F, LE, M, MO, P, US). Santa Clara, Rhder 1131 (A + GH, P). Cuba, Wright 1240 (NY, W). Sagra 1828 (LE). Poeppin s.n. (LE). Oriente, Santa Ana, Shafer 8585 (A + GH, NY, US). Los Palacios, Pinar del Rio, Shafer 11929 (MO, NY, US). Oriente, Leon 15486 (A + GH, NY, US). Pinar del Rio, Leon 4380 (A + GH). Oriente, Ekman 8563 (F, US). Pinar del Rio, Roig 1085 (F). Isle of Pines, Britto & Wilson 14857 (US). Sierra de Micora, Oriente, Ekman 6763 (US). Pinar del Rio, Killip 13546 (US). St. Clara, Leon & Roca 8109 (NY). Isla de Pinos, Ule 376 (NY). P. d. Rio, Leon & Niorow 4380 (NY). St. Clara, Leon 348 (NY). Oriente, Ekman 7475, 8588 (NY). Oriente, Leon 16743 (NY). Habana, Ekman 10982 (NY).

JAMAICA: Clarendon, Proctor 27852 (A + GH, U, US). Ayton, Mlarris 6464 (F).
HAITI: Cerea Carrajal, Holdrige 1859 (F, NY, US). Dept. du Nord, Leonard 1549 (A + GH, NY, US). Plaisance, du Nord, Leonard 9394 (US). Massif de la Pelle, Ekman 6005 (NY, US).
DOMINICAN REPUBLIC: Moncion Dist., Mote Crity Prov., Valeur 1033 (C, US), 239 (US). Rio Arriba de Norte, N. San Juan, Howard 8956 (NY, US). Seibo, Higuey, Howard 9826 (A + GH, NY, US). En bosque Manabao, Liogier 20084 (F, NY). Santiago, Jimenez 1040 'US). Santo Domingo 12153 (A + GH), 12605 (A + GH, F, NY, US). Hodge 2444 (A + GH). Valeur 239 (G).
PUERTO RICO: Las Marias, Sintenis 5990 (M, MO, W). Prope Cabo - Raja, Sintenis 758 (M). San Patricio, Yagoya, Sintenis 4537 (BAF). Portorico, Navy Project, tree no 171, 172 (MAD); Ego 160 (MAD); Kramer 45 (MAD). Las Marias, Sintenis 5990 (F, GOET, LE, NY, P, US). Maricao forest, Wagner 1503 (A + GH, U). Yabacou, Wagner 923 (A + GH). Guajataca, Little (A + GH, F, NY). Britton & Britton 8093 (A + GH, NY, US). Baguas, Heller & Heller 269 (F, NY, US). Truillo Alto, Gegory LEG-164 (US). Caribian National Forest, Holdridge LRG-235 (NY, US); Same locality, Gegory LEG 163 (US). Sierra de Haguabo, Stevenson 5234 (US). Maricao National Forest, Duke 7007 (US). San Germãn, Miller 1643 (US). San Sanbestian, Sargent 266 (US). Elverde, Luguillo Div., Navy project tree 170 (US). Alade Pedra, Britton et al 2425 (NY, US), 7492 (NY). Little 13083 (NY).
LESSER ANTILLES: Montserrat, Ryan s.n. (BM, C holotype of Bucida capitata) Tabago, Broadway 4447 (F, M). Martinique, Hahn, 1464 (P); 1787, Prest s.n. (G). Virgin Is., Little 26059 (NY, US). Tortola, Virgin Is., Shafer 1146 (NY, US). Irois Pitins, LLoyd 766 (NY). Trinidad, Biley 12336 (NY); Harri 6464 (NY). Guadeloupe, Duss 3095, 3096, 3685 (NY).

4. <u>BUCHENAVIA</u> <u>KLEINII</u>

BRAZIL: Santa Catarina: morro do Rio Vermelho, 12/3/1969, Klein & Bresolin 8241 (LTR). Mato do Hoffmann, Brusque, 13 Jan. 1951, Klein 22 (BM; S, holotype). Cunhas, Itajai, 10 m., 29 Nov. 1954, Klein 870 (BM); same locality, 8 Feb. 1955, Klein 1144 (BM); same locality, 10 Mar. 1955, Klein 1182 (BM, NY); same locality, 26 July 1955, Klein 1479 (BM). Braco Joaquim, Luis Alves, Itajai, 300 m., 14 Dec. 1954, Klein 924 (BM); same locality, 350 m., 13 Jan. 1955, Klein 1075 (BM, RB, US). Horto Florestal I.N.P., Ibirama, 250 m., 27 Dec. 1954, Klein 940 (BM,NY, RB, US). Same locality, 300 m., 4 Feb. 1956, Reitz & Klein 2568 (BM). Morro da Fazenda, Itajai, 50 m., 17 Mar. 1955, Klein 1232, (BM, NY, SP). Pilões, Palhoca, 300 m., 11 Jan. 1957, Klein 2158 (BM, NY). Mata da Companhia Hering, Bom Retior, Blumenau, 250 m., 15 Dec. 1959, Klein 2342 (BM, G, M). Morro Spitzkopf, Blumenau, 700 m., 11 Mar. 1960, Klein 2424 (BM, G, M). Morro da Ressacada, Itajai, 250 m., 29 Mar. 1956, Reitz & Klein 2915 (BM, NY, US). Matador, Rio do Sul, 350 m., 27 Jan. 1959, Reitz & Klein 8319 (BM). AltO Matador, Rio do Sul, 800 m., 30 Dec. 1958, Reitz 6126 (BM, F, G, SP). Vargem Grande Lauro Müller, 350 m., 20 Feb. 1959, Reitz & Klein 8494 (BM). Paraná: Serriuha, Hatschbach 49369 (M). Rio de Cedro, Hatschbach 49368 (M). Serrinha, Hatschbach 18271 (C, F, MO, NY, S, US). Guaraquecaba, Rio de Cedro, Hatschbach 18512 (P, S). Guaraquecba, Rio do Cedro, Hatschbach 18512 (A + GH, C, F, INPA, MO, NY, SP, US). Col.Floresta, Hatschbach 20209 (C;.MO). Sao Paulo: Sao Paulo, Nativa no Jardim Botanico, Oswald, Handro s/n. (A + GH, M, NY, U, US). Santa Isabel, Igarata, 12 Dec. 1951, Kuhlmann 2751 (SP, holotype of <u>Buchenavia</u> <u>igaratensis</u>).

5. <u>BUCHENAVIA</u> <u>PALLIDOVIRENS</u>

COLOMBIA: Valle: Costa del Pacifico, Bahia de Buenaventura, Quebrada de

San Joaquin, 0-10 m, 23 Feb. 1946, Cuatecasas 19939 (isotypes BM, U, US). Rio Calima (region del Choco), La Trojita, Tree 30 m x 30 cm (sterile), Cuatrecasas 16584 (F). Valle Del Cauca: Buenaventura, 15 Nov.- 6 Dec. 1979, Rooden et al 545 (LTR).

BRAZIL: Amazonas: Rio Vaupés, Panure, Catinga, "Arbusto", 15 Nov. 1947, Pires 1043 (BM). Pará: Região do Jari, 15/10/1970, Silva 3362 (LTR).

VENEZUELA: Ivic Study Site 4 km NE of San Carlos de R Negro, Amazonas, Liesner 8654 (LTR, MO). 0 to 2 km N. and NE San Carlos de Rio Nègro, Liesner 7559 (MO).

PERU: Amazonas: Quebrada Chi Chijam entsa, Rio Cenepa, Monte, Ancuash 432 (US).

6. BUCHENAVIA SUAVEOLENS

VENEZUELA: Amazonas: San Carlos de Rio Negro, 20 km S of confluence of R. Negro and Brazo Casiquiare 2/4/1981, Clark 7848, (LTR). On the rivers Casiquiare, Vasiva and Pacimoni, 1853-54, Spruce 3198 (BM, BP, C, GOET, K, LE, W). On the banks of Lake Vasiva, also observed in Rio Pacimoni, Dec. 1853, Spruce 3190 (K, P). Rio Sanariapo, 2 July 1942, tree 15-18 m, Williams 15955 (F, RB, S, VEN). Selva ribereña del Rio Guaina, Moroa, Williams 14418 (NY, VEN). Keserva Forestal Elsipapo, Campamento Laisa de Garza, Blanco 1117 (VEN). Occasional along Rio Yatua, near Laja Catipan, Casiquiare, 6 Feb. 1954, Maguire et al 37543 (BM, holotype of B. pterocarpa). Atabapo, Davidse et al 17441 (MO). Common and subdominant along Cana Catua, Cerro Yapacana, 19. Nov. 1953, Maguire et al 36555 (BM, INPA, US). Cano Adaho, near Rio Negro, 27 Jan. 1980 (MO). Frequent on Rio Paciba, between R. Paciba and R. Casiquiare, Maguire & Wurdack 34867 (NY). Cano Yapacana, 6. Jan. 1951, Maguire et al 30763 (BM, MO, US), 30765 (MO). Frequent near mouth of R. Pacimoni, 13/1/1958, Maguire et al 42637 (LTR). Rio Guainia en la margen or horeada del Cano Pimichin, Williams 14930 (US). Frequent along flooded margins of river just above San Fernando de Atabapo, Wurdack & Adderely 42750 (LTR).

BRAZIL: Amazonas: Rio Negro, Cucui, 25/4/1975, Mascimento et al 185 (IAN, RUB). R. Univini, lago de agua Preta, Pires et al 14124 (IAN). Rio Negro, between Barra and Barcellos, Nov. 1851, Spruce 1887 in Part (BM, BP, C, FI, K, LE lectotype, NY, W). Rio Cuieriras, Kubitzki et al P21722 (INPA, LTR, M, S). In locus Vasvae, Spruce 3190 (P). Rio Negro, Enuixy, Matozini, Froes 22376 (US). Santa Isabel, R. Negro, in flooded riparian forest, 8. Oct. 1932, Ducke 25018 (K, S); same locality, 9 Mar. 1936, Ducke 25018 in Port (K, S. US). Rio Negro, localidade Anaña, Municipio de Sao Gabriel da la Choeira, Damiao 3061 (INPA). Igarape Imuta, afluente do Rio Negro, Froes 27937 (BM, IAN, UB). Barcelos, R. Negro, 19/4/1952, Frões 28442 (IAN). Rio Taruma, Gentry & Ramos 12906 (LTR). Margem direita do R. Negro, Barcellos, Damião 2881 (LTR). "Brazil", Ferreiva E Luve Lusitan (P). Rio Branco; "Guiana" (but actually by Falls on the Rio Branco, fide Schomburgh, MS.), 1839, Schomburgk 854 (BM, K, W).

7. BUCHENAVIA OXYCARPA

BRAZIL: "Brasilia", prope para, Martius (LE, M). "Brazil", Chili, Perou et fleuve de la Plata, 1836 Poeppig 2689 (G), Amazonia, Ega, dated 1831 (W), no locality and without date (BM), "Brasilia", Riedel 744 ex Herb. Hort. Petrop. (K); Rio Negro, 1825-1829, Riedel (LE). Amazonas: Manaus, margin of R. Negro, Prance et al 11738 (LTR). In inundations on the bank of the river Solimões, near Ega and elsewhere in the Province of Rio Negro, 1820, Martius (M, lectotype). Prov. R. Negro prope Ega ad ripam fluv. Solimões, Martius (K, M). Solimões Manacapura, lago do Jacaro, Cavalcante 1812 & Wilva 32567 (NY). S. Paulo de Olivença Ducke 35166 (RB). Manaus, Coelho & Coelho, s.n. (LTR). Humayata, near Tres Casas, Kurkoff 6174 (BM, BR, INA, K, LE, MO, S, US). Humayata, near Livramento, Krukoff 6733 (BM, F, K, MO, S, US). Municipio de Maraá, R.Japurá, Damião 2543 (INPA). Municipio del Limoeiro, R. Japurá, Damião 2726, 2731 (INPA). Municipio de Alvaraes, Damiao 2872 (INPA). Acorizal, Baráe, Maced et al 230 (INPA). Forest on terra firme along Rio dos Pacaás, Anderson 12249 (INPA). Cambixe, Rodrigues & Coelho 1640 (INPA). Sacau Pirera, Rodrigues & Lima 2254A (INPA). Lago do Araca Cambixe, Rodrigues & Mello 2379 (INPA) Rio Negro, Cavalcante 497 (INPA). Maués Inara Prainha, Rodrigues & Coelho 6770 (INPA). Manaus, Byron et al s/n (INPA). Rio Auati, Byron & Lima 326 (INPA). Rio Negro, Silva et al 1075 (INPA). Rio Solimões, Honda & Mello s.n. (INPA). S. Paulo de Olivenca igapo de Camatia, 2 Feb. 1937, Ducke 402 (A + GH, K, MO, NY, R, S), dated 10/4/1944 (IAN). Paraná do Careiro, 26. Oct. 1946, Ducke 2023 (BM, IAN, NY, R). Amazonas Proj-RADAM-Piraracu, 4/11/1975, Rosa 504 (IAN). Boa Vista, flooded land, Capucho 579 (IAN). Coari, Byron et al 537, 521 (INPA). Manaus, Rodrigues 8621 (INPA). Lago do Copea, Magango et al s.n. (INPA). R. Negro, Coelho s.n. (INPA). Parana do Jacare, Coelho et al s/n (INPA). R. Catrimani, Pires et al 14092 (INPA). R. Solimães, Coelho et al 324 (INPA). Na miota alagradica, Plk & Marilene 12436 (INPA). Lago do Piaurini Magango s.n. (INPA).

PERU: Loreto, Rio Mazan, Croat 20214 (NY, P). Inundation belt of Rio Itayal, Iquitos, Asplund 14302 (K, NY, R, S). Gamitanacocha, Rio Mazan, Schunke 141 (F, NY, US). Maynas, Dtto Iquitos, Rimachi 2513 (MO, NY). Quebrada del Caserio de San Pablo, Ricmachi 3297 (F). Maynas, Dtto Bajo Amazonas, Rimachi 2680 (F, MO, NY). Iquitos, Simpson & Schunke 681 (A + GH, F, NY, US). Dtto Iquitos, Davidson 5383 (A + GH). R. Amazonas, Cano above Gamboa, Plowman et al 6474 (A + GH, F, US). Bella Vista, Dadson & Torres 2996 (F). Maynas, Revilla 2254 (F, MO). Maynas, R. Amazonas, Revilla 2415 (F, MO): Rio Yavari, Revilla 2210 (F, MO). Rio Yavari, Gentry & Revilla 20822 (F). Iquitos, R. Momon, Revilla 1828 (F, MO). Davidson & Revilla

5383 (F, MO). Requena, Rio Tapiche, Gentry et al 21271 (F). Yamitana Cocha, Rio Majon, Schunke 14240 (MO). Rio Ambiyaca, R. Maranon, Mori et al 9236 (INPA, LTR). Tonantins, Rio Solimoes, Morie et al 9028 (LTR). San Martin, in rocky stream, near Tarapoto, Spruce 4945 (BM, G, K, NY, W).
COLOMBIA: Tarapecio anazonico, Loretoyacu River, Amazonas, Schultes & Black 8432a (COL); same locality Schultz & Black 8618 (COL, US).
VENEZUELA: Apure: Reserva Forestral San Camilo, Selva siempreverde Cerro Nulita, Steyermark 101829 (NY, US).

8. BUCHENAVIA FANSHAWEI

GUYANA: Essequibo: Mazaruni Station, 7 Sept. 1942, Field No. 5844 = Forest Dept. 3580 (FDG, K). Mazaruni Station, 5 May 1943, Field No. F1270 = Forest Dept. 4006 (K). Mazaruni Station, seedlings of Forest Dept. 3580 ten weeks old from forest nursery, no date, Field No. F1616 = Forest Dept. 4352 (K). Mazaruni Station, seedlings (no source) three weeks and seven months old from forest nursery, no date, Field No. F2233 = Forest Dept. 4969 (K). Mazaruni Station, towards Labbakabra Creek, 27 Aug. 1937, Sandwith 1219 (BM, FDG, K, S). Bank of Potaro River, Tumatumari, 4-6 July 1921, Gleason 401 (A + GH, K). Riverside below Tukeit, Potaro River Gorge, rare, 16 May 1944, Maguire & Fanshae 23499 (BM, K, MO, NY holotype). Mahdia River, Potaro River, 172 km. along Bartica-Potaro road, 16 Jan. 1943, Field No. F1039 = Forest Dept. 3775 (K); same locality, 21 Jan. 1943, Field No. F1064 = Forest Dept. 3800 (K). Basin of Kuyuwini River, tributary of Essequibo River, about 240 km. from mouth, 12 Feb. 1938, Smith 3033 (K, US). Berbice: New River, Courantyne River, 5 Oct. 1911, Anderson 749 (FDG, K). Comaka, Demerara River, Persaud 223 (F, G).
BRAZIL: Amazonas: Cachoeira Baixa, Rio Tarumã, Monãos, May 1950, Ducke 2278 (BM, IAN, LTR). Manaus, km. 3, Aleixo Road, wet secondary growth by road, Prance et al 11536 (INPA, LTR, S). Pará: Breves: transecto para in ventário

florestal, Pires et al 5395 (IAN).

9. BUCHENAVIA SERICOCARPA

BRAZIL: Amazonas: Manáos, Estrada do Bombeamento, "Capoeirão, terra firme, árvore pequena," 26 Nov. and 30 Dec. 1943, Ducke 1481 (K, isotype). Manaus-Porto-Velho Highway, Prance et al 20582 (LTR, M, S). Rio Tupana, Campbell, Ongley & Ramas 20828 (LTR, S). Humayta, near Livramento, on Rio Livramento, basin of Rio Madeira, on terra firma, "tree 60 ft. high", 12 Oct.- 6 Nov. 1934, Kurkoff 6916 (BM hologype of B. acuminata, F. K). Rio Urubu, Barreirinha, "terra firme", "Árvore de 7 m., futos em espiquetas, amareladas", 24 Aug. 1949, Frões 25134 (BM, UB). Barka Rio Madeira igupo cabeerira do Iago, Ducke 35174 (RB). Humayta, on plateau between Rio Léverno & Rio Ipuxana, Kurkoff 7125 (RB). Rio Urubá; beira do vio, terra baixa, Froes 25207 (INPA). Manáus, Reserva Florestal Ducke, Q-XX, Rodrigues & Osmarine 6889 (INPA). Manaus, R. F. Ducke, levantamento floristico em Capocivão, Rodrigues 9134 (INPA).

COLOMBIA: Rio Apaporis: enter 'el Rio Pacoa & el Rio Kananari, R. E. Schultes & I. Cabrera 12653 (U, US).

10. BUCHENAVIA HOEHNEANA

BRAZIL: Sao Paulo; Caraguatatuba, 8/12/1939, Hoehne & Gehrt s.n. (LTR, isotype). Bahia: Belmonte, Bahia Mata Costeira, 3/2/1967, "Arvore de 10 m x 25 cm de diâm. fruts verdes", Belem & Pinheiro 3280 (UB).

11. BUCHENAVIA GRANDIS

BRAZIL: Amazonas: Manãos, vicinity of the Cachoeira do Mindú, on "terra firme", "árvore grande", 3 Dec. 1943, Ducke, 1450 (K, isolectotype of B. huberi). Tabatinga, Estrada do Marco, on "terra firme", "árvore muito grande, com sapopemas possantes", 26 Nov. 1945, Ducke 1803 (K). Humayta, near Tres Casas, basin of Rio Madeira, on low terra firma, 14 Sept.-11 Oct. 1934, Kurkoff 6472 (BM, K, MO). Humayta, near Livramento, on Rio Livramento, basin of Rio Madeira, on terra firma, 12 Oct.-6 Nov. 1934, Kurkoff 6794 (BM, F, INA, K, MO, RB, US). Manaus, Reserva Florestal Ducke, Q.XIX, arv. 2686, Rodrigues 5562 (INPA, RB). Same locality, Rodrigues 5542 (INPA, RB). Manaus, Reserva Florestal Ducke, Q.V., Rodrigues & Coelho 7669 (INPA). Manaus, Reserva Florestal Ducke, Q.XXII,, Loureiro 3337 (INPA). Manaus, Itacoatiara, Km 130, Rodrigues 8633 (INPA). Manaus, Itacoatiara, Km 165, Rodrigues 7949 (INPA). Manaus, R. F. Ducke, Rodrigues & Osmarino 7020 (INPA). Manaus, R. F. Ducke, Rodrigues & Osmarino 8240 (INPA). Manaus, Reserva Florestal Ducke, Aluisio 123 (INPA). Manaus, Caracara Km. 39, Mello, et al 18 (INPA). Manaus, R. F. Ducke, W. Rodrigues & Louriero 5768 (INPA). Rio Negro, Jaracuá, Rodrigues 1124 (INPA). Camatian, high forest, hilly country, Frões 24040 (IAN, INPA). Manaus, Ducke, J.B. 50941 (INPA). Manaus, AM-L Km 134. "Tanimbuca", Rodrigues 7216 (INPA). Estrada Manaus, Itacoatiara Km 26, Mello & Ramos 58148, 58142 (INPA). Same locality, Reis 58141 (INPA). Forest on terra firme, Prance et al 11032 (INPA). Estrala, Manaus, Itacoatiara entre Km 118-135, Monteiro 50893 (INPA). Para: Obidos, 9 Mar. 1909, Ducke 10235 (BM); same locality, wood in elevated places, "arbor magna fl. viridibus", 15 Sept. 1927, Ducke 21349 (K, NY, RB, SO. Oriximiná, by Rio Trombetos, 5 Feb. 1918, Ducke 16976 (isolectotypes BM, P, US). In forest in the Quataquara hills near the middle of Rio Tapajoz, "arbor magna", 13 Aug. 1923, Ducke 17687 (K, S). Belterra, mata, 25/7/1947, Black 47-1077 (INPA, US). Piaui: de sete Cidades parque Nacional, Boqueirão, Barroso 104 & Guimarães (RB). Teresina, 25/6/72, Sucre & Silva 9342 (LTR).

Acre: Cruzeiro do Sul, Monteiro & Damião 509 (INPA). Proj. RADAM-Sub-base Cruzeiro do Sul-SB-8 SD., 18/2"76, Marinho 224.

VENEZUELA: Bolivar: Uandapai, Kavanagon, Grana savana, Lasner 1801 (VEN 36512).

COLOMBIA: Rio Apaporis, entre las rios Kananari & Pacoa, Soratama, Garcia-Barriga 14071 (COL, US). Comisaria del Amazonas, Isidoro Cabre 3364 (COL). Antioquia, Rio Vaupes, Amazonas, Rodrigues 976 (INPA).

GUYANA: Bartica, on the Essequibo R., De la Cruz 1863 (A + GH, F, MO, NY, US).

SURINAM: Goede Hoop, Coppename rivier, distr. Saramacca, Teunissen/LBB no 15485 (U). Bosreservaat Sectie O, Boomnumer 838, Boswezen no 2432 (U).

PERU: Dept. Madre De Dios, Parque Nacional del Manu, Foster 6244 (F, LTR). Rio Nanay, Williams 898 (US).

12. BUCHENAVIA AMAZONIA

See under the species.

13. BUCHENAVIA VIRIDIFLORA

BRAZIL: Amazonas: Rio Ituxi, Prance et al 14057 (INPA, LTR, S). Manaus, Reis 8 (INPA). Manaus-Cachoeira, baixa Taruma, Coelho (INPA 4140). Manaus, Itacoatiara, Osmarino s.n. (INPA). Municipo de Tefe, Coelho & Osmarino 580 (INPA). Manaus, km 139 de estr., Pires & Lima 113 (INPA). Itacoatiara, Km 150, Picada 18, Rodrigues et al 509 (INPA) R. Negro entre Tapuruquara e Barcelos, Silva et al 1754 (INPA). Entre Utiam e Remanso, Silva et al 1230 (INPA). Lago do Castanho-Mirim, Rodrigues et al 884 (INPA). Manaus, Porto Velho Road km 245, Prance et al 20477 (COL, LTR, M, NY, U, US). Terr. Rondonia, basin of R. Madeira, Prance et al 8842 (F, INPA, LTR, NY, S, U, US).

R. Negro, S. Vabriel, Nascimento et al 87 (LTR, RB). R. Negro, Barcellos, 20/6/1905, Ducke 7187 (LTR). Ilha Acaburug Igapó, Maia et al 435 (LTR), Proximo do R. Marupi, Pena 373 (LTR). Near Cachoeira Grande, Manáos, 31 July 1932 and 8 Jan. 1933, Ducke 25022 (K, S). Estrada do Aleixo, Manáos, 15 July 1932, Ducke 25023 (K, S); same locality 26 Dec. 1936 and 19 Mar. 1937, Ducke 426 (K, MO, S, R). Rio Branco, Boa Vista, 24 Aug. and 16 Sept. 1943, Ducke 1378 (F, K, LTR, S). Riberbank wood near Boa Vista, Rio Branco, Ule 7682 (G, K, US). Amapa: Rio Diapogue, Cachoeira Grand Rocha, Fróes 22698 (BM). Pará: Basin of Rio Trombetas, Campbell et al 22323 (LTR). Sub-base Marapi, a margem do R. Marapi, Rosa 237 (LTR).

VENEZUELA: Reserva Forestal El Sipapo, Amazonas, Blanco 1282 (US, VEN). Pedro Lamejo, S. bank of the R. Cinaruco, Apure, 30/4/1977, Davidse & Gonzales 12401 (LTR, VEN). Along the bank of R. Cinaruco, Apure, Davise & Gonzalez 12537 (LTR, VEN). Esmeralda, Upper Orinoco, Amazonas, Williams 15486 (LTR). 1 to 6 Km N. of San Carlos de Rio Negro, Liesner 7158 (LTR, MO). F. T. Amazonas, Williams 15975 (MO).

FRENCH GUIANA: Riviere "La Comte" rive droite à 50 m en âmont du Saut, Paul 1313 (U).

PERU: Loreto, Maynas, Iquitos, Rio Nanay, 31/5/1976, Rimachi 2304 (F, MO, NY).

ECUADOR: Mature forest, N. of Lake, Limonococha, Napo Prov., Oct. 1969, Mowbray 6905 (MO, NY).

14. BUCHENAVIA TOMENTOSA

BRAZIL: Base Camp, Mato Grosso, Argent in Richards 6692 (NY, P, RB, U, UB); same locality, Argent in Richards 6792 (P, U). Cerrado, E. of Base Camp, Mt., Philcox & Fereira 4396 (MO, P, RB). Mato Grosso, Gaudichaud 1833 (P). Campos, Mt., no collector (R91407). Coxipo do Ponte, Hoehne, 1087, 1088, 1089, 1090, 1091 (R). Guyabao, Mt., Mealme 1326, 1789, 2292, 2292a (S). Santa Anna da Chapadao, Silva Clarado, Mt, Mealme 2292B, 2292Ba (S). 20 km ENE of Barra do Carlos, Mt., Anderson 9846 (INPA, LTR, W). Filadolfia, Goias, Macedo 4038 (MO). 7km SW Xavantina, Mt., Ratter et al (MO). Fazenda, Ainhumas, Mt., Hatschbach & Cuimaraes 22069 (C, F, G, MO, NY). 270 km N of Xavantina, Base Camp, Mt., Santos et al 1266 (IAN, MO, NY, RB, UB). Cerrado; ca. 1 km NE of Garapu, Mt., Irwin & Soderstrom 6563 (NY, SP, U, UB, US). 10 km W. Xavantina, Mt., Ratter et al 4115 (UB). Xavantina, Mt., Ratter & Castro 1225 (NY, UB). 2 km by Road of Monte Alegre de Goias, Goias, Anderson 6960 (LTR). Mato Grosso, Becker 50 (RB). Xavantina, Mt., Irwin & Soderstrom 6349 (A + GH, C, LTR). Serra de Caiapo, Goias, Willia & Anderson 9531 (C). Goias (Mun. Rio Verde), Hatschabach 34965 (C, LTR). 15 km S of Araguaina, Goias, Irwin et al 21205 (C, LTR, MO). Goias, Hatschach 38436 (LTR). 7 km S.W. of Xavantina, Ratter & Ramos 546 (NY). Serra Roncador, 60 km N. of Xavantina, Mt., Irwin et al 15922 (LTR). Corumbá, Mt., Allem 1139 & Vieira (RB). Amazonas, Manaus-Itacoatiara, Mello et al s.n. (INPA). Manáos, near Estrada do Aleixo, 9 July and 26 Nov. 1932, Ducke 25021 (K, S, isotypes of B. callistachya). Parque Nacional do Xingú, Mt., Coelho s.n. (INPA). Guiaba Santaream e Porto Velho arredores, Mt., Silva & Pinheiro 4427 (INPA). Guiaba margem e squerda do Ribeirao dos Barbados, Mt., Macedo & Assumpcao 793 (INPA). Santo Antonio, Mt, Macedo et al 352 (INPA). Serra do Roncador, Mt., Irwin et al 16271 (LTR). Serra Azul, S. Xavantina, Mt, Irwin et al 16255 (LTR). Serra do Caiapo, Goias, Anderson 9531 (LTR). Mun. Kenedy, Goias, Plowman et al 8359 (LTR). 30 km de Brasilia Para Belo Horizonte, Mg. Pires 58042 (LTR). W. of Filadelfia in Serro de Momoneira, Goias, Prance & Silva 58518 (LTR). 1-10 km W of Alto Araguaia, Mt., Maguire et al 56252 (LTR). Porto Velho, Guaporé, Amazonas, Silva 25 (IAN). Maranhão, Ilha dos Botes, Rio Tocantins, Pires & Black 2095 (BM). Serra Pontada, Para, 11 Sept. 1973, Ducke 17677 (K, S, isotypes of B. corrugata). Santa Cruz do Martirios, Pará, Froes 30018 (BM, LTR, UB).

Banks Gurgia, Piaui, Gardner 2657 (K). Between Alegre and Ponte do Sevorino, Goias, Glaziou 21125 (C, K, LE, P, R, RB). Minas Gerais, Biribiry, Glaziou 19144 (C, K). On Sandy Plains between Alegres and São Francisco, Sept..1834, Riedel 2641 (BM, C, FI, K, LE lectotype, W).

15. BUCHENAVIA RETICULATA

BRAZIL: Amazonas: Rio Negro, about 120 km above Barcelos, Madison 6167 (F). Rio Uneiuxi, Prance et al 15494 (INPA, LTR). Above Santa Izabel, R. Negro, 5 Mar. 1936, Ducke 35167 (K, RB). Rio Padoari, afluente do R. Negro, Coelho 446 (INPA). Rlosinho Juruema, Alto R. Jutahy, Solimões, Fróes 21039 (IAN,K). Igarapé Imutã, tributary of Rio Negro, Fróes 27936 (BM, LTR, UB). Rio Negro, Fróes 22323 (BM, IAN). Mata de Igapo solo arenoso, Barcelos, Madison et al 167 (INPA). Rio Solimões, Coelho et al 306 (INPA). Pavana do Arirara, Hascimento 691 (LTR). R. Negro, Preto, Maboaby, Froes 22864 (IAN). Proj-RADAM-Piracuca 3- R. Solimões, Rio Bia, Rosa 498 (LTR).

VENEZUELA: Amazonas: Occasional shore of Lago Paciba, Maguire & Wurdack 34799 (MO, NY, VEN 37731 W). R. Casiquiare, V.V.Y.K.M.6692 (VEN 42907). Williams 15901 (G, MO, US, VEN 33052). Along Caño Yapacana, Maguire et al 30794 (VEN 31334). Above Laju Arapacua, R. Pacimoni, Maguire & Wurdack 34912 (A + GH, NY, S, VEN 37732). Rio Pacimoni - Yatua, Maguire et al 36654 (NY, VEN 37740). Caño Paciba, R. Caiquiare, Farinas et al 648 (NY, VEN). R. Casiquiare and tributaries, frequent R. Pacimoni, Maguire & Wurdack 34865 (IAN, NY, P). Frequent near mouth of Rio Pacimoni, Maguire et al 42636 (LTR). On the Rivers Casiquiare, Vosiva and Pacimoni, 1853.-54, Spruce 3453 in part (isolectotypes BM, K, LE, W). Along the River Pacimoni, frequent, and also frequent along the Rivers Guainia and Vasiva, Feb. 1854, Spruce 3453 in part (K). Frequent on banks of the River Guainia, May 1854, Spruce 3453 in part (K). Caño Yapacana, Cerro Yapacana, Alto Rio Orinoco "tree 3-10 m. high, fruit brown, frequent at laguna edge", 19 Mar. 1953, Maguire & Wurdack 34584 (BM, MO, NY, P, RB, S). Frequent along Caño Yapacana below port for Cerro Yapacana, Rio Orinoco, "tree to 20 m. high, inflorescence brown", 6 Jan. 1951, Maguire, Cowan & Wurdack 30760 (BM, NY, VEN). Miranda: Distrito Paez, drainage of the Rio Guapo, Riberon bet. Rio Guapo & Rio Chiquito, buttresses. Petiole 4 cm long; 8-10/6/77, Davidse & Gonzalez 13765 (LTR, VEN). Selvas Pluviales deo Guatopo, Bernardi 5636 (NY). Cerra del Bachiller, Western sector, virgin evergreen forest, Steyermark & Davidse 116996 (LTR).

16. BUCHENAVIA MEGALOPHYLLA

GUYANA: Demerara, Parker (K, as Pamea guianensis). Essequibo: Mazaruni Station, "shrub or small tree 8 ft. high from sand bank by river", 11 Sept. 1942, Field No F 845 in Part = Forest Dept. 3581 in Part (FDG, K); same locality, 11 Apr. 1943, Field No F845 in Part = Forest Dept 3581 in Part (FDG, K); same locality seedling of F.D.3581, Field No 1593 = Forest Dept 4329 (FDG). Basin of Essequibo River, Head Falls Sept 20 1937 (fls), Smith 2118 (F, G, MO, NY, S, U, US), Kartabo Region, Taylor 85 (A + GH.

17. BUCHENAVIA GUIANENSIS

BRAZIL: Amazonas: Manaus, Itacoatiara, km 26, Reserva Florestal Ducke, tree 15 m, 20/11/1973, Rodrigues & Coelho 9251 (INPA); same locality, N. Vulg. Tanimbuca, 1/10/1968 Aluisio 195 (INPA). Reserva Florestral Ducke, Quadra 1, 26/2/1970, Rodrigues 8719 (INPA). Reserva Florestral Ducke, Picada 900 entre 700 e 800., 7/7/1964, Rodrigues & Loureiro 5940 (INPA). "Guiarana", kms 55-60 do Rodov., Manaus-Itacoatiana, 24/10/1963, Oliveira 2766 (IAN).

"Tanimbuca F. Grande" Estrada de Munguba, Mata de t. firme, 23/5/1969 (IAN). Para: Regiãgo do Jari, Estrada entre Tinquim e Braco km 23., 9/10/1970, Silva 3354 (IAN). Rio Pará de Oeste Missao Tiriyo, Feb. 20/1970, Cavalcante 2433 (LTR). Jari do Munguba, Mata de terra firme, 23/5/1969 Silva 2042 (IAN, LTR).

FRENCH GUIANA: Aublet (BM, holotype).

18. BUCHENAVIA NITIDISSIMA

FRENCH GUIANA: Guyane-Francaise-Grand arbre-1789, Le Blond 1792 (G, holotype). Approuge, rives en amont de Crique Maripa Grand arbre, (Nom taki-take: dindyá-oudou), 3.11.1967, Oldeman 2473 (NY, U). Fleuve Tamouri en aval du premier saut, rive gauche, forét primaire, grand arbre 40 à 45 m, (local name: Greole: Amanier Sauvage), 13/3/1974, Lescure 122 (CAY). Saül, Monts la Fumee, tropical Moist Forest, 7 Dec. 1982, Mori & Boom 15343 (LTR; same locality, 16 Oct. 1982, Mori & Boom 15095 (LTR).

19. BUCHENAVIA CONGESTA

BRAZIL: Amazonas: Manãos, near Cachoeira do Mindú in a non-flooded wood in a humid spot, "arbor sat. magna" (over 30 m. fide Ducke in descr.), 3 Dec. 1943, Ducke 1465 (F); same locality, 4 Oct. 1946, Ducke 2003 (INPA, isolectotype); same locality, "Árvore grande; flôr verde brancacenta da árvore tipica", 25 Sept. 1947, Ducke 2104 (BM, INPA, NY). Cachoeira dos Araros, Rio Vaupés (near the Colombian frontier), "Arvore, 5 m." 1 Nov. 1945, Fróes 21308 (K, NY, US). Manaus, Reserva Florestal Ducke, Rodrigues & Osmarino 6884 (INPA). Estrada Manaus-cara carai km 39, 19/9/1977 (fls), Ribamer & Ramas 291 (INPA). Rio Negro, localidad Anana, Municipio de

BRAZIL: Amazonas: Igarapé do Hilário, 1975, Pena 550 (IAN). Margem do R. Negro, Pena 443 (IAN). Rio Capilari, Coda, 31/8/1950, Froes 26483 (LTR, UB). Capsoeira Fechada, Louiz 3144 (IAN). Rio puras, R. Itaxi, 1971, Prance et al 14481 (INPA, LTR, S). Rio Javari, 1976, Prance et al 23900 (LTR). Manaus, Rio Urubu, forest on terra firme, 1966, (INPA, LTR). Humayta near Tres Casas, Krukoff 6273 (MO, US); near Livramento, Krukoff 6916 (MO). Margem esquerda do rio Juruena, Rosa & Santos (INPA, US). Manaós, Ducke 23668, 25017 (RB). Serra do Lagos, Maia et al 677 (INPA). Rio Negro, Silva et al 1702 (INPA). Rio Guieras, just below mouth of R. Brancinho, 1971, Prance et al 14992 (INPA, LTR). Rio Purus, Lago Preto, 1971, Prance et al 13726 (INPA, LTR). Manaus, Parquelo, Coelho 2954 (INPA); same locality "Tanibouca" Mello & Coelho 4116 (INPA). Manaus, Rodrigues 3144 (INPA). Manaus, Picada du antigua linhu telegrafica alem do recado do S Paulo, Ducke 14530 (INPA). Margem do Igapo do Crespo, Manaus, Ducke 15006 (INPA). Borba, Margem do rio Acari, Rodrigues 1581 (INPA). Manaus, Ponta Negro, Rodrigues et al 4779 (INPA). Near Panuré on Rio Vaupés, Oct. 1852-Jan. 1853, Spruce 2507 in part (isolectotypes BM, C, K, LE, NY, US, W). Cjapo, Rio Vaupés, Sept. 1852, Spruce 2507 in part (K). Rio Demeni, tributary of R. Negro, lake of black water, 12 Oct. 1952, Fróes 28888 (BM, IAN). Jauretê, Papury, bank of river, 16 Oct. 1945, Fróes 21156 (IAN, K, US). Manáos, Pensador, riparian forest of the Igarapé, 10 Jan. 1944, Ducke 1542 (K, NY, R, SP). Manáos, Pensador, humid spot in non-flooded forest, 20 Aug. 1935 and 3 Feb. 1936, Ducke 35168 (K, RB, S). Manáos, banks of the Igarapé Mindú, 8 Sept. 1945, Ducke 1753 (IAN, K, NY, R). Manáos, along road to Aleixo, 12 Aug.-1 Sept. 1936, Krukoff 7921 (BM, K, MO, NY, S). Humayta, near Tres Casas, basin of Rio Madeira, on varzea land, 14 Sept.,-11 Oct. 1934, Krukoff 6117 (BM, F, K, LE, MO, NY, S, US), 6273 (BM, F, K, LE, NY, S). Pará: Faro, 4 Feb. 1910, Ducke 10649 (BM); same locality, 9 Oct. 1915, Ducke 15798 (BM, R). Lago de Faro, on banks in rarely flooded places, 22 June 1926, Ducke 13583 (K, RB, S). Rio Tapajoz, region of the lower

São Gabriel da Cachoeira, Damião 3060 (INPA). Manaus, Reserva Florestal Ducke, Bosque antes do barracao, Rodrigues & Loureiro 5769 (INPA).

COLOMBIA: Amazonas: Orilla derecha del rio Vaupés, Raudal Macucū, Romero-Castaneda 3475 (MO, NY). Rio Apaaporis antre el rio Pacoa & el rio Kananari, Schultes & Isidaro Cabrera 13720 (COL). Rio Apaaporis, Raudal de Jirijirimo, R.E. Schultes & I.Cabrera 14551 (COL). Vaupés, Rio Apaporis, Jirijirimo, Garcia-Barriga 13689 (BM, US).

VENEZUELA: Maroa, Rio Guainia, Terr. Amazonas, Williams 14314 (RB). T. F. Amazonas, 1 km NE of San Carlos de Rio Negro, Liesner 4193 (LTR, MO).

20. BUCHENAVIA MACROPHYLLA

VENEZUELA: Bolivar, Vic. of Bluff. Camp. at alt 0/700 m, Steyermark 75616 (VEN). Capihuara, Alto Casiquiare 3/6/1942, Williams 15759 (LTR). Isla Sebastian, R. Casiquiare, 31 Jan. 1980, Liesner & Clark 8936 (LTR, MO). Rio Yatua, 20-25 km above Piedra Arauicana, 30/9/1957, Maguire et al (LTR). Atabapo, Vecindad de la comonidad de Culebra, rio Cunucunuma, Amazonas, 1983, Steyermark & Delascio 129379 (LTR).

COLOMBIA: Bajo calima region, N of Buenaventara, Carton de Colombia concession, 8 Dec. 1981, Al Gentry 35477 (LTR). Florencia, in the cerros La Estrella, 30 Mar. 1940, Cuatrecasas 8863 (U, US, isotypees of B. stellae). Rio Kuduyari, Pacuativa, Vaupes, 19-20 Oct. 1952, Barriga 14907 (COL). Rio Vaupes, Quaracapuri Cachoeira, Allen 3385 (MO, US).

PERU: Loreto, Rio Tacsha Curaray, Croat 20364 (HBG, NY, RB, U, US). Bagua, along roadside from Chiriaco to Puente Venezuela (3.9 km NE. Chiriaco) 31/10/1978, Barbour 4353 (LTR).

FRENCH GUIANA: Riviere Tampoc, Laurent du Maroni 7897 (P). Basse Quaqui a 2 km env. en amont du village Bacovel, 1973, Granville 4792 (LTR). S. of Maripasoula, Premiers sauts du Marouini, (3 sheets with fr.), Moretti CM 824 (CAY).

waterfalls, 25 June 1918, Ducke 17065 (BM, R, RB). Rio São Manoel, Cachoeira do Calderão, on the boundary with Mato Grosso State, by Igarapé Preto, 6 Jan. 1952, Pires 3822 (BM, US). Rio Pixuna, 40 km. from the mouth of Rio Cupari, between Prainha and Agua Boa, 22 Dec. 1947, Black 47-1964 (BM, IAN). Amapá: Rio Araguari, near the Cachoeira do Paredão, "terra firme", 25 July 1951, Fróes & Black 27695 (BM, IAN). Rio Jari, "Guiarana Folha Grande", 1968, Oliveira 4641 (LTR). Rondonia: Abana, 14, 9/1963, Maguire et al 56635, 56643 (LTR). Para: Parque Nacional do Tapajoz, Silva & Rosario 4004 (INPA). Mato Grosso: Rio Aripauná, near Igarapenzinho, 1973 Berg et al P 18420 (LTR, M, S). Rio Ouro Preto affl. Rio Paca nova affl. Mamore, Kuhlmann 21474 (RB, S). Aripuana, ao lado de baixo do Tombo das An dorinhas, Gomes & Miranda 296, 452 (INPA).

21. <u>BUCHENAVIA</u> <u>PULCHERRIMA</u>

Known only from the type (see under the species).