# Revisions of African *Moraceae* (excluding *Dorstenia, Ficus, Musanga* and *Myrianthus*)

by

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*Summary.* — In continuation of de Ruiter's treatment of *Myrianthus* and *Musanga* (Bull. Jard. Bot. Nat. Belg. 46: 471-510.1976), the present paper gives a revision of the African representatives of 17 genera of the *Moraceae.* The area studied not only consists of the African Continent, but also includes Madagascar, the Comoro Islands, the Mascarenes, the Seychelles, and the Aldabra Islands. Several new combinations are made: *Antiaris toxicaria* ssp. *africana* (Engl.) C.C. Berg, *A. toxicaria* ssp. *africana* var. *usambarensis* (Engl.) C.C. Berg, *A. toxicaria* ssp. *macrophylla* (R.Br.) C.C. Berg, *A. toxicaria* ssp. *madagascariensis* (H. Perrier) C.C. Berg, *A. toxicaria* ssp. *humbertii* (Léandri) C.C. Berg, *Broussonetia greveana* (Baillon) C.C. Berg, *Treculia africana* ssp. *madagascarica* (N.E.Br.) C.C. Berg, and *T. africana* ssp. *madagascarica* var. *sambiranensis* (Léandri) C.C. Berg. Many names are brought into synonymy. Besides revising taxa, the present study aims to fill a gap in our knowledge between Asian *Moraceae* (studied by Corner, whose studies resulted in a new classification of the family) and the neotropical *Moraceae*, a subject of study by the present author. Therefore discussions about classification of the family and relationships of African *Moraceae* with moraceous taxa elsewhere are an essential part of the present paper.

## Introduction

As shown in recent studies on *Moraceae* (Corner 1962; Berg 1972b), our knowledge of the African *Moraceae* is rather poor. This is partly due to the facts that since Engler's (1898) and Rendle and Hutchinson's (1916, 1917) surveying treatments of the African *Moraceae*, the taxonomical work in this family has been mainly done on a regional basis, and that the moraceous flora of Madagascar, phytogeographically so important, has become fairly well known only since 1948 (Léandri 1948a, 1948b). Although the predominantly floristic treatments serve well for naming material from several regions, they did not truly enhance our insight into the relationships and the position of the taxa, not being

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based on the examination of essential features by comparative studies. This particularly holds for the smaller genera. A contribution to a better knowledge and understanding of these genera in behalf of an improvement of the classification is the main aim of the present taxonomical revisions.

Material of the following herbaria was used for the present study: ABI, B, BM, BR, COI, E, FHI, FHO, G, HBG, K, L, LISC, LISU, P, S, U, UPS, WAG.

An index of specimens examined for the present study has been prepared and is available on request from the Institute for Systematic Botany, State University of Utrecht, Trans. II, Heidelberglaan 2, Utrecht, Netherlands. Maps giving the distribution of the taxa treated in the present paper will be published in the series "Distributiones Plantarum Africanarum".

## Classification of the *Moraceae*

Corner's studies on Asian *Moraceae* (1962) led to a classification of the *Moraceae* that showed considerable change compared to the generally accepted system of the family proposed by Engler (1889). Corner (1962) transferred the *Conocephaloideae*, comprising the African genera *Musanga* and *Myrianthus*, to the *Urticaceae*, and divided the *Moraceae* s. str. into 6 tribes: *Moreae*, *Artocarpeae*, *Dorstenieae*, *Brosimeae*, *Olmedieae*, and *Ficeae*, involving re-arrangement of several genera. Many small genera were united to more inclusive ones (*Streblus*, *Maclura*, *Trophis*).

In the present author's opinion the *Conocephaloideae* are not more closely related to the *Urticaceae* than to the *Moraceae* s. str. It would be better to treat these three groups as subfamilies of a single family, the *Urticaceae* (Berg 1973), or as separate families. Partly as a conclusion of the present study I prefer a subdivision of the *Moraceae* s. str. into 4 tribes: *Moreae* (including *Artocarpeae*), *Dorstenieae* (including *Brosimeae*), *Castilleae* (the re-defined *Olmedieae*; Berg 1977), and *Ficeae* (cf. Berg 1973). Some arguments for this subdivision are discussed below under the separate tribes.

As clearly demonstrated by Corner (1962), several of the characters formerly used for differentiating subdivisions of the family fail. The structure of the inflorescences, which appeared to be the only sufficient basis left for a primary subdivision, proves to be less important and useful than supposed (cf. Corner 1962; Berg 1972b). At first sight quite different inflorescences prove to be morphologically less remote than presumed (see p. 271, 272; Berg 1977). Presently the *Ficeae* and the *Castilleae* may be regarded as well-defined. The former tribe is mainly defined by characters of the reproductive structures (cf. Corner 1962), but is otherwise extremely variable; the latter is defined by a combination of various characters and appears rather homogeneous. The *Dorstenieae*, mainly defined by the basically bisexual discoid (to globose or to urceolate) inflorescences, are less homogeneous, but the genera are morphologically more or less clearly linked. Some genera of the *Dorstenieae*, especially *Utsetela* and *Helianthostylis*, show distinct affinities to a group of the Moreae comprising *Bleekrodeae*, *Fatoua*, *Sloetiopsis*, and *Sloetia*, genera of which the inflorescences are essentially bisexual (see p. 281, 328). The *Dorstenieae* are clearly delimited against the *Castilleae* and the *Ficeae*. The *Moreae* look somewhat like a dump, without very distinct features, without apparent homogeneity, and partly, without clear-cut genera.

## Habit

The African *Moraceae* show considerable variation in dimensions. Beside huge trees (more than 50 m tall), e.g. in *Antiaris*, one meets modest herbs (up to 5 cm high) in *Dorstenia*. A herbaceous (to suffrutescent) habit occurs in many species of *Dorstenia* and in *Fatoua*. Most arborescent or frutescent African *Moraceae* show sympodial growth and have biseriate leaves, at least on more or less horizontal branches. In some of them, like *Treculia africana* and *Chlorophora excelsa*, seedlings already have biseriate leaves. This growth habit matches the "model of Troll" one of the categories of growth habits of trees recognized by Hallé & Oldeman (1970).

Young trees of *Antiaris* and *Chlorophora regia* have stems with spirally arranged leaves and in continuous sequence form horizontal branches with biseriate leaves. These more or less distinctly phyllomorphic branches are shed in *Antiaris*. Adult trees of *Antiaris* have a system of permanent branches bearing the leaves in spirals and forming self-pruning phyllomorphic branches. *C. regia* probably attains the features of the "model of Troll" when becoming adult.

The trees are terrestrial, only *Trilepisium madagascariense* is occasionally epiphytic and strangling, like several *Ficus* species.

*Morus mesozygia* and *Broussonetia greveana* show abortion and shedding of shoot tips connected with intermittant growth. Distinct traces of intermittant growth can also be observed in adult specimens of *Chlorophora excelsa* and *C. regia.*

Distinct resting buds occur in *Morus mesozygia* (always axillary) and in *Chlorophora excelsa* and *C. regia* (mainly apical). Small resting buds resembling those of *M. mesozygia* can be found in *Broussonetia greveana* and *Pachytrophe dimepate.* In these three species the buds are closed, but in *Ampalis mauritiana* the axillary buds are open.

Short-shoots ending in a spine are found in *Cardiogyne.*

## Leaves

The leaves of the species treated in the present paper are basically pinnately veined and brochidodromous. A more or less distinct tendency towards subtriplinerved venation is present in *Morus mesozygia, Trilepisium madagascariense,* and *Utsetala gabonensis.* In most species the differences between leaves of juvenile and adult specimens are not conspicuous. *Antiaris toxicaria, Chlorophora excelsa* and *C. regia* are exceptions.

Scale leaves only consisting of more or less modified and mostly connate stipules occur in short-shoots bearing the inflorescences (*Castilleae,* several genera of the *Dorstenieae, Treculia*), on short branches ending in a spine, as in *Cardiogyne africana,* or on the lower parts of normal shoots, especially if arising from resting buds the scales (of which are also more or less modified stipules) as can be found in several genera of the *Moreae.* The absence of normal leaves is distinctly connected with the presence of inflorescences. In *Trilepisium* scale leaves form a bud cover to protect the young inflorescence.

## Indument

Beside unicellular hairs minute pluricellular hairs can be found in most species, mainly on the lower leaf surface and on young twigs. These hairs consist of one or two cells forming a stalk and several cells forming an oblongoid or globose head. These almost microscopic hairs are globose-capitate in most African species, but oblongoid-capitate in *Trilepisium madagascariense, Mesogyne insignis,* and *Sloetiopsis usambarensis.* They are often reddish or brownish. They were not observed in *Maillardia* and *Fatoua.*

The unicellular hairs are straight, more or less curled, or curved to uncinate. Uncinate hairs are found in all members of the *Dorstenieae*, and furthermore in *Fatoua*, *Bleekrodea*, *Sloetiopsis*, and *Treculia*. They are not found in other members of the *Moreae*, although some of them (*Broussonetia greveana*, *Cardiogyne africana*) have close relatives having uncinate hairs. Uncinate hairs are wanting in all *Castilleae*.

In *Chlorophora excelsa* the areoles on the lower leaf surface are covered by small hairs, forming extra-stomatal crypts.

## Inflorescences

Almost all types of moraceous inflorescences occur in the African *Moraceae*. The inflorescence of the *Moraceae* (and the *Urticaceae*) appears to be basically a cymose system with pistillate flowers (centrally, basally) and staminate flowers (peripherally, distally) with a tendency to dorsiventral flattening resulting in adaxial orientation of the flowers. The flattening can explain the abaxial sterile groove or strip in spicate and racemose inflorescences. Condensation of the branch system, reduction of the number of flowers, and the development of unisexuality are the main lines in the differentiation of the inflorescence of the *Moraceae*. Condensation results in spicate, racemose, or capitate inflorescences, or in inflorescences with a (plane, convex, or concave) discoid, globose, or urceolate receptacle; the bracts may form a more or less distinct involucre. In contrast to the unisexual inflorescences in bisexual inflorescences the cymose pattern is more or less well-preserved or traceable (cf. Bernbeck 1932). *Bleekrodea madagascariensis* distinctly shows the presumed basic structure of the moraceous inflorescence.

There is a pronounced tendency to shorten the single elongate axis (of the spicate or racemose inflorescence) to a clavate to globose or even discoid axis (of the capitate inflorescence), involving reduction of the number of flowers, even to one, as in *Maillardia*. In this process the pistillate inflorescence (usually) preceeds. In some genera (*Treculia*, *Cardiogyne*) the staminate and pistillate are (almost) similar, in other genera they are slightly different as in *Ampalis*, *Chlorophora* (*excelsa* and *regia*), but there are also genera (*Sloetiopsis* and *Maillardia*) with very different inflorescences in the two sexes. These two genera have many-flowered staminate inflorescences and single-flowered pistillate ones. Shortening of the elongate axis usually results in indistinctness or disappearance of the sterile groove.

More or less pronounced pseudanthy occurs in the groups of the *Moraceae* (*Castilleae* and *Dorstenieae*) with discoid to urceolate receptacles, especially if they are involucrate or bear marginal bracts. Reduction in such inflorescences can also result in uniflorous pistillate inflorescences.

After having discredited several characters formerly used for a primary subdivision of the *Moraceae*, the structure of the inflorescence appeared to be left for this purpose (cf. Corner 1962). The unisexual discoid involucrate inflorescence was regarded as characteristic for the "*Olmediae*". For several reasons (cf. Berg 1977) *Olmedia*, *Antiaropsis*, and *Sparattosyce* had to be excluded from this tribe and transferred to the *Moreae*. These genera can be linked with undoubted members of the *Moreae*; *Olmedia* is linked with *Trophis*, which has mainly spicate or racemose inflorescences, but in *Trophis involucrata* capitate-involucrate pistillate inflorescences; the other two genera are linked with *Phyllochlamys* (= *Streblus* sect. *Phyllochlamys*), a genus with capitate, involucrate inflorescences. According to Corner (1962) the inflorescences of *Phyllochlamys* can be regarded as derived from spicate (or racemose) ones. The cymose inflorescences of *Bleekrodea* are morphologically related to those of *Utsetela* and the neotropical genus *Helianthostylis*, both belonging to the *Dorstenieae*. *Fatoua* (with which *Bleekrodea* appears to be related) shows that cymose and spicate (to racemose) inflorescences are not remote structures, either. As these cases show or suggest, several apparently distinct types of the inflorescence are morphologically related, and features of the inflorescences thus have less value for a primary subdivision of the family than formerly supposed.

For well-founded considerations about the differentiation of the inflorescence and its significance for classification, functional aspects relating to pollination and dispersal should be taken into account, which is hardly possible at this moment, through lack of knowledge of them.

The inflorescences are borne in pairs in the leaf axils (which appears to be the basical situation in the *Moraceae* and the *Urticaceae*) or solitary (as commonly in *Chlorophora excelsa* and *C. regia*, *Morus mesozygia*, *Ampalis mauritiana*, and *Broussonetia greveana*) or on scaled short-shoots in the axils of the leaves or also on older branches (in *Antiaris*, *Mesogyne*, *Treculia*, *Dorstenia*, and *Scyphosyce*), down to the main branches (in *Treculia*). In *Antiaris* and *Mesogyne* the short-shoots may bear both pistillate (on the lower nodes) and staminate inflorescences, thus somewhat simulating the situation in a flower with regard to the position of male and female structures. The short-shoots may produce several to many inflorescences almost simultaneously or successively. In *Trilepisium* the inflorescences are initially enclosed in scaled buds in the leaf axils. In some genera (e.g. *Morus*) most fertile shoots are more or less intermediate between a normal shoot and a short-shoot; they form scale leaves at the base, and most inflorescences are borne there. The short-shoots may develop into normal shoots.

## Staminate flowers

Inflexed stamens springing back at anthesis and ejecting their pollen are found in many species of the *Moreae* s.l. These stamens, with introrse anthers and a small connective, are adapted to windpollination. In the groups having these stamens the perianth is well-developed, the number of stamens is mostly four or five, and the pistillode is usually present and often rather large. In groups in which the stamens are straight in the bud, or if inflexed or incurved not springing back at anthesis (as in *Dorstenia* and *Bosqueiopsis*), the perianth often shows a reduction in the number and/or the size of the tepals, often accompanied by a reduction of the number of stamens, as well of the size of the pistillode. Moreover, the flowers may become more or less disorganized (as in *Antiaris*). In *Trilepisium* the perianth is lacking. If the perianth is more or less reduced or lacking, other structures are involved in the protection of the stamens, which is brought about in a peculiar manner in *Trilepisium.*

The inflexed stamens, characteristic for all *Urticaceae*, have been used for delimiting the subfamily *Moroideae* of the *Moraceae.* But as stated by Corner (1962), this feature cannot be used for delimitation at the subfamily or the tribe level, not even at the genus level. Under *Maclura* Corner brought together species with inflexed and others with straight stamens. There are several examples of pairs of (probably) more or less closely related taxa one of which has inflexed stamens, the other straight stamens: *Trophis-Sorocea*, *Chlorophora* (*excelsa* and *C. regia*)*-Bagassa*, *Maclura-Cudrania*, *Phyllochlamys-Antiaropsis*, and *Malaisia-Prainea.*

## Pistillate flowers

With the exception of *Treculia* all genera treated have pistillate flowers with a well-developed perianth; this is indistinct if it is completely or largely fused with the receptacle. In *Treculia* the perianthless pistillate flowers are placed in cavities formed by the basally fused parts of the interfloral bracts. In the genera with free pistillate flowers and free pistils the perianth mainly varies in the degree to which the tepals are connate, Differences in the fruiting perianth are more important because of the role they play in the protection and dispersal of the fruits. These differences refer to the degree in which they develop further, to their substance or texture, and to their colour.

## Fruit

A white pulpy exocarp splitting open in two valves and pushing upward (or outward) or ejecting the endocarp body occurs in several genera: *Dorstenia, Scyphosyce, Utsetela, Sloetiopsis, Bleekrodea, Fatoua,* and besides in several species of *Streblus* sensu Corner, in some species of *Ficus* (cf. Corner 1962), in *Antiaropsis,* and possibly in *Sparattosyce.* The exocarp has a thick fleshy base which may occupy about half of the length of the fruit. The endocarp body is clasped by the two valves. The valve at the seed-bearing side is rather straight and thicker than the other, which is curved over the endocarp body and towards the top strongly narrows to about the width of the lateral vascular bundle. The endocarp is released by a break at the top of the narrowed part (actually the vascular bundle). The stress on the endocarp body caused by the exocarp is suddenly released when the connecting part breaks. If small, the endocarp is often whitish or pale brown and may be more or less tuberculate (as in *Fatoua* and some *Dorstenia* species). These small endocarp bodies are probably ejected. The uneven surface of the endocarp body is probably advantageous for ejection, as in seeds of *Oxalidaceae* (cf. Overbeek 1923, 1926). Overbeek (1924) described the ejecting mechanism of fruits of *Dorstenia contrajerva,* said to be a pincer mechanism. It was further studied by Schleuss (1958). This study also contains an account of the development of the fruit of *Dorstenia.* If the endocarps are large, they are usually smooth and often black (*Dorstenia* species, *Sloetiopsis*). They are probably not ejected but only pushed away; or if the exocarps are relatively thin (as in *Antiaropsis*) they probably only slip away abruptly. In *Dorstenia, Utsetela* and *Bleekrodea* the endocarp can only be released after tearing of the surrounding tissue (the upper part of the infructescence or the fruiting perianth).

In some genera of the *Moraceae,* like *Broussonetia* and *Chlorophora* (*excelsa* and *regia*), the oblongoid fruit has an indehiscent white and thinly fleshy exocarp with a short stipe, as in the dehiscent fruit. A drawing of the fruit of *Broussonetia papyrifera* given by Seringe (1855) suggests the (occasional?) occurrence of a thickly fleshy (and dehiscent) exocarp in that genus. It is conceivable that the fruit as occurring in *Chlorophora* is derived from the dehiscent fruit. In *Morus, Ampalis,* and *Pachytrophe* the exocarp is also more or less succulent. In the broad bases of their fruits these genera differ distinctly from *Broussonetia* and *Chlorophora.* On the other hand, the fact that the exocarp becomes thicker toward the parts containing the (lateral) vascular bundles, as found in the dehiscent fruit, suggest that this broad-based indehiscent fruit is also derived from the dehiscent fruit. Broad-based fruits also occur in some *Streblus* species, like *S. ascendens, S. pendulinus,* and *S. sclerophylla* (Corner 1970).

In *Treculia* the exocarp is thin-fleshy in *T. africana,* but coriaceous in *T. acuminata* and *T. obovoidea.*

It may be said that drupes are rather common among the *Moraceae* with free fruits. In other *Moraceae,* like *Maillardia,* the fruit is adnate to the fleshy fruiting perianth and forms a drupe-like structure with it. In *Antiaris, Mesogyne, Trilepisium,* and *Bosqueiopsis* the fruit (adnate to the perianth) forms a drupaceous whole with the surrounding fleshy receptacle.

In most *Moraceae* the endocarp is woody, crustaceous (or coriaceous). It has functionally replaced the testa, which is usually thin or very thin. The testa usually shows a more or less extensive system of vascular bundles departing from the hilum. Below the hilum there usually is an oblong to orbicular thickened part of the testa to which the vascular bundles are often confined. Depending on the position of the embryo and the hilum, the thickened part is apical or lateral. The significance of the thickened part is not clear.

The embryo shows much variation. In several small-seeded *Moreae* (*Fatoua, Morus, Chlorophora,* and *Broussonetia*) the seed contains endosperm and an embryo with almost plane cotyledons and a long radicle. In other genera of the *Moreae* (*Pachytrophe, Treculia*) traces of endosperm can be found. The cotyledons vary from equal to very unequal, from plane to conduplicate to plicate, and from flat to almost cylindrical; the radicle varies from long to very short.

## Pollination

Except for *Treculia* all African members of the *Moreae* have stamens that bend outward abruptly and elastically at anthesis and eject their pollen. Transport of this pollen demands more or less open habitats (semi-deciduous or deciduous forests, forest edges, riversides). This may explain the remarkable abundance of *Chlorophora* just behind littoral bush, as in the Ivory Coast (Aubréville et al. 1947; cf. Aubréville 1959). A short period of leaflessness just before flowering (as occurs in *Antiaris*, *Chlorophora*, and *Morus*) is advantageous for wind pollination. *Sloetiopsis* which often inhabits dense forests is there almost confined to the side of streamlets, places where air movement may be expected. According to Osmaston (1965) *Antiaris* is probably also wind pollinated. If passive release of pollen by mere dropping is effective enough, wind pollination may also occur in *Trilepisium* where the inflorescences initially point downwards. The remarkable affixture of the anthers of *T. africana* might also be an indication of wind pollination. However, many labels report that the staminate inflorescences are odoriferous. The strong sweet smell is said to be pleasant, unpleasant, or disgusting, and seems to attract beetles which may use the staminate inflorescences as brood-places. Labels also report that the inflorescences of *Trilepisium madagascariense*, and the staminate inflorescences of *Mesogyne insignis* are sweetly scented.

## Dispersal

It is known that the fruits of *Antiaris*, *Chlorophora excelsa*, *Treculia africana*, and *Cardiogyne* are eaten by various animals. It may be assumed that greenish infructescences somewhat resembling those of *Chlorophora exelsa* (like those of *Morus mesozygia*) and the infructescences with a coloured and more or less fleshy receptacle or fruiting perianth are also eaten and dispersed by animals.

The situation is different in a group of species the fruits of which have a white pulpy dehiscent exocarp which pushes upwards or ejects the endocarp body. These fruits, enclosed by a green (or, in several *Dorstenia* species, a brownish to purplish) receptacle and enveloped by a green (or in *Scyphosyce manniana* slightly purplish) perianth and often hidden under the leaves, are inconspicuous. The smaller whitish or larger blackish endocarp bodies are dropped close by the plant and might be transported further by water. Many of the species concerned are gregarious. In several of them this is due to the presence of repent rhizomes, but in other species, like *Sloetiopsis usambarensis*, the way of dispersal may provide an explanation for this phenomenon, as well as for the fact that the species are usually found along streams. In this group of species only *Bleekrodea madagascariensis* has a reddish fruiting perianth, which has to be torn to release the endocarp body. The colour of the perianth, contrasting with the black endocarp might attract animals.

## Chemical substances

In many members of the *Moreae* a yellow dye occurs in several parts of the plant. This may often be more or less accumulated in certain parts imparting to them a yellow or orange colour, e.g. in the bark of the roots, in the tepals and bracts as in *Cardiogyne africana*, or in the connectives of the anthers.

The latex of *Treculia africana* and *Antiaris toxicaria* is said to be toxic. This may be ascribed to cardiac glycosides in *A. toxicaria*, in *T. africana* to a poisonous substance, possibly similar to that of *Parartocarpus*. Conspicuous change in colour of the latex from whitish to brownish or reddish, after exposure to the air is known in *Antiaris toxicaria*, *Treculia africana* and in *Trilepisium madagascariense*. The latex of *Trilepisium* is a dye. Latex and even laticiferous elements seem to be lacking in *Fatoua madagascariensis* (Léandri 1948b).

## Chromosome numbers

Chromosome numbers of only a few of the African *Moraceae* treated in the present study are known:

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|---|---|---|
| — *Antiaris africana* | 2n = 28 | Le Coq (1964) |
| (= *A. toxicaria* ssp. *africana* var. *africana*?) | | |
| — *Antiaris usambarensis* | 2n = 28 | Le Coq (1964) |
| (= *A. toxicaria* ssp. *africana* var. *usambarensis*?) | | |
| — *Antiaris welwitschii* | 2n = 24 | Mangenot & Mangenot (1958) |
| (= *A. toxicaria* ssp. *africana* var. *welwitschii*?) | | |
| — *Bosqueia angolensis* | 2n = 28 | Gadella & Kliphuis (1969) |
| (= *Trilepisium madagascariense*) | | |
| — *Scyphosyce manniana* | 2n = 28 | Cameroun, near Loum<br>*Leeuwenberg & Berg* 9759) |

Judging from the indices of chromosome numbers (Le Coq 1963; Fedorov 1969) 2n = 28 seems to be a common chromosome number in the *Moraceae*.

## Distribution

The *Moreae* have their center in Asia, which is also evident from the distribution and the relationships of the African members of the tribe. Eight of the eleven genera (distinguished by provisionally adopting a very narrow genus concept) occur in Madagascar. Only *Treculia* and *Cardiogyne* (only known from a single locality in Madagascar) also occur on the African continent, inhabited by five genera. These genera or species have their closest relatives in Asia. If in anticipation we adopt a broader genus concept, we may even say that none of the genera is endemic to Africa, possibly except for the genus which might be formed by *Chlorophora excelsa* and *C. regia.* These species appear to be related to the neotropical genus *Bagassa* (see p. 273). Most of the species of this tribe are not (true) components of (humid) rain forests. *Chlorophora excelsa, Morus mesozygia, Treculia africana,* and *Sloetiopsis usambarensis* have a wide distribution in tropical Africa. *Chlorophora regia* is confined to a rather small area in West Africa, the other two species of *Treculia* inhabit the rain forest area ranging from S.E. Nigeria to the Lower Congo River. *Cardiogyne africana* chiefly inhabits coastal areasi n East Africa. *Maillardia borbonica* is an endemic of Mauritius, *M. montana* extends from Madagascar to the Comoro Islands and Aldabra Atoll. Except for *Fatoua madagascariensis* the Madagascan *Moreae* are more or less widely distributed on the island.

In Asia the *Dorsteniae* are only represented by some *Dorstenia* species. The tribe has distinct trans-atlantic connections. In contrast to the *Moreae,* the *Dorstenieae* are more or less centered in western Africa. Many of the species are true components of humid rain forests, especially of the undergrowth, and are (almost) confined to the rain forest area between the Cross River in S.E. Nigeria and the Lower Congo River. Furthermore, many species have small areas. But *Trilepisium madagascariense,* extending outside the rain forest areas, ranges from West Africa to Madagascar and to the Seychelles; *Bosquieopsis gilletii* and *Dorstenia kameruniana* have rather wide, in their disjunctions more or less similar areas, the former from East Africa to the Lower Congo River, the latter up to S.E. Guinea (Mount Nimba). The *Castilleae* are chiefly neotropical, extending to Africa only with the two closely related monotypic genera *Antiaris* and *Mesogyne. Antiaris toxicaria* ranges from Senegal to Madagascar and from Sri Lanka to the Tonga Islands. In Africa it extends far outside rain forest areas. *Mesogyne,* with a peculiar disjunct area (Eastern Tanzania — São Tomé) appears to be a component of the rain forest and in this aspect resembles most of its neotropical relatives.

Most arborescent species of the African *Moraceae* (as far as treated in the present paper) may inhabit relatively dry regions, or at least more or less open vegetations. They occur in semi-deciduous or deciduous forests, gallery forests, in forest islands or as solitary trees in savanna regions, or along streams. *Chlorophora excelsa* and *Antiaris toxicaria* may be co-dominant in forests bordering savanna areas (observed in Togo). Those arborescent species often occur in secondary vegetations or as lone trees spared in cultivated areas. Most of them (appear to) penetrate into rain forests areas, where some of them (e.g. *Treculia africana*) are mostly found along streams. They are not frequent in the dense humid upland forests. They probably appear there due to accidental clearings (cf. Aubréville 1959). The *Chlorophora* species and *Antiaris toxicaria* are known to be light demanding (Aubréville 1959; Voorhoeve 1965).

*Sloetiopsis usambarensis* is a remarkable species. It may inhabit (as a shrub or a small tree) dense primary forests, but (as a small, much-branched shrub) also rocks in riverbeds or coastal scrub vegetations. This suggests that the seeds germinate under quite different (light) conditions. Other species, like *Bosquieopsis gilletii*, may also prove to have this property.

True components of humid rain forests are the two *Scyphosyce* species, *Utsetela gabonensis*, *Treculia acuminata*, and *Mesogyne insignis*. All are components of the undergrowth. The main area of these species extends from S.E. Nigeria to the Lower Congo River. *Treculia obovoidea*, also occurring in this region, may too be regarded as a true component of the humid rain forest, although the small to medium-sized trees often occur along streams.

Several taxa show considerable ecological amplitude with regard to humidity (*Cardiogyne africana*, *Sloetiopsis usambarensis*, several Madagascan species). Drought conditions may influence habit (*Sloetiopsis usambarensis*), leaf characters (*Sloetiopsis usambarensis*, *Antiaris toxicaria*), and leaf-fall.

Infra-specific or specific differentiation in relation to the kind of soil or to altitude, as suggested for several Madagascan *Moraceae* (cf. Léandri 1948a, 1948b; Perrier de la Bâthie & Léandri 1952) is not apparent.

**Key to the tribes of the *Moraceae* s. str.**

1.a. Inflorescences urceolate,, the opening entirely closed by (ostiolar) bracts . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ficeae*

b. Inflorescences mostly spicate, capitate, or discoid, if urceolate then the opening not entirely closed . . . . . . . . . . . . . . . . . . . . . . 2

2.a. Inflorescences discoid to turbinate, sometimes cyathiform or capitate, often more or less distinctly involucrate; stamens straight in the bud, or, if inflexed, then straightening gradually . . . . . . . . . . . . . . . . . . . . . 3

b. Inflorescences mostly spicate to racemose or capitate or sometimes shortly branched cymes (in some Asian genera discoid and involucrate or urceolate, subinvolucrate in *Treculia* and some Asian genera) usually unisexual; stamens often inflexed and bending outward elastically at anthesis . . . . . . . *Moreae*

3.a. Inflorescences bisexual or rarely unisexual by reduction, interfloral bracts usually peltate uncinate; hairs always present; self-pruning branches lacking . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Dorstenieae*

b. Inflorescences unisexual, bracts never peltate; uncinate hairs lacking; with self-pruning branches . . . . . . . . . . . . . . . . . . . . . . *Castilleae*

## Dorstenieae Gaudich.
## in Freyc., Voy. Monde Bot.: 491, 510 (1830)

*Trees*, shrubs, or herbs (*Dorstenia*). *Leaves* distichous or in a spiral; stipules connate or not; uncinate hairs general; wood without septate fibres. *Inflorescences* solitary or paired, rarely in small groups on short-shoots, mostly bisexual, discoid to globose; involucre lacking or if present generally not consisting of several series of imbricate bracts; often peltate bracts among the flowers; stamens straight or curved (but not elastically springing back); sometimes a distinct pistillode; perianth of the pistillate flower with connate tepals. *Fruit* free or forming a drupaceaous whole with the receptacle; seeds large or small, without or with endosperm; testa generally having a thickened part with vascular strands; embryo often not oriented longitudinally in the seed, cotyledons often unequal.

In this circumscription (cf. Berg 1973) the tribe comprises *Dorstenia, Scyphosyce, Utsetela, Bosqueiopsis,* and *Trilepisium,* and further the neotropical genera *Brosimum, Trymatococcus,* and *Helianthostylis.*

Because of the inflexed stamens *Dorstenia* was formerly classed far from the *Brosimeae* (cf. Trécul 1847; Bureau 1873; Engler 1889). The inflexed stamens of *Dorstenia* do not suddenly spring back at anthesis to release the pollen, as in many members of the tribe *Moreae* and in the *Urticaceae*, and have therefore been regarded as distinct.

When the diagnoses of the *Dorstenieae* and the *Brosimeae*, as given by Corner (1962) in a key to the tribes of the *Moraceae*, are compared, the two tribes approach each other: the diagnoses do not include essential differentiating characters. In Corner's concept the tribe *Dorstenieae* only comprises the genus *Dorstenia*, which is very uniform to the basic characters of inflorescence and flower. That uniformity is not affected by combining the species formerly put in *Craterogyne* with *Dorstenia*. However, *D. djettii* is a remarkable exception in having interfloral peltate bracts, like *Bosqueiopsis* and the neotropical genus *Brosimum*. In this feature *D. djettii* distinctly links *Dorstenia* with genera formerly placed in the *Brosimeae*.

*Scyphosyce* resembles in habit and habitat many species of *Dorstenia.* It is not very difficult to connect the structure of the inflorescence of *S. manniana* via that of *S. pandurata* with the inflorescence of *Dorstenia. S. manniana* has an inflorescence with free flowers and a pistillate flower with free tepals. *S. pandurata* has basally fused staminate flowers and a pistillate flower with connate tepals whereas in the inflorescence of *Dorstenia* all flowers are fused except for their upper parts. *Scyphosyce* and *Dorstenia* have the same type of fruit (with a white thick-fleshy dehiscent exocarp, pushing upward or ejecting the endocarp body). The same type of fruit also occurs in *Utsetela.*

*Utsetela* (inserted in the *Dorstenieae* on the basis of the structure of the inflorescence, only distinct when fruiting) in its inflorescence resembles *Bleekrodea.* Thus *Bleekrodea* links the *Dorstenieae* with a group of the *Moreae* comprising, beside *Bleekrodea, Sloetiopsis, Sloetia* [according to Corner (1962) to be regarded as members of the broad genus *Streblus*], and *Fatoua.* In this group bisexual inflorescences are predominant, as in the *Dorstenieae.* Moreover, this group of genera matches most *Dorstenieae* in their indument and several genera of the *Dorstenieae* in their fruits. But they distinctly differ in the stamens, which suddenly spring back at anthesis. The inflorescence of *Utsetela* also resembles the bisexual inflorescences of the neotropical genus *Helianthostylis*; however, in the latter the fruit is not free but fused with the receptacle. The capitate staminate inflorescences of *Helianthostylis* do not have a distinct receptacle but are compactly branched like the inflorescence of *Bleekrodea.*

The striking resemblance between *Bleekrodea* and *Utsetela* is puzzling. The main difference between these taxa is found in the type of stamens. The difference between inflexed stamens which bend outward elastically and straight stamens or inflexed stamens which do not bend outward elastically appears not to be important for classification and delimination of genera in the *Moreae* (cf. Corner 1962) which is not surprising considering the lack of homogenity in this tribe. Several characters which are distinctive for groups of the *Urticales* like inflexed stamens for the *Urticeae* s. str., are apparently distributed at random in the *Moreae.* On the other hand, differences in the type of stamens seem to be fundamental with regard to evolutionary patterns in the *Urticales,* especially in relation to pollination.

Beside connections to several genera of the *Dorstenieae,* the *Bleekrodea-Fatoua-Sloetiopsis* group appears to be connected to the *Urticaceae* s. str. through *Fatoua.* The presence of primitive features in the inflorescences and flowers and the presumably primitive dehiscent fruits suggest that the *Bleekrodeae-Fatoua-Sloetiopsis* group and several genera of the *Dorstenieae* are still close to an ancestral (?) morphological complex to which several differentiation lines go back. Some of these lines involve adaptations to wind pollination (in *Bleekrodea*, etc.), in others to insect pollination (*Utsetela*, etc.).

The inflorescences of *Bosqueiopsis* resemble those of the neotropical genus *Trymatococcus*. In these two genera, and besides in *Trilepisium* and the neotropical genera *Brosimum* and *Helianthostylis* the pericarp, the (lower part of the) perianth of the pistillate flower, and the receptacle are fused and form a drupaceous whole. In the characters of the (bisexual) inflorescences (especially when fruiting) *Helianthostylis* resembles *Trymatococcus* and links *Utsetela* with other members of the *Dorstenieae*. Therefore, it appears impossible to separate *Utsetela* and *Helianthostylis*, the characters of the inflorescences of which approach those of *Bleekrodea*, from the other genera of the *Dorstenieae*.

It has to be mentioned that Bureau (1873) placed *Fatoua*, *Sloetia* and *Bleekrodea* in the tribe *Dorstenieae*, in which Engler (1889, 1915) also placed *Sloetiopsis* and *Neosloetiopsis*, thus disregarding differences in the structure of the inflorescence (see p. 363).

### Key to the genera of the *Dorstenieae*

1.a. Staminate flowers without a perianth and before anthesis enclosed by the expanded margin of the receptacle; young inflorescences in scaly buds; stipules fully amplexicaul; twigs mostly glabrous . . . . . . . . . . . 5. *Trilepisium*
b. Staminate flowers with a perianth; inflorescences not in buds; stipules not fully amplexicaul; twigs mostly with hairs . . . . . . . . . . . . . . 2
2.a. Inflorescences cyathiform; low undershrubs . . . . . . . . . 2. *Scyphosyce*
b. Inflorescences discoid to turbinate (or naviculate) or capitate; trees, shrubs, undershrubs or herbs . . . . . . . . . . . . . . . . . . . . . . . . 3
3.a. Inflorescences capitate, with 4 subtending bracts; infructescences globose with 4 subtending bracts; infructescences globose with scattered remnants of the staminate flowers; leaves subtriplinerved . . . . . . . . . . . . 3. *Utsetela*
b. Inflorescences discoid to turbinate (or naviculate), with marginal bracts; remnants of staminate flowers crowded on the upper surface of the receptacle; leaves pinnately veined or (in *Bosqueiopsis*) subtriplinerved . . . . . 4
4.a. Inflorescences with persistent, peltate, interfloral bracts; overy and fruit adnate to the receptacle; leaves subtriplinerved; trees or shrubs . 4. *Bosqueiopsis*
b. Inflorescences without interfloral bracts (or with caducous, peltate, interfloral bracts in *D. djettii*); ovary and fruit free; leaves pinnately veined; shrubs, undershrubs or herbs . . . . . . . . . . . . . . . . . . . . . 5. *Dorstenia*

1. **Dorstenia** L., Sp. Pl.: 121 (1753). — Type species: *D. contrajerva* L.

*Kosaria* Forsk., Fl. Aegypt Arab.: 164 (1755).
*Craterogyne* Lanj., Rec. Trav. Bot. Neérl. **32**: 272 (1935). — Type

species: *C. africana* (Baill.) Lanj. [= *Dorstenia* africana (Baill.) C.C. Berg].

*Ctenocladus* Engl., Bot. Jahrb. **57**: 246 (1921), nom. reject., = *Ctenocladium* Airy Shaw, Kew Bull. **18**: 272 (1965). — Type species: *Ctenocladus mildbraedii* Engl. = *Ctenocladium mildbraedii* (Engl.) Airy Shaw.

Four of the five species which together form the genus *Craterogyne* namely *C. africana* (Baill.) Lanj., *C. kameruniana* (Engl.) Lanj., *C. oligogyna* (Pellegr.) Lanj., and *C. djettii* (Guillaumet) N. Hallé & Aké Assi, show relationships to *Dorstenia elliptica* Bur., the only species of *Dorstenia* sect. *Nothodorstenia* Engl. The fifth species, *C. dorstenioides* (Engl.) Lanj., shows a distinct relationship to *Dorstenia turbinata* Engl. which belongs to another group of *Dorstenia*, related to sect. *Nothodorstenia.*

Because of the resemblances of the *Craterogyne* species with *Dorstenia* species and the lack of good differential characters between *Craterogyne* and *Dorstenia*, the two genera must be united. The five *Craterogyne* species are now to be referred to as *Dorstenia africana* (Baill.) C.C. Berg, *D. kameruniana* Engl., *D. oligogyna* (Pellegr.) C.C. Berg, *D. djettii* Guillaumet, and *D. dorstenioides* (Engl.) M. Hijman & C.C. Berg, respectively (see Berg & Hijman 1977). Except for *D. dorstenioides*, those species can be placed in the section *Nothodorstenia.*

The revision of this group of *Dorstenia* species does not fit very well in the present paper and will be published separately.

Mainly due to the presence of (caducous) peltate interfloral bracts *D. djettii* links *Dorstenia* with other members of the tribe *Dorstenieae.*

*Ctenocladus* was based on a monstrosity. It has to be rejected for that reason (Intern. Code Art. 17). The inflorescences of the type specimen (which might belong to *Dorstenia psilurus*) have developed in an abnormal way by repeated braching.

2. **Scyphosyce** Baillon, Adansonia **11**: 293 (1875); Engl., Monogr. Afr. Pfl. **1** (*Moraceae*): 30 (1898); Hutch. in Prain, Fl. Trop. Afr. **6** (2): 221 (1917). — Type species: *S. manniana* Baillon.

*Cyathanthus* Engl. in Engl. & Prantl, Nat. Pflanzenfam., Nachtr. **1**: 120 (1897). — Type species: *C. zenkeri* Engl. (= *S. manniana* Baillon).

Small monoecious *undershrubs* with rhizomatous stems and ascending or erect leafy twigs. *Leaves* distichous, pinnately veined; stipules subamplexicaul, free. *Inflorescences* solitary to several together on short-shoots in the leaf axils, bisexual, cup-shaped to funnel-shaped, pedunculate, with 4 reniform, imbricate bracts on the margin of the receptacle; staminate flowers many, in several series, partly in small groups, pedicellate; perianth tubular, (3-)4(-5)-lobed to -fid; stamens 1-2(-3), straight before anthesis, anthers narrow, latrorse; pistillode lacking; pistillate flowers solitary in the centre of the receptacle, free; perianth with 2(-3) free or 4 connate tepals; ovary free, stigmas 2. *Fruit* (¹) free from the enlatged green perianth; exocarp white, fleshy, dehiscent, pushing the endocarp body; endocarp thin; testa (¹) thin with a suborbicular thickened vascularized part below the small hilum; cotyledons (alsmost) equal, thick and fused, radicle subapical and short.

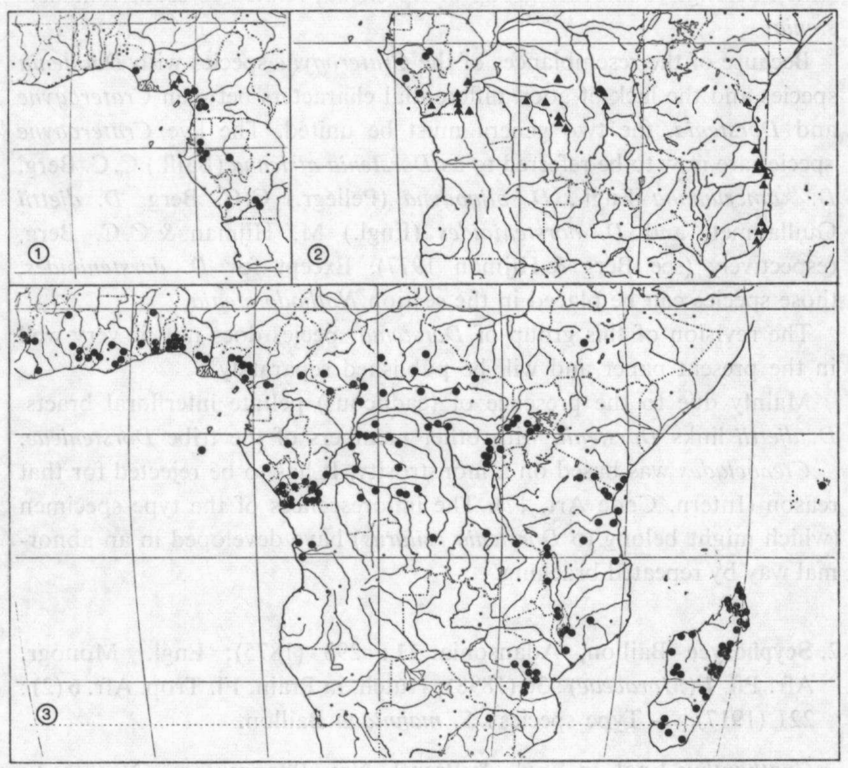

Fig. 1. — Distribution of species of the *Dorstenieae*: map 1, ● *Scyphosyce manniana*, ▲ *S. pandurata*; map 2, ● *Utsetela gabonensis*, ▲ *Bosqueiopsis gilletii*; map 3, *Trilepisium madagascariense*.

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(¹) Characters of fruit and seed only refer to *S. manniana*.

Baillon (1875) founded the genus *Scyphosyce* by describing *S. manniana*. In 1897, Engler described *Cyathanthus*, but he soon (1898) recognized this genus as identical with *Scyphosyce* and transferred *C. zenkeri* to *Scyphosyce*. Two other species were added to the genus *Scyphosyce*: *S. gilletii* (De Wildeman & Th. Durand 1903) and *S. pandurata* (Hutchinson 1917, 1919). Only the latter proved to be distinct from *S. manniana*.

The two species show interesting differences in the inflorescence. In *S. manniana* both the staminate flowers and the pistillate flower arise from the bottom of the cup-shaped to tunnel-shaped receptacle. At anthesis the staminate flowers are almost sessile but in fruit distinctly pedicellate. In *S. pandurata* the (apparently) sessile staminate flowers arise (apparently) from the middle of the funnel-shaped receptacle. However, the tissue surrounding the pistillate flower (which arises from the bottom of the receptacle) is probably formed by the fused pedicels of the staminate flowers. The perianth of staminate flowers of *S. manniana* consists of 2 free conduplicate tepals, sometimes accompanied by a reduced third one. In *S. pandurata* the perianth of the pistillate flower consists of 4 basally connate tepals.

In *S. manniana* the very thin testa coheres with the endocarp which looks like a testa.

In habit the *Scyphosyce* species call to mind several *Dorstenia* species.

### Key to the species of *Scyphosyce*

1.a. Periderm of the twigs not peeling off; pistillate flower with 2(-3) free tepals; S.E. Nigeria to Zaire . . . . . . . . . . . . . . . . . . . . . 1. *S. manniana*
b. Periderm of the twigs peeling off; pistillate flower with 4 connate tepals; S.E. Nigeria . . . . . . . . . . . . . . . . . . . . . . . . 2. *S. pandurata*

2.1. **Scyphosyce manniana** Baillon, Adansonia **11**: 293 (1875); Hutch. in Prain, Fl. Trop. Afr. 6 (2): 221 (1917). — Type: *Mann* 1727, Gabon, Monts de Cristal (P; isotype K). — Fig. 2.

*Cyathanthus zenkeri* Engl. in Engl. & Prantl, Nat. Pflanzenfam., Nachtr. **1**: 120 (1897). — Type: *Zenker* 905, Cameroun, near Bipinde (B; isotypes G, K, P).

*Scyphosyce zenkeri* (Engl.) Engl., Monogr. Afr. Pfl. **1** (*Moraceae*): 31, t. 10 (1898).

*S. gilletii* De Wild., Ann. Mus. Congo, Bot., ser. 5, **1**: 26 (1903); Hauman, Fl. Congo, Ruanda-Urundi **1**: 98 (1948). — Type: *Gillet* s.n., Zaire, near Kinshasa (BR).

*Undershrubs* up ca. 50 cm tall; leafy twigs sometimes branched, 1-4 mm thick, (rather) densely whitish to brownish hirtellous to puberulous with straight to curved hairs; periderm not peeling off. *Leaves* often crowded in the upper part of the twigs, elliptic to lanceolate, mostly broadly to narrowly obovate to subpandurate or oblanceolate, not or hardly inequilateral, (1.5-)5-18 cm long, (0.5-)2-7 cm broad, chartaceous, acuminate to subcaudate, at the base (sub)obtuse to subcordate, at least one half auriculate; margin entire or more or less distinctly crenate to (sometimes coarsely) dentate towards the apex; above (almost) glabrous beneath sparsely to rather densely puberulous to hirtellous (partly with uncinate hairs) especially on the main veins, sometimes almost glabrous; above veins slightly prominent to plane, beneath more or less prominent, 6-15 pairs of secondary veins, usually without parallel tertiary veins; petioles 2-12 mm long, (rather) densely hirtellous, with straight to curved hairs; stipules 2-15(-20) mm long, lanceolate to narrow-ovate, with a prominent costa, the apex mucronate to (sub)aristate, puberulous to almost glabrous, dark brown, subpersistent. *Inflorescences* solitary to several together, at least initially deflexed, 2-4 mm in diameter, cup-shaped to funnel-shaped; bracts ciliolate; the 3-11 mm long peduncle and receptacle glabrous or with sparse appressed unicellular hairs and/or reddish globose-capitate pluricellular hairs, at the base of the peduncle usually a reniform to deltoid, mucronate, ciliolate bract; staminate flowers arising from the bottom of the receptacle, partly in groups of 2-3; perianth 1.5-2.5 mm high, (irregularly) (3-)4(-5)-lobed to -fid, upper part puberulous or only ciliolate, pedicels up to ca. 4 mm long; stamens 1-2(-3), filaments 2-3 mm long, very sparsely to densely hairy, the upper part glabrous, anthers (0.3-)0.5-0.8 mm long, 0.15-0.3 mm broad, connective rather narrow, sometimes apiculate; pistillate flower sessile on the bottom of the receptacle; perianth 2-3 mm high, with 2 free, conduplicate, imbricate, sparsely puberulous to glabrous, ciliolate tepals, sometimes a third plane, lanceolate to narrowly ovate tepal; ovary ca. 1 mm high, style 2-3 mm long, sometimes puberulous, stigmas ca. 1.5 mm long, filiform to vittiform, minutely puberulous. *Infructescences* ca. 7 mm in diam.; fruiting perianth ca. 1-1.2 cm high, fruit ca. 8-10 mm long, endocarp body ca. 6-7 x 4-6 mm, endocarp thin, brown to blackish (with a paler, reticulate venation somewhat rugose); testa thin, cohering

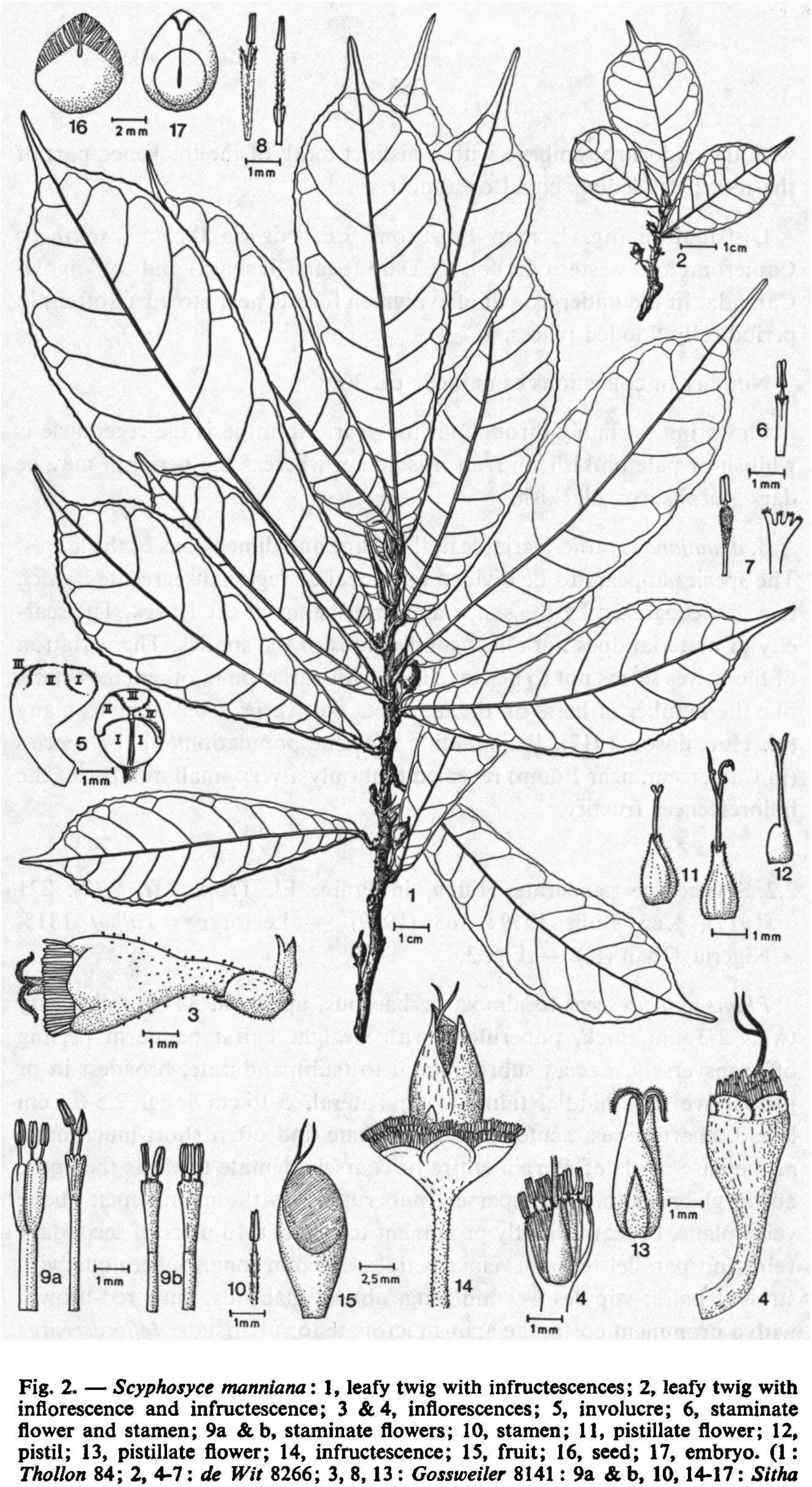

Fig. 2. — *Scyphosyce manniana*: 1, leafy twig with infructescences; 2, leafy twig with inflorescence and infructescence; 3 & 4, inflorescences; 5, involucre; 6, staminate flower and stamen; 9a & b, staminate flowers; 10, stamen; 11, pistillate flower; 12, pistil; 13, pistillate flower; 14, infructescence; 15, fruit; 16, seed; 17, embryo. (1: *Thollon* 84; 2, 4-7: *de Wit* 8266; 3, 8, 13: *Gossweiler* 8141: 9a & b, 10, 14-17: *Sitha* 1938a; 11, 12: *de Wit* 398 or 8266).

with the endocarp; embryo with a distinct mark of the thickened part of the testa; cotyledons equal or almost so.

Distribution (fig. 1, map 1): From S.E. Nigeria through southern Cameroun and western Gabon to Zaire (near Kinshasa) and to Angola-Cabinda. In the undergrowth of evergreen forests near streams, (often) in periodically flooded places.

Number of collections examined: ca. 30.

Flowering probably throughout the year. At anthesis the receptacle is whitish or pale pinkish; in fruit it is green, whereas the perianth may be dark purplish or blackish.

*S. manniana* is rather variable in the shape and dimensions of the leaves. The species appears to be divided into local or regional segregates which may be recognized by the shape and dimensions of the leaves. The scarcity of material does not allow subdivisions of the species. The variation of the leaves seems not to be correlated with variation in other characters, like the number of hairs on the filaments that varies from none to many (cf. Hutchinson 1917). Examination of some populations of the species (in Cameroun, near Loum) revealed that only a very small number of the inflorescences fructify.

2.2. **Scyphosyce pandurata** Hutch. in Prain, Fl. Trop. Afr. **6** (2): 221 (1917), Kew Bull. **1919**: 263 (1919). — Lectotype: *Talbot* 1315, Nigeria, Oban (K). — Fig. 3.

*Plants suffrutescent* to almost herbaceous, up to ca. 30 cm tall. Leafy twigs 2-3 mm thick, puberulous with straight hairs; periderm peeling off transversely. *Leaves* subrhomboid to (sub)pandurate, broadest in or just above the middle, (almost) equilateral, 5-16 cm long, 2.5-6.5 cm broad, chartaceous, acute to subacuminate and often short-mucronate, at the base cordate; margin entire or coarsely dentate towards the apex; above glabrous, beneath sparsely puberulous on the main veins; above veins plane, beneath slightly prominent to plane, 8-13 pairs of secondary veins, no parallel tertiary veins; petioles 3-6 mm long, puberulous with straight hairs; stipules 6-9 mm long, almost glabrous, dark red-brown, with a prominent costa, the apex mucronate to subaristate. *Inflorescences* solitary, receptacle funnel-shaped, ca. 5 mm high, 3-4 mm in diam.; peduncle 0.5-1.5 cm long, peduncle and receptacle with sparse minute white unicellular hairs and less sparse reddish globose capitate pluricellu-

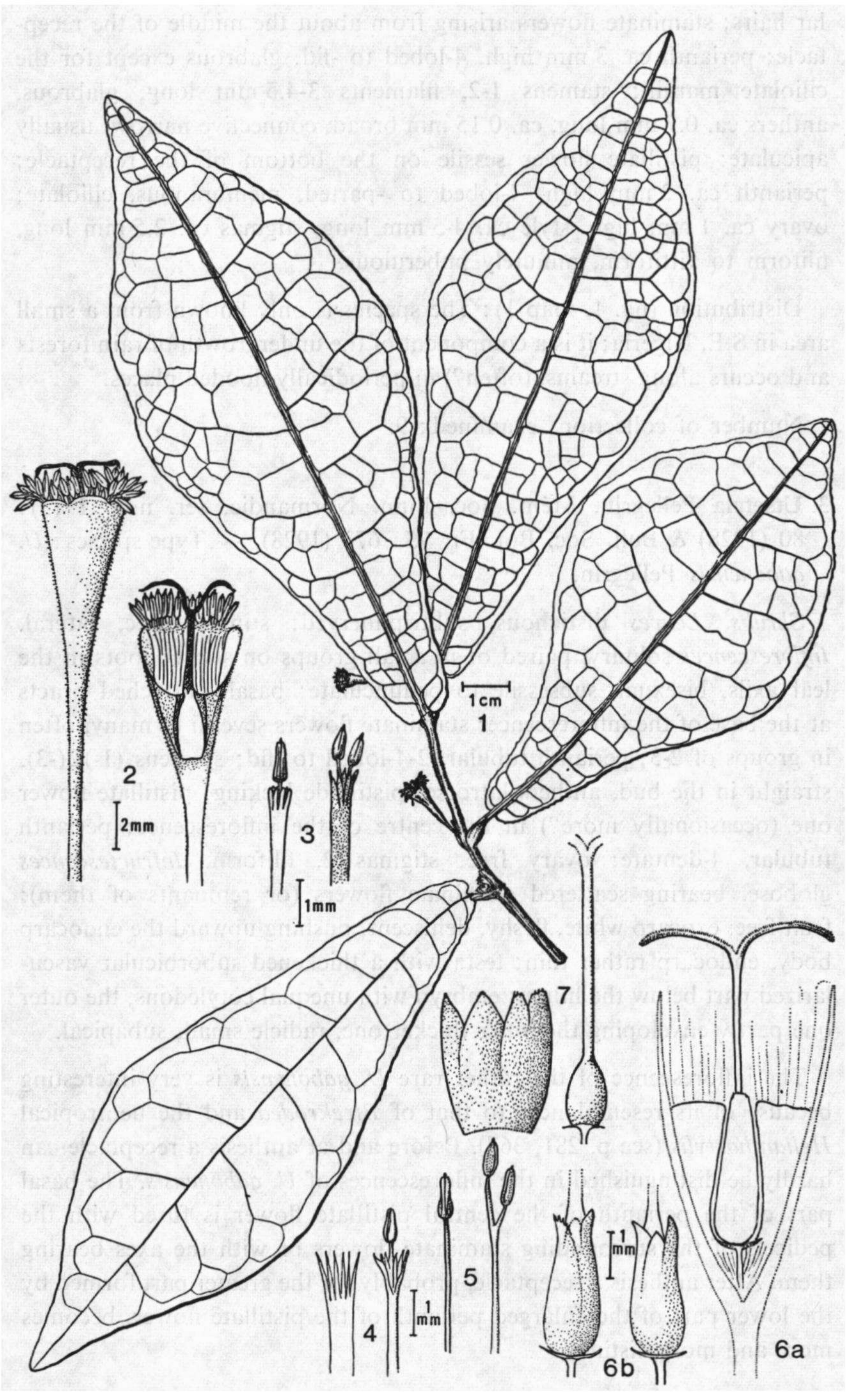

**Fig. 3.** — ***Scyphosyce pandurata*: 1, leafy twig with inflorescences; 2, inflorescence; 3, staminate flowers; 4, staminate flower and perianth; 5, stamens; 6a & b, pistillate flower; 7, perianth and pistil (*Latilo* 45806).**

lar hairs; staminate flowers arising from about the middle of the receptacle; perianth ca. 3 mm high, 4-lobed to -fid, glabrous except for the ciliolate margin; stamens 1-2, filaments 3-4.5 mm long, glabrous, anthers ca. 0.7 mm long, ca. 0.15 mm broad, connective narrow, usually apiculate; pistillate flower sessile on the bottom of the receptacle; perianth ca. 3 mm high, 4-lobed to -parted, membranous, ciliolate; ovary ca. 1 mm high, style ca. 4-5 mm long, stigmas ca. 2.5 mm long, filiform to vittiform, minutely puberulous.

Distribution (fig. 1, map 1): The species is only known from a small area in S.E. Nigeria; it is a component of the undergrowth of rain forests and occurs along streams, (often?) in periodically flooded places.

Number of collections examined: 9.

3. **Utsetela** Pellegrin, Mém. Soc. Linn. Normandie, ser. nov. **1** (3): 80 (1928) & Bull. Soc. Bot. Fr. **75**: 673 (1928). — Type species: *U. gabonensis* Pellegrin.

*Shrubs. Leaves* distichous, subtriplinerved; stipules free, lateral. *Inflorescences* solitary, paired or in small groups on short-shoots in the leaf axils, bisexual, subsessile to pedunculate; basally attached bracts at the base of the inflorescence; staminate flowers several to many, often in groups of 2-3; perianth tubular, 2-4-lobed to -fid; stamens (1-)2(-3), straight in the bud, anthers latrorse; pistillode lacking; pistillate flower one (occasionally more?) in the centre of the inflorescence; perianth tubular, 4-dentate; ovary free, stigmas 2, filiform. *Infructescences* globose, bearing scattered staminate flowers (or remnants of them); fruit free, exocarp white, fleshy, dehiscent, pushing upward the endocarp body, endocarp rather thin; testa with a thickened suborbicular vascularized part below the hilum; embryo with unequal cotyledons, the outer one partly enveloping the inner thicker one, radicle small, subapical.

The inflorescence of the rather rare *U. gabonensis* is very interesting because of its resemblances to that of *Bleekrodea* and the neotropical *Helianthostylis* (see p. 281, 367). Before and at anthesis a receptacle can hardly be distinguished in the inflorescences of *U. gabonensis*. The basal part of the perianth of the central pistillate flower is fused with the pedicels of the surrounding staminate flowers or with the axes bearing them. After anthesis a receptacle, probably for the greater part formed by the lower part of the enlarged perianth of the pistillate flower, becomes more and more distinct.

The infructescence is very similar to that of *Helianthostylis* (see Berg 1972a, 1972b). The young inflorescence is reminiscent of that of *Bleekrodea*. In *Utsetela* the fruit, with dehiscent exocarp, is free (as in *Bleekrodea*, but unlike *Helianthostylis*). The endocarp body is possibly released through a rift in the fruiting perianth (c.q. receptacle) as in *Bleekrodea*.

3.1. **Utsetela gabonensis** Pellegrin, Mém. Soc. Linn. Normandie, ser. nov. 1 (3): 81, t. 6 (1928) & Bull. Soc. Bot. Fr. 75: 673 (1928). — Type: *Le Testu* 1930, Gabon, near Tchibanga (P; isotypes B, BM, K). — Fig. 4.

*Shrubs* (branched or unbranched) up to 2.5 m (or more?) tall; latex white; leafy twigs 1-3.5 mm thick, puberulous with white to brown retrorse uncinate hairs. *Leaves* elliptic to lanceolate, mostly broadest in or above the middle, not or slightly inequilateral, (2-)3-19 cm long, (0.5-)1-8 cm broad, chartaceous, acuminate to caudate or to subacute, at the base acute to obtuse; margin (faintly) repand, more often coarsely dentate to lobed towards the apex; sparse hairs on the main veins and the margin; above the costa prominent, the other veins slightly prominent to plane or slightly impressed, beneath veins prominent, 3-8 pairs of secondary veins, the lower pair departing from the costa at an acute angle, the other pairs departing from the costa from about the lower third of the lamina upwards at less acute angles, without or with few parallel tertiary veins; stipules 2-5 mm long, ovate to deltoid, subaristate, with a prominent costa, sparsely puberulous, subpersistent. *Inflorescences* mostly solitary or paired, or sometimes more together in the leaf axils, 3-4 mm in diam.; peduncle up to 2 mm long, puberulous with straight and uncinate white to brownish hairs; perianth of the staminate flower 1-2 mm high, tubular, often more or less narrowed towards the base, irregularly 2-4-lobed to 2-4-fid, puberulous with partly uncinate hairs; stamens free or basally connate, filaments 1-4.5 mm long, slender, anthers 0.4-0.8(-1.0) mm long, 0.2-0.5 mm broad, apiculate or not, connective rather broad; perianth of the pistillate flower ca. 3 mm long, puberulous with partly uncinate hairs; style 2-3 mm long, stigmas 1-4 mm long; bracts up to 7-8, in 2-3 series, with straight, relatively long, brownish, and uncinate, white to brownish hairs, the 3-4 outer ones deltoid to ovate, large (to ca. 3.5 mm long), the inner ones narrowly ovate to lanceolate or linear, usually much smaller. *Infructescences* (sub)globose, 6-9 mm in diam.; peduncle up to 3.5 mm long; receptacle densely puberu-

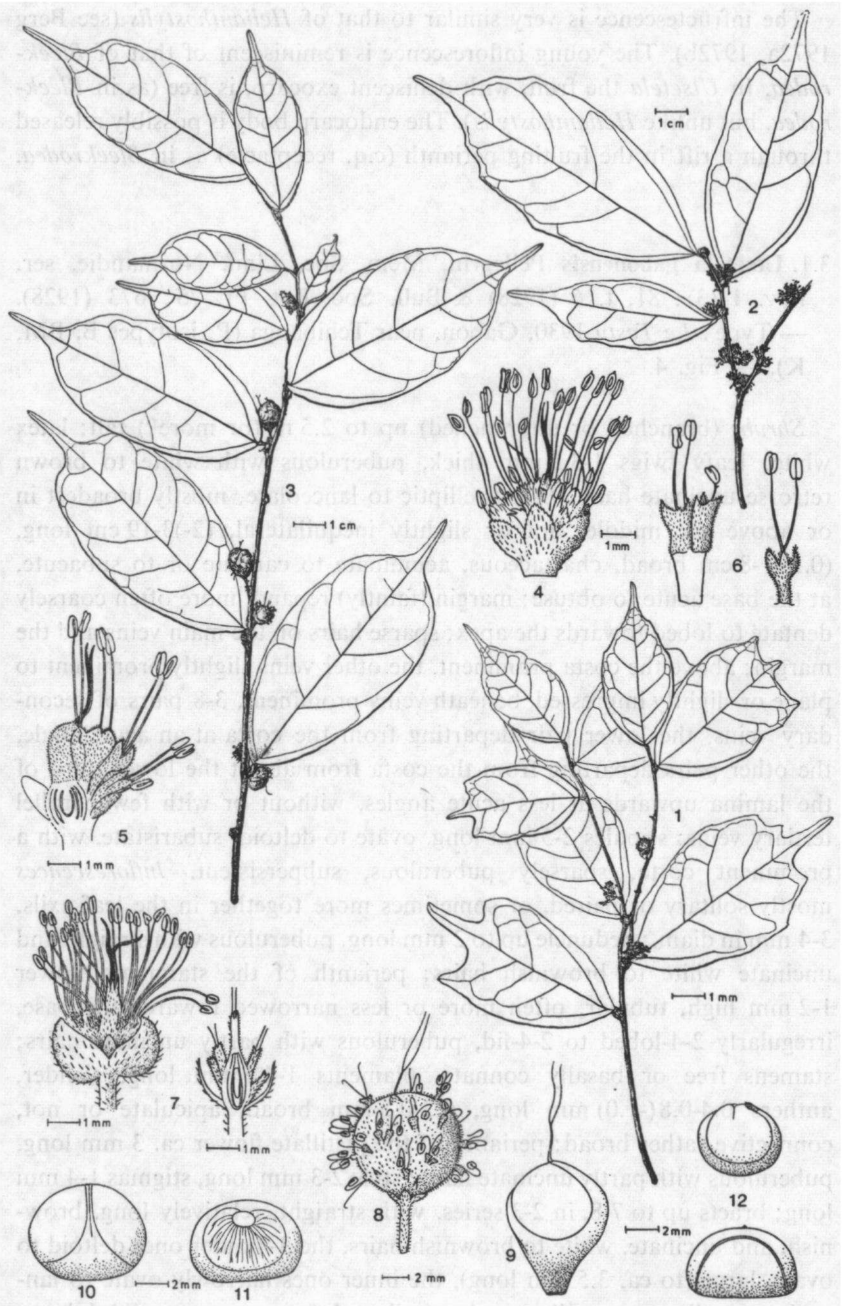

**Fig. 4.** — ***Utsetela gabonensis*** **: 1 & 2, leafy twigs with inflorescences; 3, leafy twig with infructescences; 4, inflorescence; 5, pistillate and staminate flowers; 6, staminate flowers; 7, inflorescence; 8, infructescence; 9, fruit; 10, endocarp body; 11, seed; 12, embryo (1, 4-6 :** ***Le Testu*** **1930; 2 :** ***Le Testu*** **8012; 3, 8-12 :** ***Le Testu*** **5807; 7 :** ***Lebrun*** **5879).**

lous with uncinate hairs; filaments in the persisting staminate flowers often reflexed; endocarp body ca. 8 × 6-7 mm; seed ca. 7 × 5-6 mm.

Distribution (fig. 1, map 2): Known from some localities in Gabon, a single locality in Congo (along the Lower Kouilou River, near Sounda), and a single locality in Zaire (Kivu, Terr. Panzi, Lumuna); in the undergrowth of forests.

Number of collections examined: 13.

Flowering probably throughout the year.

According to a field note of *Le Testu* 8012, the inflorescence may contain more than one pistillate flower.

4. **Bosqueiopsis** De Wild. & Th. Dur., Bull. Herb. Boiss., ser. 2, **1**: 839 (1901); Engl., Bot. Jahrb. **51**: 435 (1914); Hutch. in Prain, Fl. Trop. Afr. 6 (2): 217 (119); Hauman, Fl. Congo, Ruanda-Urundi **1**: 96 (1948). — Type species: *B gilletii* De Wild. & Th. Dur.

Monoecious or (androdioecious?) *shrubs* or *trees*. *Leaves* distichous, subtriplinerved to pinnately veined; stipules free, subamplexicaul. *Inflorescences* bisexual or staminate, discoid to subglobose, usually pedunculate, with interfloral peltate bracts and 1-3 rows of imbricate basally attached marginal or subtending bracts; staminate flowers several to many; perianth 3-4-fid to 3-4-parted; stamens (1-)2, inflexed before anthesis, gradually straightening at anthesis, anthers latrorse; pistillode lacking; pistillate flower solitary, immersed in the centre of the receptacle and adnate to it; ovary adnate to the perianth; stigmas 2, vittiform. *Infructescences* with a yellow to orange fleshy receptacle; endocarp crustaceous; testa rather thick with a thickened, suborbicular, apical, not distinctly vascularized part; cotyledons unequal, thick, radicle very short, in a lateral pit of the embryo.

Four *Bosqueiopsis* species have been described and kept separated mainly on the basis of differences in the shape and dimensions of the leaves. These differences are not very distinct and cannot be used for distinguishing taxa, not even on an infraspecific level.

On the other hand, differences in habit and habitat between groups of populations of the single species *B. gilletii* in Zaire and in East Africa, suggesting the presence of ecological differences, may prove to be constant and significant. At this moment, however, the scarcity of collections and the poor data given by the labels do not provide a sufficient basis for distinguishing subspecies. A subdivision on the basis of these characters should be made only after ample consideration, in view of the rather broad ecological amplitude of many arborescent African *Moraceae* (see p. 278, 279).

The distinctly inflexed stamens which gradually straighten out at anthesis, and the tendency to produce unisexual inflorescences are remarkable features of *B. gilletii*.

The name *Trymatococcus parvifolius* was probably erroneously published by Engler (1915) together with the drawing which also accompanied the description of *Bosqueiopsis parvifolia* Engler (1914).

The bisexual inflorescences and infructescences of *Bosqueiopsis* resemble those of the neotropical genus *Trymatococcus*.

4.1. **Bosqueiopsis gilletii** De Wild. & Th. Dur., Bull. Herb. Boiss., ser. 2, **1**: 840 (1901); Engl., Bot. Jahrb. **51**: 435, t. 2 (1914). — Type: *Gillet* 1742, Zaire, Kimuenza (BR). — Fig. 5.

*B. lujae* De Wild., Pl. Nov. Herb. Hort. Then. **1** (7): 239, t. 56 (1907). — Type: *Luja* 78, Zaire, Sankuru River (BR).

*B. carvalhoana* Engl., Bot. Jahrb. **51**: 436, t. 3 (1914). — Type: *de Carvalho* s.n., Moçambique (COI; isotype B).

*B. parvifolia* Engl., Bot. Jahrb. **51**: 437, t. 4 (1914). — Type *Koerner* 2259, Tanzania, Amani (B).

*Trymatococcus parvifolius* Engl., Pflanzenw. Afr. **3** (1): 27, t. 15 (1915), without description, plate based on *Koerner* 2259.

*Shrubs* or *trees* up to 25 m tall; latex white to yellowish or greyish, Leafy twigs 1-3(-5) mm thick, sparsely to densely puberulous with retrorse, uncinate or curved hairs. *Leaves* (elliptic to) oblong to lanceolate, mostly tending to obovate or oblanceolate, distinctly to hardly inequilateral, (1-)2-14(-21) cm long, (0.7-)1.5-6(-12.5) cm broad, chartaceous to subcoriaceous, acuminate, at the base acute to obtuse; margin entire; above almost glabrous, beneath on the veins puberulous with uncinate hairs; above veins slightly prominent to plane, beneath especially the main veins prominent, 3-6 pairs of secondary veins, the basal pair departing from the costa at an acute angle, the others (often not distinctly paired) departing from the costa from about the middle of the lamina upwards, at less acute angles, without parallel tertiary veins; petioles

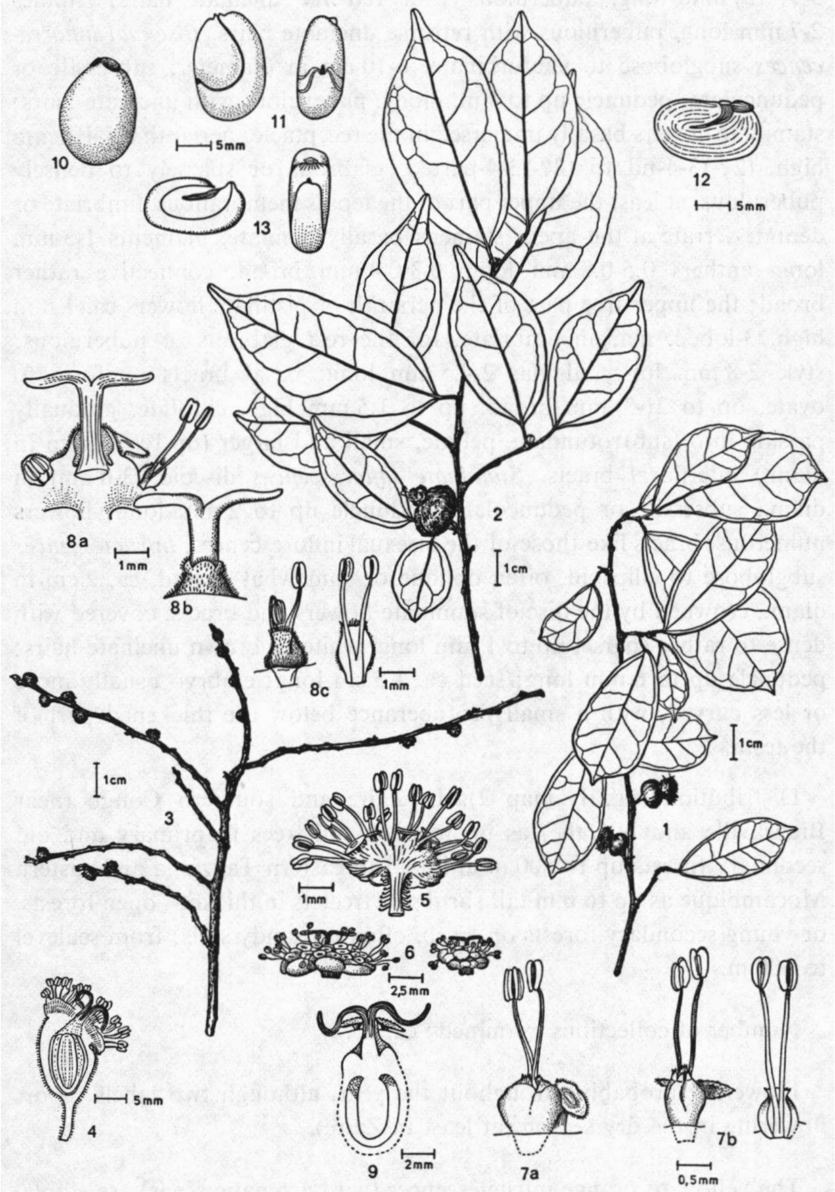

**Fig. 5. — *Bosqueiopsis gilletii*: 1, leafy twig with inflorescences; 2, leafy twig with infructescence; 3, leafless twig with staminate inflorescences; 4, bisexual inflorescence; 5, staminate inflorescence; 6, staminate inflorescences with abortive pistillate flower; 7a & b, staminate flowers and bracts; 8a, b & c, abortive pistillate flower and staminate flowers; 9, pistillate flower; 10, seed; 11, embryo; 12, seed; 13, embryo (1, 2: *Carlier* 272; 3: *Schlieben* 5437; 4, 5, 7a & b, 9: *Gillett* 17956; 6, 8a, b & c: *Collin* 17; 10, 11: *Torre & Paiva* 10051; 12, 13: *s. coll.* s.n.).**

3-9(-15) mm long, puberulous with retrorse uncinate hairs; stipules 2-7 mm long, puberulous with retrorse uncinate hairs. *Bisexual inflorescences* subglobose to subturbinate, 6-10 cm in diameter, subsessile or pedunculate; peduncle up to 4 mm long, puberulous with uncinate hairs; staminate flowers basally immersed in the receptacle; perianth 0.5-1.5 mm high, (2?-)3-4-fid to (2?-)3-4-parted, glabrous or sparsely to densely puberulous, at least the upper part of the tepals membranous, fimbriate or dentate-serrate at the apex; stamens basally connate, filaments 1-3 mm long, anthers 0.5-0.8 mm long, 0.3-0.4 mm broad, connective rather broad; the upper free part of the perianth of pistillate flowers ca. 1 mm high, 3-lobed, margin fimbriate, for the rest glabrous or puberulous; style 2-8 mm long, stigmas 2-4.5 mm long; basal bracts reniform to ovate, up to 2(-3) mm broad, up to 1.5 mm high, ciliolate, gradually passing into (sub)rotundate, peltate, small and larger (up to 1.5 mm in diam.) interfloral bracts. *Staminate inflorescences* discoid, 3-6 mm in diam., subsessile or pedunculate; peduncle up to 2 mm long; flowers numerous; bracts like those of the bisexual inflorescences. *Infructescences* subglobose to ellipsoid, often oblique or somewhat curved, ca. 2 cm in diam., crowned by the disc of staminate flowers and bracts, covered with dense to rather sparse, up to 1 mm long, white or brown uncinate hairs; peduncle up to 6 mm long; seed ca. 1.5 cm long; embryo usually more or less curved, with a small protuberance below the thickened part of the testa.

Distribution (fig. 1, map 2). In Zaire and southern Congo (near Brazzaville and N'Gabé) as up to 35 m tall trees in primary and old secondary forests up to 500 m altitude; in eastern Tanzania and eastern Moçambique as up to 6 m tall shrubs or treelets in thickets, open forests, or young secondary forests or scrub, often on sandy soils; from sealevel to 500 m.

Number of collections examined : ca. 45.

Flowering probably throughout the year, although two labels report flowering in the dry season (at least in Zaire).

The yellow to orange infructescences (with aromatic seeds) are edible. The wood is used for carpentry.

In some of the collections staminate inflorescences were found. These discoid inflorescences may have a central abortive pistillate flower with more or less well-developed style and stigmas. On the basis of the available herbarium material it is not possible to ascertain if bisexual and staminate inflorescences are borne on separate trees or on the same tree.

5. **Trilepisium** Thouars, Gen. Nov. Madag.: 22 (1806); DC., Prodr. **2**: 639 (1825); Benth. & Hook., Gen. Pl. **1** (2): 605 (1865). Proposal *Bosqueia* versus *Trilepisium*: Taxon **17**: 731 (1968), **19**: 293 (1970), and **24**: 239 (1975). — Type species: *Trilepisium madagascariense* DC.

*Bosqueia* Thouars ex Baillon, Adansonia **3**: 338 (1863); Benth. & Hook., Gen. Pl. **3**(1): 379 (1880); Engl., Monogr. Afr. Pfl. **1** (*Moraceae*): 35 (1898); De Wild. & Th. Dur., Bull. Herb. Boiss., ser. 2, **1**: 839 (1901); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 218 (1917); Léandri, Not. Syst. **13**: 176 (1948). — Lectotype species: *B. thouarsiana* Baillon (= *Trilepisium madagascariense* DC.); see Capuron, Taxon **17**: 732 (1968).

*Bosquiea* Benth. & Hook., Gen. Pl. **3**(1): 370 (1880).

*Pontya* A. Chev., Végét. Ut. Afr. Trop. Fr. **5**: 263 (1909), nomen; Bull. Soc. Bot. Fr. **58** (Mém. 8a): 210 (1912); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 219 (1917). — Type species: *P. excelsa* A. Chev. (= *Trilepisium madagascariense* DC.).

Monoecious *trees*. *Leaves* distichous, pinnately veined to subtriplinerved; stipules fused, fully amplexicaul. *Inflorescences* solitary or sometimes in pairs on short shoots in the axils of leaves, initially enveloped by two modified stipules, bisexual, discoid to turbinate, pedunculate, with a 6-8-lobed to -fid submembranaceous involucre, the upper part of the receptacle submembranous, bent inwards and with its margin fused with the inner surface of the receptacle, covering many free stamens, at anthesis circumscissile and leaving a tubular and torn part aouund the perianth of the single central pistillate flower and a marginal and torn part; anthers latrorse; pistillate flower basally embedded in the receptacle, perianth tubular; ovary adnate to the perianth; stigmas 2, vittiform. *Infructescences* oblongoid to globose, crowned by the remains of the submembranous part of the receptacle and the stamens, the receptacle fleshy, red to blackish; endocarp crustaceous; testa rather thin, with a thickened suborbicular vascularized part below the hilum; embryo with a distinct mark of this part of the testa; cotyledons thick, equal and fused, radicle short, apical or subapical.

The genus *Trilepisium* was described by Du Petit-Thouars (1806) and placed in the *Rosaceae.* De Candolle (1825) published the epithet *madagascariense* and regarded the genus as related to the *Rosaceae.* From this family *Trilepisium* was definitely excluded by Bentham & Hooker (1865) and henceforth almost neglected, until Capuron (1968) recognized it as identical with the genus *Bosqueia,* established by Baillon (1863), which genus was even partly based on material having served for the description of *Trilepisium.* Capuron's finding resulted in a proposal to conserve the name *Bosqueia.* This proposal was not carried (cf. Taxon **19**: 293. 1970 and **24**: 239. 1975).

Within *Bosqueia* 13 species have been described. From material of this genus Chevalier (1912) described the new genus *Pontya* with *P. excelsa* as the sole species. All the described species prove to belong to the resurrected *T. madagascariense.* In spite of the considerable variation, no infra-specific taxa with a sound basis can be distinguished.

Because of the highly evolved inflorescence *Trilepisium* occupies a rather isolated position within the *Dorstenieae.*

*Inflorescence*: The peculiar inflorescences of *Trilepisium* are borne on short-shoots in the axils of the leaves. Two modified and more or less differently shaped coriaceous stipules form the scales of the bud, enclosing the single young, laterally compressed inflorescence and often a minute leaf which belongs to the upper stipule. The short-shoot may develop into a normal shoot. At anthesis the inflorescence appears from between the scale-like stipules and points downwards. It soon becomes discoid to broadly turbinate. The inflorescence has a central pistillate flower, basally embedded in the receptacle and a ring of stamens of the perianthless staminate flowers in several rows. Before anthesis the stamens are completely covered by a membranous structure bending over the stamens from the margin of the receptacle to near the base of the free part of the perianth of the pistillate flower. At anthesis this membrane tears all round and leaves a tubular to more or less infundibuliform, irregularly torn part around the perianth of the pistillate flower and a marginal, also irregularly torn part. The membranous structure probably represents the enlarged peripheral part of the receptacle (occurring in some *Dorstenia* species). Its slightly thickened margin is adnate to the inner rim of the stamen-bearing part of the receptacle. The inflorescence has a (sometimes) irregularly 6-8-lobed to -fid involucre, quite separate from the stamen-covering membranous structure. The present interpretation of the structure of the inflorescence of *Trilepisium* has to be tested by an anatomical study for which well-preserved young inflorescences are required.

The way in which the young stamens are protected is rather complicated, the evidently not very effective protection by the (too weak) enlarged margin of the receptacle is supplemented by the more effective protection provided by the firm, modified stipules.

*Bosquiea spinosa excluded*: *B. spinosa* Engl., Bot. Jahrb. **40**: 548 (1908) & Pflanzenw. Afr. **3**(1): 33 (1915). It proved to belong to the Ulmaceous genus *Chaetacme*. Rendle [in Prain, Fl. Trop. Afr. **6**(2): 14. 1916] put this species into the synonomy of *Chaetacme microcarpa* Rendle. Afterwards it is found in the synonomy of *Chaetacme aristata* Planchon, see Fl. Trop. W. Afr., ed. 2, **1**: 593 (1958); Letouzey, Fl. Cameroun **8**: 57 (1968).

5.1. **Trilepisium madagascariense** DC., Prodr. **2**: 639 (1825). — Type: *Du Petit-Thouars* s.n., Madagascar (P). — Fig. 6 and 7.

*Bosqueia thouarsiana* Baillon, Adansonia **3**: 339, t. 10 (1863); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 34, t. 7 (1952). — Type: *Du Petit-Thouars* s.n., Madagascar (P); very probably belonging to the same collection as the type of *T. madagascariense*.

*B. thouarsiana* var. *acuminata* Baillon, Adansonia **3**: 339 (1863). — Based on the same type as the species.

*B. thouarsiana* var. *pyriformis* Baillon, Adansonia **3**: 339 (1863); Léandri, Not. Syst. **13**: 179 (1948). — Type: *Boivin* s.n., Madagascar, Nossi Bé (P).

*B. boiviniana* Baillon, Adansonia **3**: 340, t. 10 (1863); Léandri, Not. Syst. **13**: 179 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 36, t. 7 (1952). — Type: *Boivin* s.n. (comm. Richard), Madagascar, Nossi Bé (P).

*B. phoberos* Baillon, Adansonia **8**: 72, t. 4 (1867); Aubrév., Fl. For. Côte d'Ivoire **1**: 68 (1958). — Type: *Boivin* s.n., Tanzania, Zanzibar (P; isotypes BM, K).

*B. angolensis* Ficalho, Pl. Ut. Afr. Port.: 27 (1884); De Wild. & Th. Dur., Bull. Herb. Boiss., ser. 2., **1**: 839 (1901). — Type: *Welwitsch* 456, Angola, Golungo Alto, near Sange (B, BM, G, K, LISU, P; the specimen in LISU probably served for the description of *B. angolensis*, that in B for the description of *B. welwitschii*).

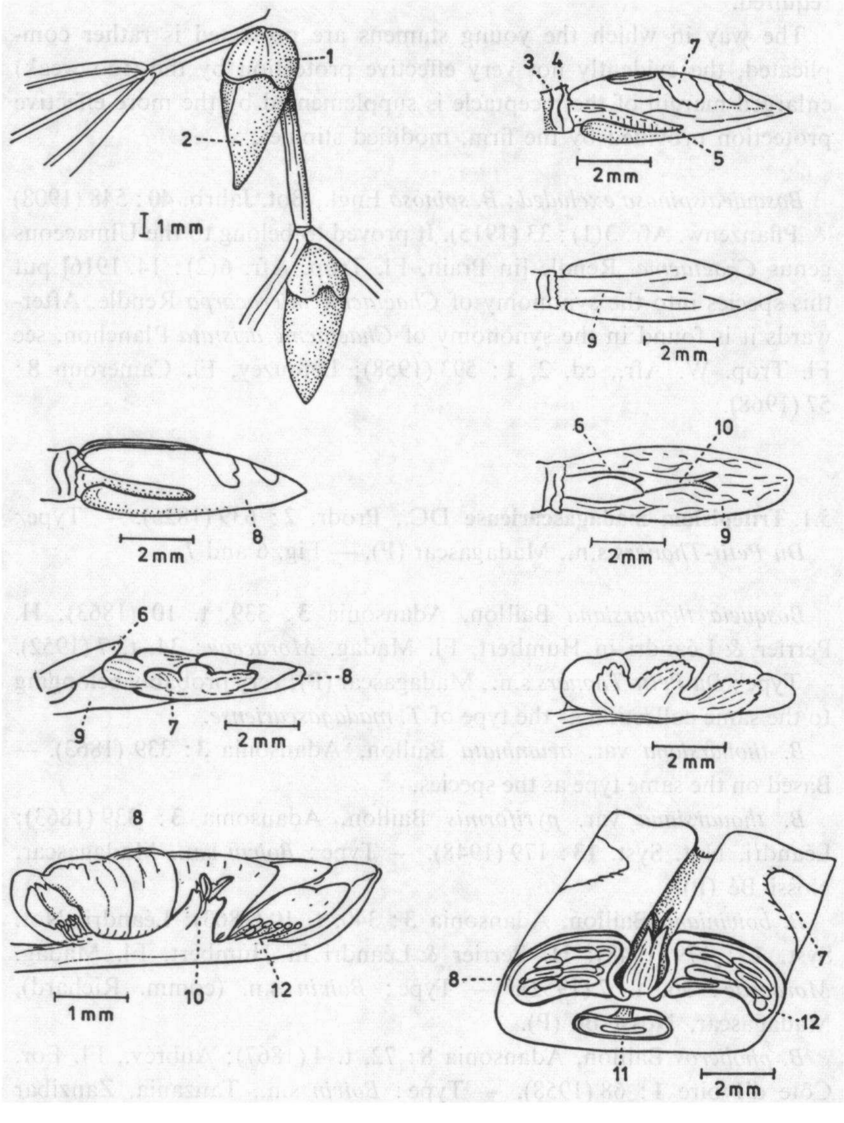

**Fig. 6. — Young inflorescence of *Trilepisium madagascariense*: 1, lower bud scale (= fused, modified stipules); 2, upper bud scale (= fused, modified stipules); 3 & 4, scars of bud scales; 5, reduced leaf; 6, shoot apex; 7, involucre; 8, expended margin of the receptacle; 9, peduncle; 10, pistillate flower; 11, ovary; 12, stamens (*Garcia* 886).**

*B. welwitschii* Engl., Monogr. Afr. Pfl. 1 (*Moraceae*): 36 (1898); Engl., Bot. Jahrb. **51**: 439, t. 5 (1914); Hutch. in Prain, Fl. Trop. Afr. 6(2): 218 (1917).

*Centrogyne angolensis* Welw., herbarium label, name published by Benth. & Hook., Gen. Pl. 3(1): 370 (1880).

*Bosqueia gymnandra* J.G. Baker, Fl. Mauritius Seychelles: 283 (1877). — Type: *Horne* 417, Seychelles (K).

*B. cerasifolia* Volkens ex Engl., Monogr. Afr. Pfl. 1(*Moraceae*): 36 (1898); Engl., Bot. Jahrb. **51**: 439, t. 5 (1914); Hutch. in Prain, Fl. Trop. Afr. 6(2): 219 (1917). — Type: *Volkens* 1935, Tanzania, Kilimanjaro region (B; isotypes BM, BR, G).

*B. carvalhoana* Engl., Pflanzenw. Afr. 3(1): 33 (1915), nomen subnud.

*B. danguyana* Léandri, Not. Syst. **13**: 178 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 35, t. 7 (1952). — Lectotype: *Perrier de la Bâthie* 9956, Madagascar, Analamazaotra (P).

*B. calcicola* Léandri, Not. Syst. **13**: 179 (1948); Perrier de la Bâthie & Léandri in Humbert, Fl. Madag. *Moraceae*: 35, t. 7 (1952). — Type: *Perrier de la Bâthie* 9841, Madagascar, Tsingy-mavo, near Ampandrano, on the Ranobe River (P).

*B. orientalis* Léandri, Not. Syst. **13**: 180 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 38, t. 7 (1952). — Type: *Perrier de la Bâthie* 9898, Madagascar, between Fénérive and Lake Aloatra (P).

*B. manongarivensis* Léandri, Not. Syst. **13**: 180 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 38 (1952). — Type: *Perrier de la Bâthie* 2321, at the base of Massif of Manongarivo, along the Sambirano River (P).

*B. occidentalis* Léandri, Not. Syst. **13**: 181 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 39, t. 7 (1952). — Type: *Perrier de la Bâthie* 1382, Madagascar, near Ankirihitra (P).

*Pontya excelsa* A. Chev., Végét. Ut. Afr. Trop. Fr. **5**: 263 (1909), nomen; Bull. Soc. Bot. Fr. **58**(Mém. 8d): 210 (1912), descr.; Hutch. in Prain, Fl. Trop. Afr. 6(2): 219 (1917). — Lectotype: *Chevalier* 20990, Guinea, between Lola and N'ZO (P; isotypes B, BR).

*Trees*, mostly up to 20-25 m, sometimes up to 40 m tall; latex white, turning red or brownish; leafy twigs (0.5-)1-4 mm thick, usually glabrous, sometimes with sparse minute uncinate hairs. *Leaves* elliptic to oblong to lanceolate, sometimes subrotundate, broadest in or often above the middle and then to broadly or narrowly obovate or oblanceolate, (1-)2-12(-18) cm long, (0.5-)1.5-6.5(-8) cm broad, coriaceous to subcoriaceous, usually

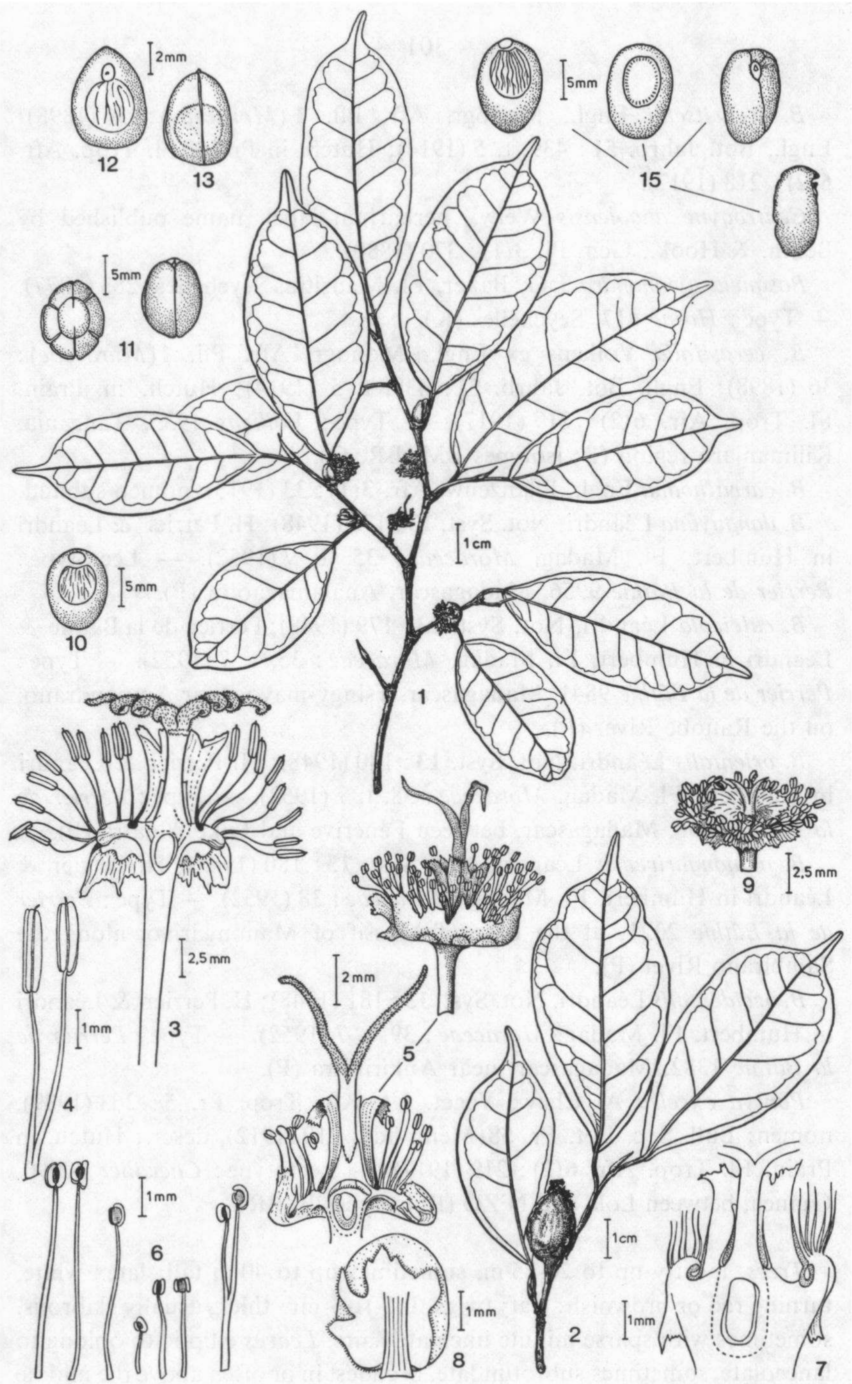

Fig. 7. — ***Trilepisium madagascariense*****: 1, leafy twig inflorescences; 2, leafy twig with infructescence; 3, inflorescence; 4, stamens; 5, inflorescence; 6, stamens; 7, inflorescence; 8, involucre; 9, inflorescence; 10, seed; 11, embryo; 12, seed; 13, embryo; 14, seed, 15, embryo (1, 2, 10, 11 : *Breteler* 2732; 3, 4 : *Gossweiler* 4394; 5, 6 : *Simao* 506; 7, 8 : *Gossweiler* 6514; 9 : *Mendonça* 141; 12, 13: *Capuron* 948; 14, 15 : *Devred* 2454).**

shortly or long-acuminate, sometimes subcaudate, subacute, obtuse or emarginate, at the base acute to obtuse, often subauriculate; margin entire, rarely near the base incised to near the costa; glabrous on both sides, beneath often with minute oblongoid-capitate white pluricellular hairs; above veins slightly prominent to plane, the costa sometimes slightly impressed, beneath the costa prominent, the other veins less prominent to plane, 4-10(-12) pairs of secondary veins, the basal pair of secondary veins often distinct, often departing from the costa at more acute angles than the other secondary veins, without parallel tertiary veins; petioles 3-15 mm long; stipules 2-12 mm long, coriaceous, glabrous or sometimes with sparse minute uncinate hairs and/or ciliolate. *Inflorescences* (2-)5-8(-10) mm in diam.; peduncle 2-12 mm long; receptacle and peduncle glabrous or sometimes with sparse uncinate hairs; involucre glabrous or with sparse uncinate hairs and/or ciliolate; stamens many, often 2 or more basally connate, filaments (0.5-)10 mm long, anthers ca. 0.3-2.0 mm long, ca. 0.3-0.6 mm broad, especially the longer ones often apiculate; occasionally 2 pistillate flowers; perianth 1.5-3 mm high, 4-lobed or irregularly incised to fimbriate, ciliolate; style (1-)2-9 mm long, stigmas 2-8 mm long, straight or twisted. *Infructescences* often slightly oblique or curved, ca. 0.8-2.5(-3) cm long, ca. 0.15-1.5(-2.5) cm in diam.; receptacle glabrous or with sparse hairs, fleshy; peduncle up to 20(-30) mm long; seed ellipsoid to subglobose, ca. 6-16 mm long, ca. 4-14 mm broad.

Distribution (fig. 1, map 3): From Guinea to Angola and trough Zaire, the Central African Republic, and Uganda to S. Kenia, from there southwards to northern Natal (Republic of South Africa); besides in S. Ethiopia, in Annobon, Madagascar, and the Seychelles, according to Horne (coll. 417) on all islands, but not common. On the continent as evergreen trees in primary or secondary forests in regions with evergreen or semi-deciduous forests, often along streams, also in montane forests up to 2000(-2500?) m altitude; rare, frequent, or dominant. In Madagascar widely distributed, mostly as evergreen trees in wet to dry forests, on various soils, from sealevel to 1300 m.

Number of collections examined: ca. 330 (African continent), ca. 100 (Madagascar), 5 (Seychelles).

In the whole area flowering throughout the year, with tops at the beginning and the end of the year; probable regional differences in (main) flowering times could not be established because of the scarce data available.

The stamens (and involucre) are purple. McWhriter (coll. 228) reported that the inflorescences have a pleasant scent.

The wood can be used for construction. The fruits (seeds) are locally eaten. The latex turning red is tinctorial.

The trees of *T. madagascariense* are mostly small or medium-sized. They may reach a height of 40 m. These tall trees possibly occur more frequently at higher elevations (montane forests). In dry habitats (in Madagascar) the habit may be shrub-like. The trees are evergreen, but may periodically shed their leaves in dry habitats (Madagascar). They are occasionally epiphytic when young and strangling when older (*Leeuwenberg* 9511, Cameroun, near Nkongsamba).

The data from labels do not give certainty about the colour of the infructescences at full maturity. The infructescence turns from green to yellow, brownish or reddish. As a rule it finally turns blackish or dark purple, but it may retain a yellow or reddish to blood-red colour, even at full maturity. In the mature infructescence there is a mealy layer between the coloured outer layer of the receptacle and the endocarp.

*T. madagascariense* is very variable in leaf characters, dimensions of floral parts, and the shape and dimensions of the infructescence. On the African continent the species is rather uniform in its leaf characters. The lamina is usually elliptic to oblong or broadly ovate and more or less distinctly subtriplinerved. On the average the leaves are narrower in East Africa. A more pronounced difference between the representatives of the species in East Africa and in Central and West Africa is found in the length of the anthers. In the former area it varies from 0.3-1.0 mm. In the south-western part of the area (from S.E. Kenia to Natal) the anthers are ca. 0.3-0.5 mm long. In Uganda and the adjacent parts of Tanzania, Kenia, and Zaire the anthers usually are somewhat longer (8.5-1.0 mm). From central Zaire westwards the anthers mostly have a length of 1-2 mm, although specimens with shorter stamens may (regionally) occur. The increase of the length of the anthers from East to West appears to be continuous, and the differences in length cannot serve for distinguishing infra-specific taxa. The differences in the shape and dimensions of the infructescences seem to be distributed at random.

In contrast to the continental representatives of the species the Madagascar ones show considerable variation in the leaf characters. The differences in the leaves cannot be correlated with other morphological differences. As on the continent, the floral parts and the infructescences show much variation. The length of the anthers varies from 0.5 to 1.5 mm. Whereas the twigs of the continental specimens are (always?) glabrous, the Madagascan ones may bear sparse short uncinate hairs. But as a whole the Madagascan representatives of *T. madagascariense* cannot be satisfactorily distinguished from the continental ones, nor these two groups from the specimens from the Seychelles.

The difference in variation between the continental and the Madagascan representatives may be considered as an argument for subdividing the species, but this serves no purpose, unlike in *Treculia africana*, where regional differentiation justifies to distinguish infra-specific taxa for Madagascar.

In the material collected in Madagascar three groups of specimens can be distinguished on the basis of differences in leaf characters. They are, however, connected by intermediate forms. The variation in the shape, dimensions, and the texture of the leaves may be partly caused by differences in habitat, especially with regard to exposure and humidity conditions. But the variation does not appear to be related to area, altitude, soil, etc.

### Group A

*Leaves* (rigidly) coriaceous, tending to obovate or oblanceolate, sometimes suborbicular, the apex obtuse, very shortly acuminate, or emarginate, the base usually acute, the basal pair of secondary veins usually not distinct. *Fruit* longer or shorter than 10 cm.

This group comprises about 30% of the collections, among wich several showing resemblances to those of group C, like the lectotype collection of *Bosqueia danguyana.*

*Collections:* e.g., *Capuron* 948, 8626, 8704, 8795, 9012, 9128, 10564, 11420, 11474, 20574, 27131, 27696; *Service Forestier Madagascar* 2866, 2918, 12581, 15105, 15117, 16538, 16930.

### Group B

*Leaves* large, coriaceous, many of them longer than 10 cm, the apex mostly long-acuminate, the base often obtuse, the basal pair of secondary veins not distinct. *Fruit* over 10 cm long.

This group comprises about 10% of the collections, among which the type collections of *B. orientalis* and *B. manongarivensis.* A few collections ranked in this group somewhat resemble those of group C. The material of this group in leaf characters resembles the collections from the Seychelles.

*Collections:* e.g., *Capuron* 9152, 20345; *Humbert & Capuron* 23985; *Perrier de la Bâthie* 2321, 9898; *Service Forestier Madagascar* 14508.

### Group C

*Leaves* variable in shape, small or medium-sized, subcoriaceous to coriaceous, the apex long or shortly acuminate, the base acute or obtuse, the basal pair of secondary veins distinct or not. *Fruit* shorter or longer then 10 cm.

This group, the most variable and the least clear-cut of the three, comprises about 60% of the collections, among which the type collections of *B. thouarsiana*, *B. boiviniana*, *B. calcicola*, and *B. occidentalis.* Several of the collections (e.g., *Capuron* 11306, 28146; *Humbert & Capuron* 24575; *Perrier de la Bâthie* 9956) placed in this group approach those of group A, a few (e.g., *Capuron* 18209, *Service Forestier Madagascar* 19054) those of group B.

*Collections:* e.g., *Boivin* s.n.; *Capuron* 1000, 6767, 6772, 8647, 8718, 9006, 9101, 11509, 11661, 27333, 28355; *Perrier de la Bâthie* 1133, 1382, 2193, 9841, 9931, 9960, 10006, 15420, 17439; *Service Forestier Madagascar* 2844, 5388, 5396, 5404, 8050, 10646, 12622, 12716, 12836, 13032, 13262, 16850, 19312, 19373.

## Castilleae C.C. Berg
Acta Bot. Neerl. **26**: 78 (1977)

*Trees* or *shrubs*, (always?) with spirally arranged self-pruning branches bearing the *leaves* in two rows; stipules rarely connate; uncinate hairs lacking; latex bitter, white or yellowish, usually turning pinkish or brown; wood fibers usually septate; cardiac glycosides present in several genera. *Inflorescences* mostly in groups on short-shoots in the leaf axils, unisexual, usually discoid, with an involucre of imbricate, basally attached bracts; perianth if present and well-developed (usually) with imbricate tepals; stamens usually straight; pistillodes rare; pistil mostly more or less adnate to the perianth. *Fruit* adnate to the perianth; seeds large, without endosperm; vascular strands in the testa often not confined to a thickened part; embryo longitudinal, cotyledons (usually) equal and thick radicle short and apical.

The neotropical genus *Olmedia* (as well as the palaeotropical genera *Antiaropsis* and *Sparattosyce*) had to be excluded from the group of genera ranked among the *Olmedieae* and the tribe had to be renamed (Berg 1977). An important character of the neotropical *Castilleae* is the occurrence of self-pruning branches, connected with the architecture and growth of the trees. Adopting the distinctions made by Hallé and Oldeman (1970) the members of the *Castilleae* can be inserted in the "model of Cook" the "model of Roux" or the "model of Corner". The authors placed *Antiaris* in the "model of Roux". Young specimens of *Antiaris* show the features of the "model of Cook" because of shedding of branches, which phenomenon was (probably) indepently reported for *Antiaris* by Lynch (1877), Trimen (1898), and de Wit (1963). Nothing is known about growth habit and presence of self-pruning branches in *Mesogyne.*

In the neotropical *Castilleae* the more or less bitter, watery component of the latex turns pinkish brown or sometimes blackish after exposure to the air. The same change of colour is reported for *Antiaris.* Although the *Castilleae* have these features of the latex in common, latex with a bitter taste and/or turning pinkish or brownish appears to be rather widely distributed in the *Moraceae.*

The closely related genera *Antiaris* and *Mesogyne* differ from the neotropical members of the tribe in the arrangement of the bracts. In the neotropical genera the bracts form a distinct involucre of imbricate bracts, even in the infructescence. In the two Old World genera the bracts are partly scattered, especially in the fruiting pistillate inflorescence. In contrast to the neotropical genera, *Antiaris* and *Mesogyne* have a thickened part in the testa, containing the greater part of vascular bundels in the testa. Moreover, the buds forming permanent branches are placed above the insertion of the selfpruning branches in *Antiaris*, but beside the insertion of the selfpruning branches in the New World representatives. In spite of the differences the two groups of genera match very well.

### Key to the genera of the *Castilleae*

1.a. Stipules semi-amplexicaul; staminate inflorescences with many involucral bracts; fruiting perianth densely hairy; cotyledons equal . . . . . 6. *Antiaris*
b. Stipules fully amplexicaul; staminate inflorescences with 4 involucral bracts; fruiting perianth sparsely hairy; cotyledons unequal . . . . . . . 7. *Mesogyne*

6. **Antiaris** Lesch., Ann. Mus. Hist. Nat. Paris **16**: 478 (1810), nom. conserv.; Corner, Gard. Bull. Singapore **19**: 244 (1962). Type species: *A. toxicaria* Lesch.

Monoecious or dioecious *trees*. *Leaves* (at least on twigs) distichous, pinnately veined; stipules free, semi-amplexicaul. *Inflorescences* on short-shoots in the axils of the leaves or below the leaves, with 1-2 pistillate inflorescences (on the lower nodes of the short-shoot) and/or up to ca. 8 staminate ones. *Staminate inflorescences* discoid, pedunculate, many basally attached bracts, those on the margin of the receptacle in 1-3 rows, imbricate, forming an involucre; flowers many, with 2-7 free tepals; stamens 2-4, straight before anthesis, anthers latrorse to extrorse; pistillode absent. *Pistillate inflorescences* sessile or pedunculate, with an involucre of several basally attached imbricate bracts, flower 1, occasionally 2; perianth 4-lobed, the lower part adnate to the receptacle; ovary adnate to the embedded part of the perianth, stigmas 2. *Infructescences* with an orange to scarlet, fleshy receptacle, forming a whole with the fruit; endocarp crustaceous; testa thin, with a large suborbicular closely vascularized thickened part below the hilum; embryo longitudinally aligned, cotyledons (almost) equal, radicle short and apical.

The Asian and Australasian species, all described in the past century, were united with *A. toxicaria* Lesch. by Corner (1962). African and Madagascan representatives of the genus were described only in this century by Engler (1902), Perrier de la Bâthie (1927), and Léandri (1948).

Before Engler described three African species in *Antiaris*, African material of this genus had already been referred to Asian *Antiaris*. Hiern (1900) regarded the collections made by Welwitsch in Angola as possibly belonging to *Ipo toxicaria* Pers. (= *A. toxicaria* Lesch.). African representatives of the genus were named *Antiaris toxicaria* var. *africana* by Scott Elliot (in Chevalier 1909). How closely African *Antiaris* is related to Asian *Antiaris* appeared from Corner's study (1962) on this genus. According to Corner the species recognized may be united into one broadly construed species, *A. toxicaria*.

On the basis of non-essential differences (variation in leaf characters and the size and shape of the infructescences, connected with geographical distribution and ecology) Corner recognized:

*A. toxicaria* Lesch. var. *toxicaria* (from Sri Lanka to Celebes)
*A. toxicaria* Lesch. var. *macrophylla* (R. Br.) Corner (from the Philippines to Tonga)

*A. toxicaria* Lesch. var. *welwitschii* (Engl.) Corner (tropical Africa)
*A. africana* Engl. (Western and Central tropical Africa)
*A. madagascariensis* H. Perrier (Madagascar)
*A. humbertii* Léandri (Madagascar)

Mature infructescences, when dried, are ellipsoid to pyriform and up to 1.5 cm long in Africa, subglobose and 2-3 cm in diameter in Madagascar, and ellipsoid to pyriform and usually longer than 1.5 cm in the rest of the area of *Antiaris*. Var. *macrophylla* and *A. humbertii* are distinct in leaf shape and in the number of secondary leaf veins, respectively.

Until recently three species of *Antiaris* were generally recognized in Africa: *A. africana* Engl., *A. welwitschii* Engl., and *A. usambarensis* Engl. Corner put *A. usambarensis* into the synonymy of *A. toxicaria* var. *welwitschii.*

The material from the African continent is rather uniform in the characters of the inflorescence, flower, and infructescence. The main differences are found in the indument of twigs and leaves and in the venation (and texture) of the leaves.

Juvenile specimens (saplings, young trees, suckers) of the three taxa distinguished in Africa are rather similar and have their own combination of leaf and indument characters.

Regarding the variation within *Antiaris* and its segregates, it is clear that, even without adopting a broad species concept, all species recognized hitherto have to be brought together under one species, *A. toxicaria.* In this concept the following subdivision of the species appears to be proper:

**Antiaris toxicaria** Lesch.
— ssp. **toxicaria**
— ssp. **macrophylla** (R. Br.) C.C. Berg stat. et comb. nov., based on *Antiaris macrophylla* R. Br. in Flinders, Voy. Terra Austr. **2**: 602, t. 5 (1814).
— ssp. **africana** (Engl.) C.C. Berg
— — var. **africana**
— — var. **welwitschii** (Engl.) Corner
— — var. **usambarensis** (Engl.) C.C. Berg
— ssp. **madagascariensis** (H. Perrier) C.C. Berg
— ssp. **humbertii** (Léandri) C.C. Berg

On the main this subdivision is in accordance with Corner's views on *Antiaris.* Delimitation of the infra-specific taxa is based on non-essential differences in the indument, in leaf characters, and dimensions of the fructescences, in connection with their distribution. However, the distinct morphological resemblances between members of var. *welwitschii* and ssp. *toxicaria* are less reflected by the present subdivision. Except for ssp. *humbertii* (of which only four collections are known) all subspecies show more or less parallel variation patterns.

**Antiaris challa** (Schweinf.) Engl., Afr. Pflanzenw. **3**(1): 33 (1915); Mildbr. & Burret, Bot. Jahrb. **46**: 264 (1911); Blatter, Rec. Bot. Surv. India **8**(4): 446 (1923); Swartz, Fl. Trop. Arab.: 25 (1939); Corner, Gard. Bull. Singapore **19**: 248 (1962). — Syntypes: *Schweinfurth* 416, Yemen, Gebel Bura (LE), and *Schweinfurth* 982, Yemen, Regma, near Hodjela = Holeida? (not seen).

*Ficus challa* Schweinf., Bull. Herb. Boiss., ser. 1, **4**(App. II): 144 (1896).

Engler (1915) regarded *Ficus challa* as identical with *Antiaris usambarensis*. *Schweinfurth* 416 (seen in LE) belongs without doubt to *Antiaris toxicaria*. In its leaf characters it matches ssp. *africana* var. *africana*. As long as no fruiting material is available, the position of the taxon remains uncertain.

6.1. **Antiaris toxicaria** Lesch., Ann. Mus. Hist. Nat. Paris **16**: 478, pl. (1810); Hiern, Cat. Welw. Afr. Pl. **4**: 1020(1900).

6.1.a. **Antiaris toxicaria** Leschenault ssp. **africana** (Engl.) C.C. Berg comb. et stat. nov. — Lectotype: *Warnecke* 336, Togo, near Lome (B; isotypes E, G, K, L, P).

*A. africana* Engl., Bot. Jahrb. **33**: 119 (1902); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 224 (1917); Fl. Trop. W. Afr., ed. 2., **1**(2): 612 (1958); Corner, Gard. Bull. Singapore **19**: 247 (1962).

*Trees* up to 40(-60) m tall, with or without buttresses; latex white or yellowish turning pinkish or brownish; leafy twigs 1.5-5 mm thick, at least when dry more or less wrinkled and the periderm usually peeling off in small flakes, with yellowish to brown, patent or appressed-puberulous to hirtellous to subtomentose to hirsute, or to strigulose indument.

*Leaves* oblong to elliptic, or sometimes to lanceolate, usually broadest in or above the middle, more or less inequilateral, (2-)6-17(-22) cm long, (1.5)3-12 cm broad, subcoriaceous to coriaceous, shortly acuminate to apiculate, obtuse or sometimes subacute, at the base (subacute to) obtuse to (sub)cordate; margin subentire to denticulate towards the apex; above scabrous to scabridulous or smooth, the costa, especially in the lower part, more or less densely puberulous or hirtellous (to subtomentose), beneath sparsely appressed-puberulous to almost glabrous, or patent-puberulous to hirtellous to hirsute or to strigulose and often more or less scabrous; veins slightly prominent to plane above, beneath more or less prominent, the veinlets hardly or distinctly prominent, (5-)7-14 pairs of secondary veins, tertiary veins often partly parallel; petioles 3-9 mm long, with sparse or dense indument; stipules 3-10(-15) mm long, puberulous to pubescent to hirtellous or to hirsute, caducous. *Inflorescences* in the axils of the leaves or on (already) leafless twigs, on short-shoots bearing bract-like stipules. *Staminate inflorescences* 6-12(-20) mm in diam., mostly more or less lobed, at anthesis the margins deflexed; peduncle (4-)6-14(-18) mm long, densely puberulous to shortly velutinous, sometimes bracteate; receptacle puberulous to shortly velutinous, bracts (sub)ovate to oblong to elliptic, imbricate, up to ca. 1 mm long and below several scattered bracts extending to the peduncle; flowers many; perianth 1-1.5(-1.7) mm high, with (2-)3-5(-7) free, more or less spathulate, flat, cucullate or subpeltate, puberulous tepals; stamens (2-)3-4, filaments 0.2-0.4 mm long, anthers 0.8-1.8 × 0.4-0.7 mm, connective rather narrow, apiculate or not. *Pistillate inflorescences* 3-4 mm high, ca. 3 mm in diam., ellipsoid (to turbinate), sessile to pedunculate; peduncle up to 3 (or 6) mm long, densely puberulous to short-velutinous; receptacle bearing up to 12, mostly ca. 8 imbricate, reniform to ovate, puberulous bracts in several rows; flower 1(-2); free part of the perianth ca. 2 mm high, 4-parted, puberulous; style up to 1 mm long, stigmas filiform to vittiform, (2-)5-7(-10) mm long, minutely puberulous. *Infructescences* ellipsoid, sometimes nearly ovoid or globose, 1-1.5 cm long, 0.8-1 cm in diam., short- or long-apiculate, receptacle fleshy, brownish short-velutinous (with swollen hairs), with scattered bracts; peduncle 3-12 mm long; endocarp body ca. 10 mm long, endocarp crustaceous; seed ca. 7-9 mm long, testa (at least in dried material) adhering to the endocarp, rather thin, vascularized, closely so in a suborbicular to oblong, not distinctly thickened part below the hilum; embryo often marked by the thickened part of the testa and vascular bundles departing from that part; cotyledons equal or nearly so.

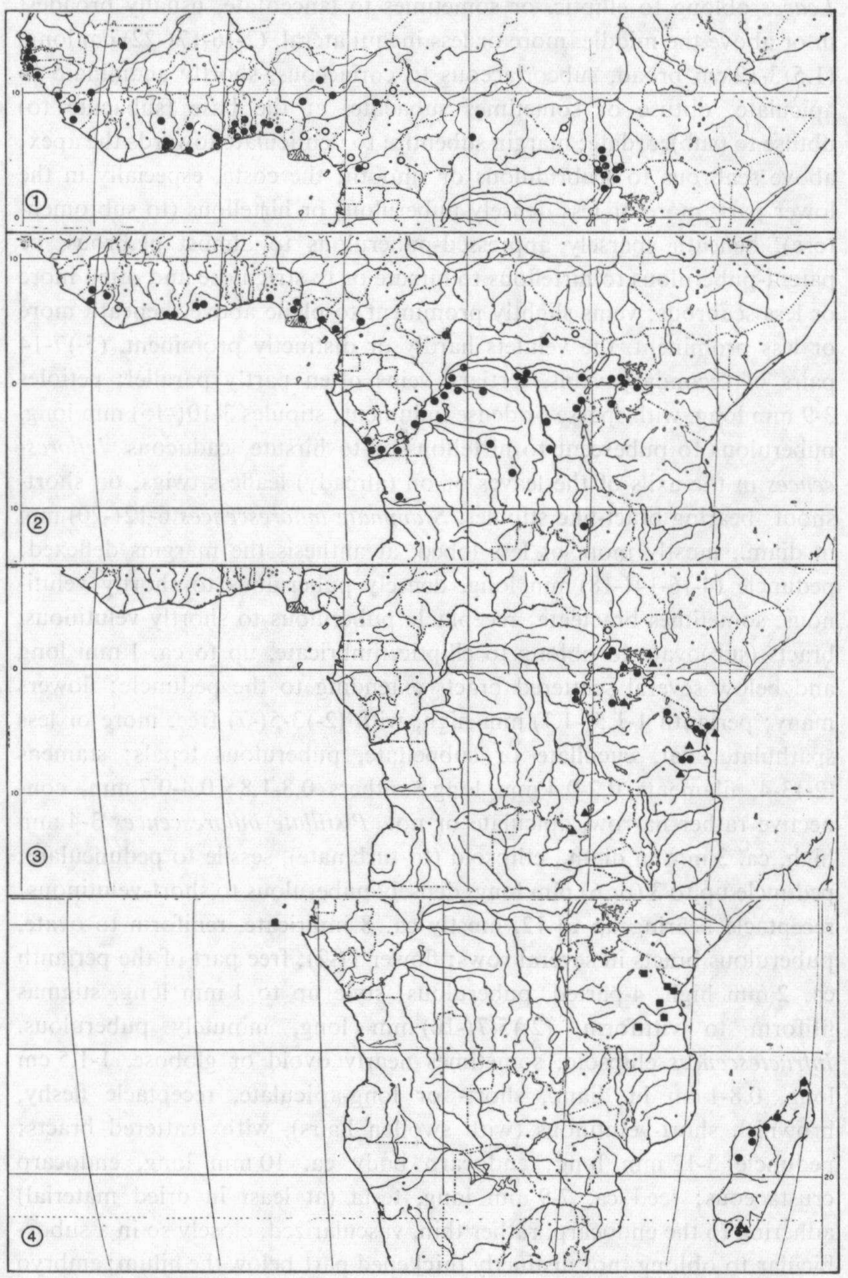

**Fig. 8.** — Distribution of taxa of the *Castilleae*: map 1, *Antiaris toxicaria* ssp. *africana* var. *africana*, ● adult specimens, ○ juvenile specimens probably belonging to var. *africana*; map 2, *A. toxicaria* ssp. *africana* var. *welwitschii*, ● adult specimens, ○ juvenile specimens probably belonging to var. *welwitschii*; map 3, *A. toxicaria* ssp. *africana* var. *usambarensis*, ● adult specimens, ○ juvenile specimens probably belonging to var. *usambarensis*, ▲ juvenile specimens of uncertain identity; map 4, ● and ?● *A. toxicaria* ssp. *madagascariensis*. ▲ *A. toxicaria* ssp. *humbertii*, ■ *Mesogyne insignis*.

*Juvenile specimens*: Leafy twigs hirtellous, subtomentose, hirsute or (sub)hispid, the hairs of the same length and then relatively long or of different length; leaves often oblong to lanceolate, chartaceous to subcoriaceous (to coriaceous); above hirsute to (sub)hispid, usually scabridulous because of persisting hair bases, sometimes almost glabrous except for the hirsute main veins; beneath hirsute to subtomentose or (sub)hispid; margin usually distinctly dentate; apex long-acuminate to subacute; veins, especially the main ones, prominent beneath.

The juvenile features are more or less pronounced, probably depending on the age. Many specimens show transitions to the features of the adult specimens of the varieties distinguished. Suckers (which may arise from the roots) of adult trees also show juvenile features. These features are sometimes found in adult, at least flowering trees.

Distribution (fig. 8, maps 1-4): From Senegal to Tanzania, southward to Angola and Zambia, in forests in wet to dry situations, from sealevel to 800 m altitude; rare, common, or locally predominant.

Number of collections examined: ca. 290.

The infructescences are eaten by antilopes, monkeys, and birds. The wood is a timber and is used for making canoes, the (inner) bark is used for making cloth, hammocks, sacks etc. (cf. Voorhoeve 1965). The latex is used for adulterating rubber, it is poisonous (when brought into the blood-stream), and is regionally used to prepare arrow poison. (Kerharo & Bouquet 1950; Walker 1953; Irvine 1961).

Three varieties can be distinguished within ssp. *africana*: var. *africana*, var. *welwitschii*, and var. *usambarensis*. In the regions where the (presumed) areas of var. *welwitschii* and var. *africana* overlap or approach each other, intermediate forms are (often) found. From the relatively scarce material we may cautiously conclude that the drier the habitat, the more pronounced the features of var. *africana*. On the other hand, the features of var. *welwitschii* are usually more distinct in regions with humid rain forests.

In East Africa material previously assigned to *A. usambarensis* shows a mixture of the characters of var. *africana* and var. *welwitschii*. Some of the East African specimens are exactly intermediate between the two taxa, like the type collection of *A. usambarensis*. Other specimens tend in their features towards either var. *africana* or var. *welwitschii*. The intermediate forms in East Africa are not quite like those found in West Africa.

The nature and the pattern in the variation of *Antiaris* in Africa raise the question if the differences, especially between var. *africana* and var. *welwitschii*, are genetically determined (by different chromosome numbers?, see p. 277) or mainly due to environmental factors. I am inclined to regard the environmental (climatological) conditions as important.

The varieties of ssp. *africana* are not clear-cut neither in their morphological features nor in their distributional areas. Uncertainty about the cause of the variation justifies distinction of the varieties, certainly with regard to var. *africana* and var. *welwitschii*. Distinguishing these varieties leads to recognition of var. *usambarensis*, partly because the type of *A. usambarensis* cannot be placed in one of the primary varieties.

The axillary short-shoots often produce both pistillate and staminate inflorescences, either (almost) simultaneously or successively. But they may produce only staminate ones or sometimes only pistillate ones. It is possible that part of the specimens only produce staminate inflorescences (depending on their age?). Trees may bear only staminate inflorescences beyond the main flowering time. For some regions [Angola, Liberia, see Hiern (1900); Voorhoeve (1965)] the trees (of var. *welwitschii*) are reported to be always dioecious. At anthesis separate flowers can be hardly distinguished in the staminate inflorescences.

The cotyledons are mostly strongly coherent or sometimes partly fused.

### 6.1.a′. **Antiaris toxicaria** Lesch. ssp. **africana** (Engl.) C.C. Berg var. **africana**. — Fig. 9.

*A. toxicaria* var. *africana* Scott Elliot ex A. Chev., Végét. Ut. Afr. Trop. Fr. 5: 259 (1909). — Syntypes: *Chevalier* 16107 and 16217, Ivory Coast, respectively Bouroukrou and Dabou (K, P).

*A. kerstingii* Engl., Pflanzenw. Afr. 3(1): 33, t. 20A (1915), very briefly described, but with a good plate. — Type: *von Sokode* s.n., Togo, Basari (B?, not seen).

*Leafy twigs* puberulous, hirtellous to subtomentose, or strigose, sometimes hirsute; periderm usually distinctly peeling off. *Leaves* subcoriaceous to coriaceous; above hirtellous to subhispid(ulous), (scabridulous to) scabrous by persisting hair bases or more frequently by short rigid hairs, the costa often strigose to hirtellous; beneath hirtellous,

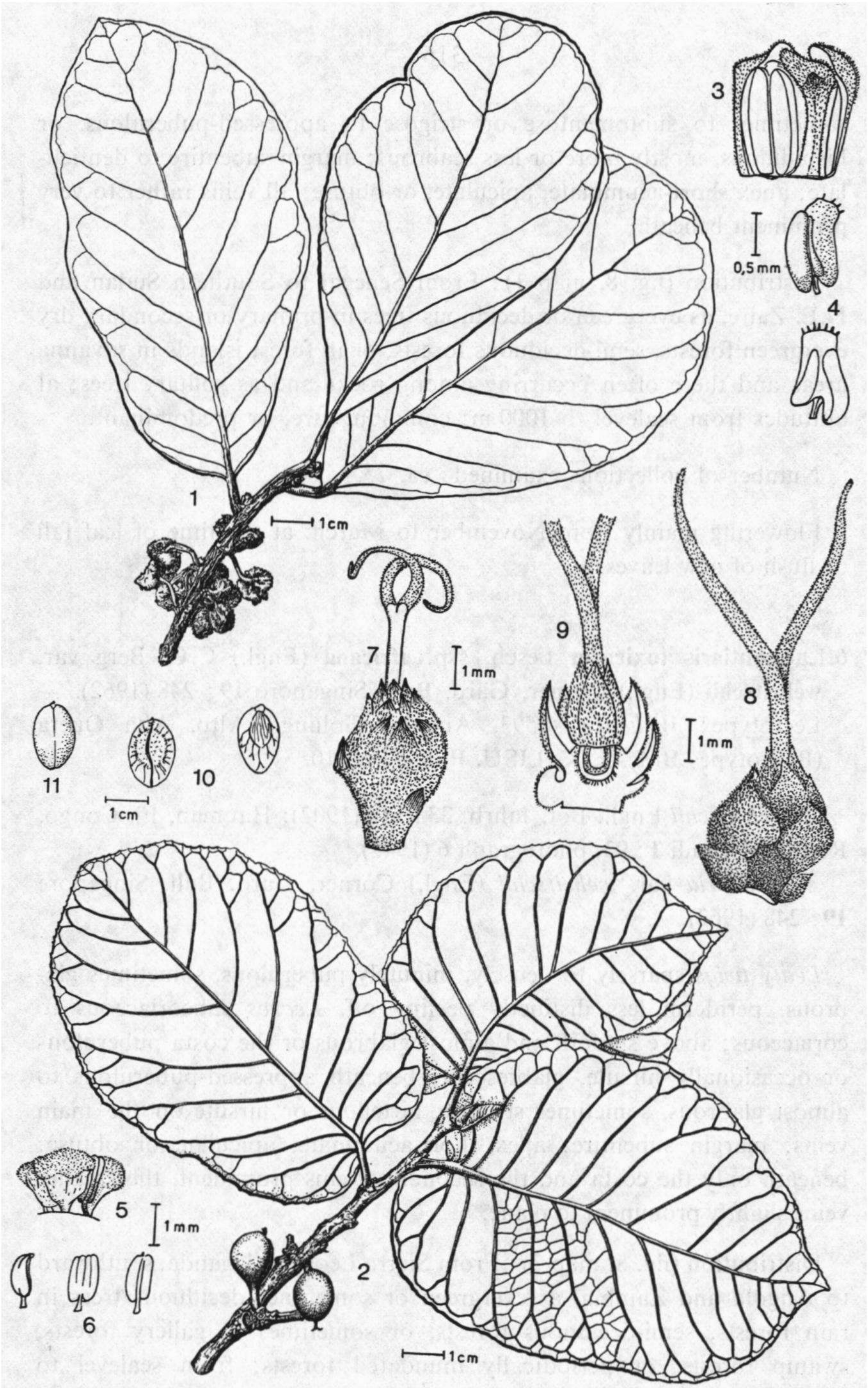

**Fig. 9. — *Antiaris toxicaria* ssp. *africana* var. *africana*: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3, staminate flower; 4, stamens; 5, staminate flower; 6, stamens; 7 & 8, pistillate inflorescences; 9, pistillate flower; 10, seeds; 11, embryo (1, 10, 11 : *Kersting* A 571; 2 : *Esperito Santo* 1741; 3, 4, 7 : *Dalziel* 177; 5, 6 : *de Wilde* 1373; 8, 9 : *d'Orey* 296).**

sometimes to subtomentose or strigose to appressed-puberulous, or hispidulous, mostly more or less scabrous; margin subentire to denticulate; apex short-acuminate, apiculate, or obtuse; all veins rather to very prominent beneath.

Distribution (fig. 8, map 1): From Senegal to Southern Sudan and N.E. Zaire, as evergreen or deciduous trees in primary or secondary dry evergreen forests, semi-deciduous forests, or in forest islands in savanna areas and there often occurring among rocks and as solitary trees; at altitudes from sealevel to 1000 m; common, rare, or predominant.

Number of collections examined: ca. 75.

Flowering mainly from November to March, at the time of leaf fall or flush of new leaves.

6.1.a". **Antiaris toxicaria** Lesch. ssp. **africana** (Engl.) C.C. Berg var. **welwitschii** (Engl.) Corner, Gard. Bull. Singapore **19**: 248 (1962). — Lectotype: *Welwitsch* 2593, Angola, Golungo Alto, Alta Queta (B; isotypes BM, G, K, LISU, P). — Fig. 10.

*A. welwitschii* Engl., Bot. Jahrb. **33**: 118 (1902); Hauman, Fl. Congo, Ruanda-Urundi **1**: 93, photograph 6 (1948).
*A. toxicaria* var. *welwitschii* (Engl.) Corner, Gard. Bull. Singapore **19**: 248 (1962).

*Leafy twigs* sparsely to densely, minutely puberulous, sometimes glabrous, periderm less distinctly peeling off. *Leaves* subcoriaceous to coriaceous; above smooth and almost glabrous or the costa puberulous or occasionally hirsute, glabrescent; beneath appressed-puberulous to almost glabrous, sometimes strigose, hirtellous or hirsute on the main veins; margin subentire; apex short-acuminate, apiculate or obtuse; beneath only the costa and the secondary veins prominent, the smaller veins slightly prominent to plane.

Distribution (fig. 8, map 2): From Sierra Leone to Uganda, southward to Angola and Zambia, as evergreen or sometimes deciduous trees in rain forests, semi-deciduous forests, or sometimes in gallery forests, swamp forests, or periodically inundated forests; from sealevel to ca. 1300 m; common or rare.

Number of collections examined: ca. 105.

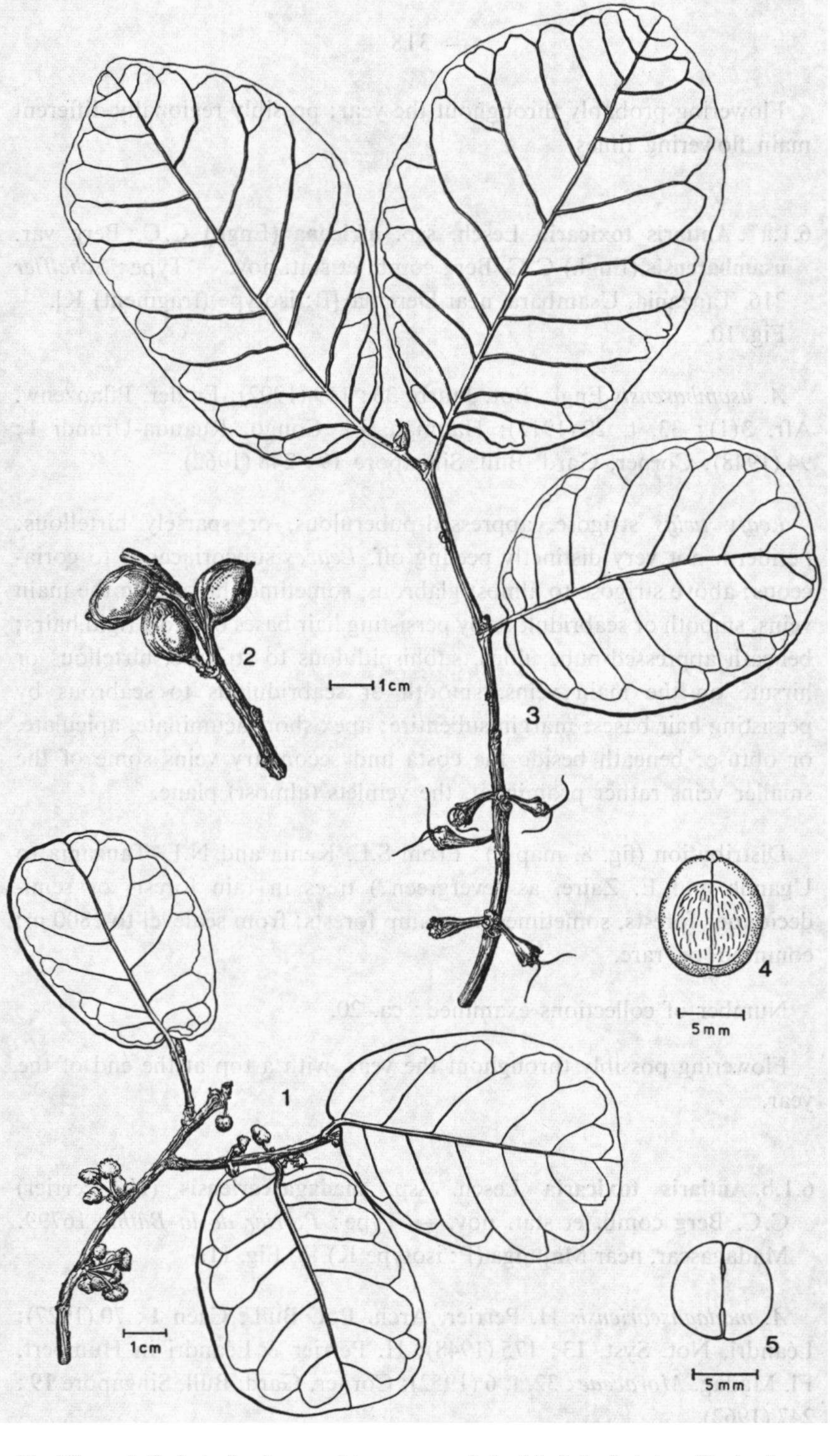

Fig. 10. — *Antiaris toxicaria* ssp. *africana* var. *welwitschii*: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3, twig with infructescences (1 : *Flamigni* 10490; 2 : *Devred* 762; 3 : *Toka* 26). — *Antiaris africana* ssp. *africana* var. *usambarensis*: 4, seed; 5, cross section of embryo (*Gille* 282).

Flowering probably throughout the year; possibly regionally different main flowering times.

**6.1.a‴. Antiaris toxicaria** Lesch. ssp. **africana** (Engl.) C.C. Berg var. **usambarensis** (Engl.) C.C. Berg comb. et stat. nov. — Type: *Scheffler* 216, Tanzania, Usambara, near Derema [B; isotype (fragment) K]. — Fig. 10.

*A. usambarensis* Engl., Bot. Jahrb. **33**: 119 (1902); Engler, Pflanzenw. Afr. **3**(1): 33, t. 20 (1915); Hauman, Fl. Congo, Ruanda-Urundi **1**: 94 (1948); Corner, Gard. Bull. Singapore **19**: 248 (1962).

*Leafy twigs* strigose, appressed-puberulous, or sparsely hirtellous; periderm not very distinctly peeling off. *Leaves* subcoriaceous to coriaceous; above strigose to almost glabrous, sometimes hirsute on the main veins, smooth or scabridulous by persisting hair bases or short rigid hairs; beneath appressed-puberulous, subhispidulous to strigose, hirtellous or hirsute on the main veins, smooth or scabridulous to scabrous by persisting hair bases; margin subentire; apex short-acuminate, apiculate, or obtuse; beneath beside the costa and secondary veins some of the smaller veins rather prominent, the veinlets (almost) plane.

Distribution (fig. 8, map 3): From S.E. Kenia and N.E. Tanzania to Uganda and E. Zaire, as (evergreen?) trees in rain forests or semi-deciduous forests, sometimes in swamp forests; from sealevel to 1800 m; common or rare.

Number of collections examined: ca. 20.

Flowering possibly throughout the year, with a top at the end of the year.

**6.1.b. Antiaris toxicaria** Lesch. ssp. **madagascariensis** (H. Perrier) C.C. Berg comb. et stat. nov. — Type: *Perrier de la Bâthie* 16799, Madagascar, near Majunga (P; isotype K). — Fig. 11.

*A. madagascariensis* H. Perrier, Arch. Bot. Bull., Caen **1**: 70 (1927); Léandri, Not. Syst. **13**: 175 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae* : 32, t. 6 (1952); Corner, Gard. Bull. Singapore **19**: 247 (1962).

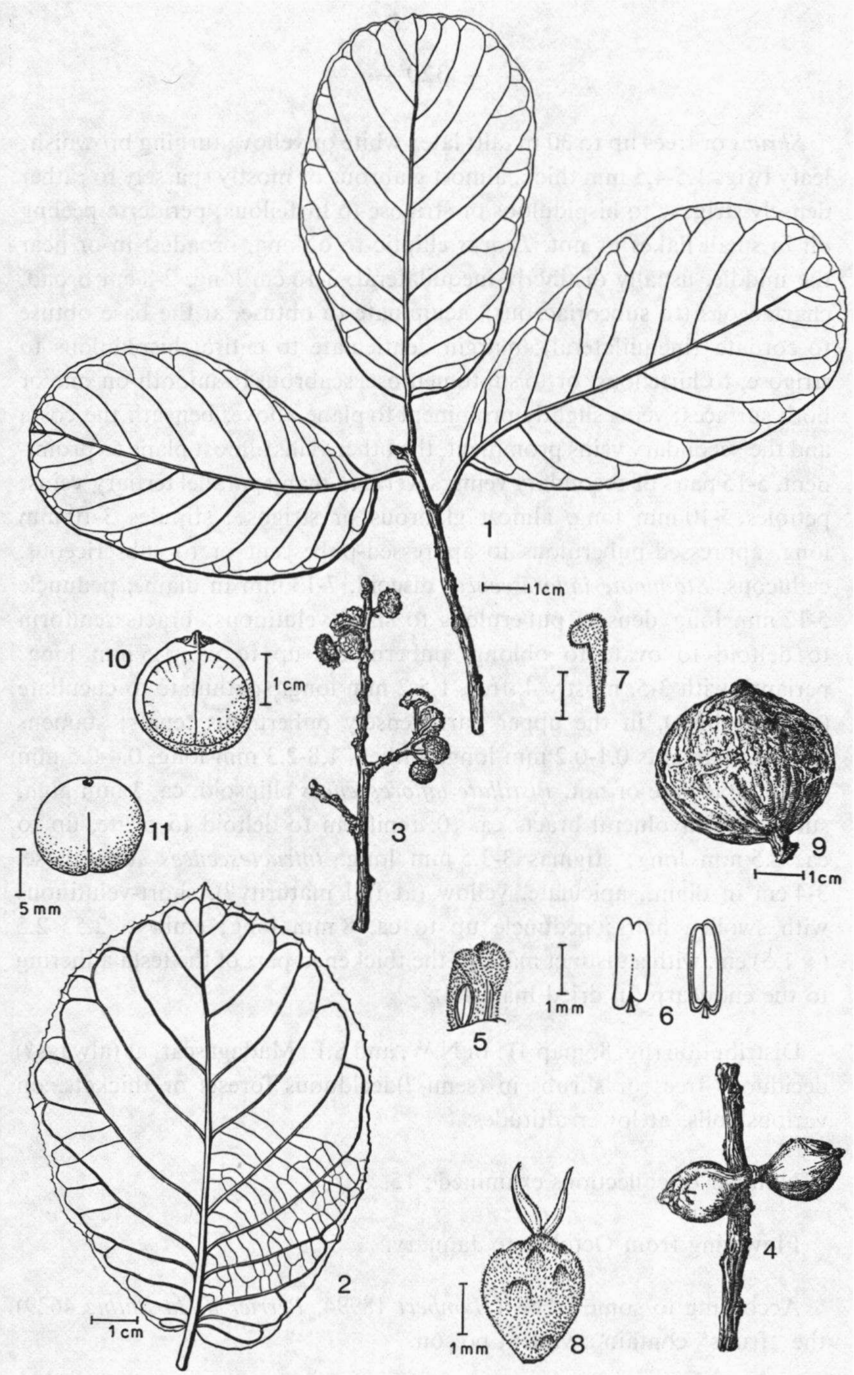

Fig. 11. — *Antiaris toxicaria* ssp. *madagascariensis*: 1, leafy twig; 2, leaf; 3, twig with staminate inflorescences; 4, twig with pistillate inflorescences; 5, staminate flower; 6, id., stamens; 7, id., tepal; 8, pistillate flower; 9, infructescence; 10, embryo; 11, embryo (1, 9, 10: *Serv. For. Madag.* 13412; 2, 4: *Capuron* 18846; 3, 5-8: *Capuron* 8544; 11: *Perrier de la Bâthie* 16799).

*Shrubs* or trees up to 30 m tall; latex white or yellow, turning brownish; leafy twigs 1.5-4.5 mm thick, almost glabrous or mostly sparsely to rather densely strigose to hispidulous or strigose to hirtellous; periderm peeling off in small flakes or not. *Leaves* elliptic to oblong, broadest in or near the middle, usually distinctly inequilateral, 3-16 cm long, 2-8 cm broad, chartaceous (to subcoriaceous), acuminate to obtuse, at the base obtuse to cordate (inequilateral); margin denticulate to entire; hispidulous to strigose, to hirtellous, or to subtomentose, scabrous to smooth on one or both surfaces; veins slightly prominent to plane above, beneath the costa and the secondary veins prominent, the other veins almost plane to prominent, 5-15 pairs of secondary veins, several to many parallel tertiary veins; petioles 5-10 mm long, almost glabrous or strigose; stipules 3-10 mm long, appressed-puberulous to appressed-pubescent or to subsericeous, caducous. *Staminate inflorescences* discoid, 7-13 mm in diam.; peduncle 5-12 mm long, densely puberulous to short-velutinous; bracts reniform to deltoid to ovate to oblong, puberulous, up to ca. 1.5 mm long; perianth with 3-5, mostly 4, free, 1.5-2 mm long, spathulate to cucullate (to subpeltate), in the upper part densely puberulous tepals; stamens (2-)3-5, filaments 0.1-0.2 mm long, anthers 1.8-2.3 mm long, 0.4-0.5 mm broad, apiculate or not. *Pistillate inflorescences* ellipsoid, ca. 3 mm high, subsessile; involucral bracts ca. 10, reniform to deltoid to ovate, up to ca. 0.5 mm long; stigmas 3-3.5 mm long. *Infructescences* subglobose, 3-4 cm in diam., apiculate, yellow (at full maturity?), short-velutinous with swollen hairs; peduncle up to ca. 8 mm long; embryo 2.5 × 2.5 (× 1.5) cm, with a distinct mark of the thickened part of the testa adhering to the endocarp (in dried material).

Distribution (fig. 8, map 4) : In N.W. and S.E. Madagascar, as (always?) deciduous trees or shrubs in (semi-?)deciduous forests or thickets, on various soils, at lower altitudes.

Number of collections examined : 15.

Flowering from October to January.

According to some labels (*Humbert* 18994, *Perrier de la Bâthie* 4629) the "fruits" contain a violent poison.

The two Madagascan subspecies are distinct by their large, (sub) globose infructescences. Ssp. *humbertii* (only known by four collections of fruiting specimens growing in xerophytic bush) differs from ssp.

*madagascariensis* in the smaller number of secondary leaf veins and the very rough leaf surface.

Ssp. *madagascariensis* shows the same variation in indument and venation as ssp. *africana*, although less pronounced.

Although trees of ssp. *madagascariensis* can grow to a height of 30 m, several collections have been made from flowering or fruiting small trees or even shrubs. Corner (1962) mentioned the occurrence of shrubby plants in ssp. *macrophylla*.

The hairs on the leaves are patent to appressed, straight or curved, very short and rigid, or longer and weaker, straight, curved, or almost crinkled. The different types of hairs gradually pass into each other. The roughness of the leaf surface is caused by short rigid hairs and/or the persisting swollen bases of longer hairs.

In general appearance two not highly distinct groups of specimens can be distinguished within the collected material of ssp. *madagascariensis*.

### Group A

*Leaves* tending to be elliptic and broadest above the middle, with a shortly acuminate to obtuse apex, with relatively long hairs and therefore the leaf surface not or hardly scabrous, and further with prominent tertiary (and quaternary) veins beneath; the periderm of the *twigs* (also invested with relatively long hairs) peels off in small flakes.

This group comprises, among other collections: *Capuron* 18846, *Homolle* 358, *Humbert* 18994, and *Serv. For. Madagascar* 13142.

### Group B

*Leaves* tending to be oblong and long-acuminate (to subacute) at the apex, usually with short hairs, with the leaf surface smooth or scabrous, with tertiary and quaternary veins slightly prominent to (almost) plane beneath; the periderm of the *twigs* usually not peeling off in small flakes.

This group comprises, among other collections: *Capuron* 24578 (leaves scabrous on both surfaces), *Léandri et al.* 2117, 2735, *Perrier de la Bâthie* 4629, 16799.

6.1.c. **Antiaris toxicaria** Lesch. ssp. **humbertii** (Léandri) C.C. Berg comb. et stat. nov. — Lectotype: *Humbert* 12320, Madagascar, between Tsivory and Anadabolava (P). — Fig. 12.

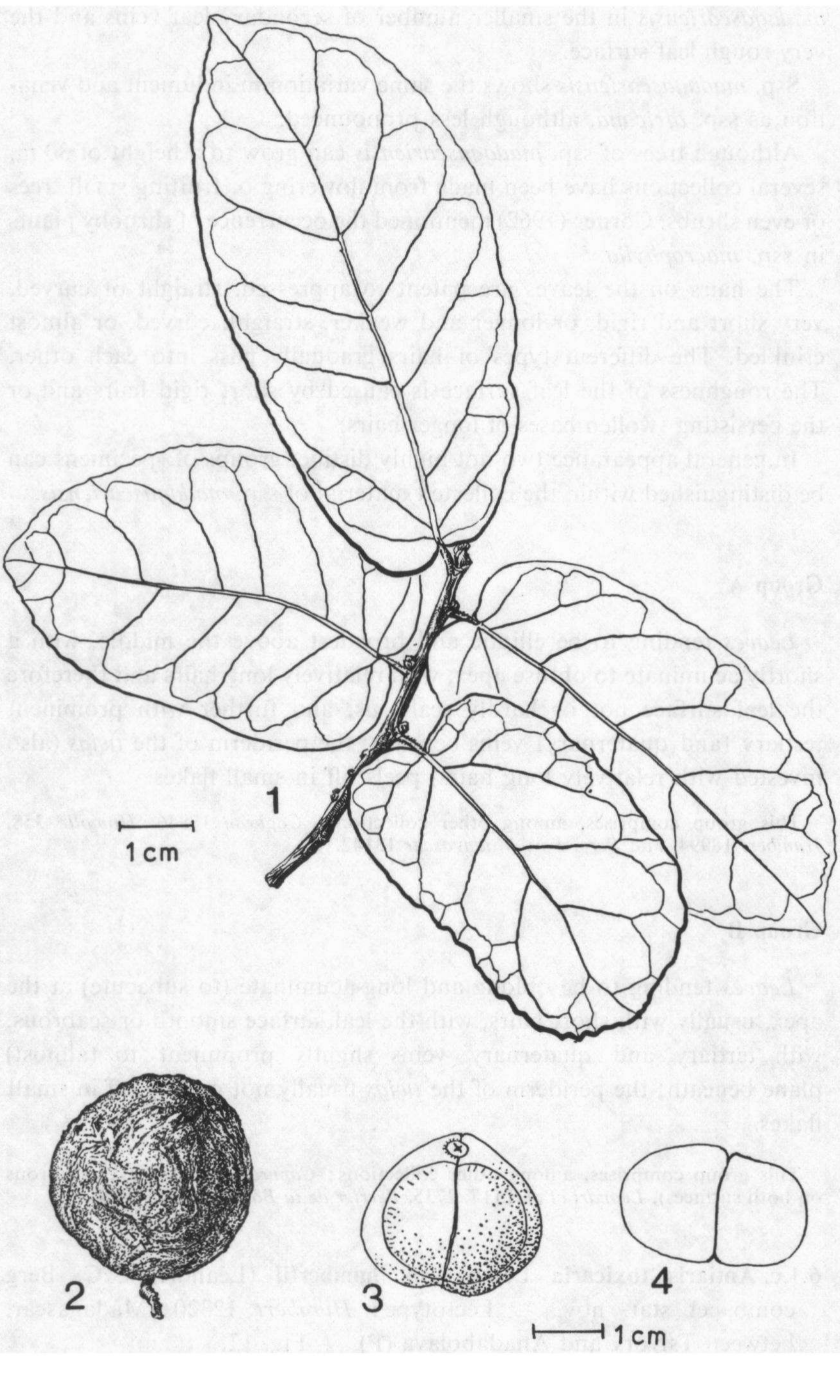

Fig. 12. — ***Antiaris toxicaria*** **ssp.** ***humbertii*****: 1, leafy twig; 2, infructescence; 3, embryo; 4, cross section of embryo (*Capuron* 22430).**

*A. humbertii* Léandri, Not. Syst. **13**: 175 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 32, t. 6 (1952); Corner, Gard. Bull. Singapore **19**: 247 (1962).

Small *trees* or *shrubs* with white to yellow latex (turning brownish?). Leafy twigs 1-3 mm thick, strigose to hispidulous. *Leaves* elliptic to oblong, broadest in or near the middle, usually distinctly inequilateral, 2-8.5 cm long, 1-5 cm broad, chartaceous (to subcoriaceous), shortly acuminate to obtuse or sometimes to subacute, at the base obtuse to cordate; margin denticulate to faintly repand or subentire; both surfaces very rough by short rigid patent hairs, beneath on the main veins some longer appressed hairs; veins slightly prominent to plane above, beneath prominent, 4-8 pairs of secondary veins, parallel tertiary veins few or lacking; petioles 2-5 mm long, hispidulous to strigose; stipules 2-4 mm long, strigose. *Infructescences* subglobose, ca. 2.5-3 cm in diam., velutinous with short swollen hairs, shortly pedunculate to subsessile; endocarp body 2.5-3 cm in diam., endocarp subcrustaceous; testa (at least in dried material) adhering to the endocarp, thin, below the hilum a thickened, closely vascularized, suborbicular, ca. 1.5 cm broad part leaving a distinct mark on the embryo; embryo (in dried material) ca. 1.5 × 2.5 cm, cotyledons equal.

Distribution (fig. 8, map 4): Madagascar, only known from the Mandrare Basin, in xerophytic bush, at altitudes up to 900 m.

The collections examined: 4.

Fruiting specimens collected from December to February.

The leaf characters of this subspecies might prove to be due to very dry conditions.

7. **Mesogyne** Engl., Bot. Jahrb. **20**: 147 (1894); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 222 (1917); Corner, Gard. Bull. Singapore **19**: 224, 250 (1962). — Type species: *M. insignis* Engl., see Hutch., Gen. Flow. Pl. **2**: 171 (1967).

Monoecious *shrubs* or small *trees*. *Leaves* (at least on the twigs) distichous, pinnately veined; stipules free, fully amplexicaul. *Inflorescences* on leafless short-shoots in the leaf axils, usually 1-2 pistillate ones (on the lower nodes) and up to 6 (or more) staminate ones. *Staminate* *inflorescences* discoid to hemispherical, with 3-4 basally attached imbricate bracts forming an involucre, pedunculate, with several to many flowers; perianth 2-4-parted; stamens 4-2, straight before anthesis; anthers extrorse to latrorse; pistillode lacking or rare. *Pistillate inflorescences* uniflorous, sessile, involucre with several basally attached imbricate bracts; flowers basally adnate to the receptacle; ovary basally adnate to the 3-4-lobed perianth, stigmas 2. *Infructescences* with a red, fleshy receptacle forming a whole with the fruit; endocarp crustaceous; testa with a large, oblong, thickened, closely vascularized part below the hilum; embryo longitudinally aligned; cotyledons very unequal; radicle apical and short.

In 1894 Engler established the genus *Mesogyne* and described two species: *M. insignis* on material from Tanzania and *M. henriquesii* on material from São Tomé. He placed *Mesogyne* in the *Dorstenieae*. The results of Tippo's study (1938) on the anatomy of the wood of *Moraceae* and allied groups could already raise doubt about the accepted position of the genus. Corner (1962) referred the genus to the *Olmedieae* and placed it close to *Antiaris*. He even suggested to unite the two genera.

The close relationships between these genera are clear, but uniting them now would be premature. Unequal cotyledons are unusual in the *Castilleae*, as well as the very small number of involucral bracts of the many-flowered staminate inflorescence. Knowledge about the habit, growth, and presence of self-pruning branches may assist in establishing the position of *Mesogyne*.

The nature of the differences within the genus do not justify the maintainance of two species.

7.1. **Mesogyne insignis** Engl., Bot. Jahrb. **20**: 148, t. 5 (1894), Engl., Monogr. Afr. Pfl. **1** (*Moraceae*): 30, t. 11 (1898). — Lectotype: *Holst* 2290, Tanzania, Usambara, near Nguelo (B). — Fig. 13.

*M. henriquesii* Engl., Bot. Jahrb. **20**: 148 (1894); Exell, Cat. Vasc. Pl. S. Tomé: 309 (1944). — Type: *Quintas* 164, São Tomé, near Angolares (COI, not seen; isotype B).

*Shrubs* or *trees* up to 15(-40?) m tall; leafy twigs 1-3(-4) mm thick, sparsely appressed-puberulous. *Leaves* (elliptic to) oblong (to lanceolate), broadest in or above the middle, usually more or less inequilateral, 5-26 cm long, 1.5-9 cm broad, chartaceous to subcoriaceous (to coria-

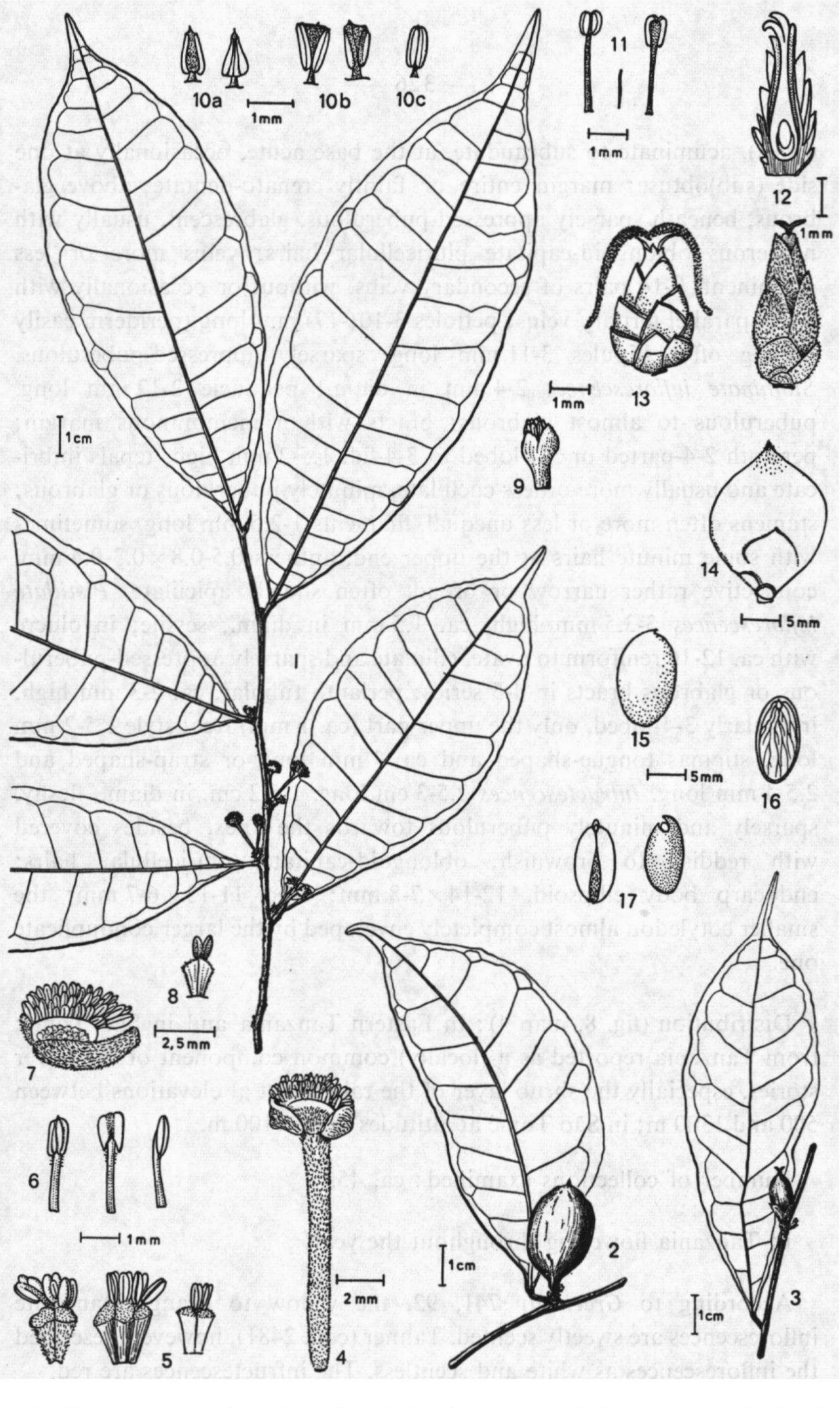

Fig. 13. — ***Mesogyne insignis*****: 1, leafy twig with staminate inflorescences; 2, leaf and pistillate inflorescence; 3, leaf and infructescence; 4, staminate inflorescence; 5, staminate flowers; 6, stamens; 7, staminate inflorescence; 8 & 9, staminate flowers; 10a, b & c, stamens; 11, stamens and pistillode; 12 & 13, pistillate inflorescences; 14, young infructescence; 15, endocarp body; 16, seed; 17, embryo with a small cotyledon (1 : *Drummond & Hemsley* 1841; 2, 12 : *Drummond & Hemsley* 1692; 3 : *Faulkner* 1346 ; 4-6 : *Warnecke* 461; 7, 8 : *Drummond & Hemsley* 1694; 9-11 : *Quintas* 1062; 13 : *Chevalier* s.n.; 14-17 : *Semsei* 1447).**

ceous), acuminate to subcaudate, at the base acute, occasionally at one side (sub)obtuse; margin entire or faintly crenato-dentate; above glabrous, beneath sparsely appressed-puberulous, glabrescent, usually with numerous oblongoid-capitate pluricellular hairs; veins more or less prominent, 9-14 pairs of secondary veins, without or occasionally with a few parallel tertiary veins; petioles 3-10(-17) mm long (periderm easily peeling off); stipules 3-11 mm long, sparsely appressed-puberulous. *Staminate inflorescences* 2-4 mm in diam.; peduncle 2-12 mm long, puberulous to almost glabrous; bracts with a membranous margin; perianth 2-4-parted or 3-4-lobed to 3-4-fid, 1.5-2 mm high, tepals imbricate and usually more or less cucullate, minutely puberulous or glabrous; stamens often more or less unequal, filaments 1-2.5 mm long, sometimes with some minute hairs at the upper end, anthers 0.5-0.8 x 0.3-0.4 mm, connective rather narrow or broad, often shortly apiculate. *Pistillate inflorescences* 3-3.5 mm high, ca. 1.5 mm in diam., sessile; involucre with ca. 12-16 reniform to ovate, ciliolate and sparsely appressed-puberulous or glabrous bracts in 4-5 series; perianth tubular, ca. 2-3 mm high, irregularly 3-4-lobed, only the upper part (ca. 1 mm) free; style 1.5-2 mm long, stigmas tongue-shaped and ca. 1 mm long or strap-shaped and 2.5-4 mm long. *Infructescences* 2.5-3 cm long, 1.5-2 cm. in diam., fleshy, sparsely and minutely puberulous towards the apex, besides covered with reddish to brownish, oblongoid-capitate, pluricellular hairs; endocarp body ellipsoid, 12-14 x 7-8 mm; seed 11-13 x 6-7 mm; the smaller cotyledon almost completely enveloped by the larger conduplicate one.

Distribution (fig. 8, map 4): In Eastern Tanzania and in São Tomé; from Tanzania reported as a (locally) common component of the lower stories, especially the shrub layer of the rain forest at elevations between 500 and 1300 m; in São Tomé at altitudes up to 1100 m.

Number of collections examined: ca. 45.

In Tanzania flowering throughout the year.

According to *Greenway* 741, 92, the yellow to orange staminate inflorescences are sweetly scented. Tanner (coll. 2481), however, described the inflorescences as white and scentless. The infructescences are red.

The material from São Tomé differs from that from Eastern Tanzania in the longer (2.5-4 mm long) and strap-shaped stigmas, in the less deeply divided perianth of the staminate flower, in the somewhat shorter (2-4 mm long) peduncle of the staminate inflorescence, and often in the somewhat thicker (coriaceous) leaves. Because of the scarcity of material nothing can be concluded about the constancy of these differences. Therefore it is not desirable to distinguish infraspecific taxa at this moment.

In the staminate inflorescences of East African specimens the inner flowers are often 4-merous, whereas the peripheral ones are often 2-merous and less well-developed, their stamens usually being smaller and often irregularly shaped.

## Moreae

*Trees* or *shrubs* (sometimes climbing and/or armed) rarely herbs (*Fatoua*). *Leaves* in two rows or in spirals, stipules mostly free; uncinate hairs general; occasionally septate wood fibres (*Prainea*) or cardiac glycosides (*Streblus*, *Antiaropsis*) present. *Inflorescences* usually unisexual, mostly spicate, racemose or capitate [and sometimes (sub)involucrate because of the presence of several (large) basal bracts], sometimes cymose or discoid and involucrate; bracts often peltate; stamens straight or inflexed and then mostly springing back elastically; pistillodes general; perianth of the pistillate flower with free or connate tepals, sometimes lacking. *Fruit* free or adnate to the perianth; seeds large or small with or without endosperm, testa mostly with a thickened part having vascular strands, embryo very diverse.

In this circumscription of the tribe (cf. Berg 1973) the *Artocarpeae*, as defined by Corner (1962), are included. Reasons for combining the two tribes were the rather faint differentiating characters between the groups and the lack of sufficient homogeneity of each of them. Corner (1962 : 214) already considered fusing of the *Moreae* and the *Artocarpeae*.

The main problem in the *Moreae* is generic delimitation, owing to insufficiently understood and far from transparent patterns of variation and differentiation, gaps in our knowledge of several complexes of characters (morphological, anatomical, chemical), and uncertainty about the significance of the characters for delimitation. Especially for this tribe the differentiation of inflorescences, flowers, infructescences, and fruits have to be considered in connection with pollination and dispersal, data on which are very scarce.

The *Moreae* show some remarkable features : the incidental presence of characters characteristic for other tribes, for example septate wood fibres (*Prainea*), cardiac glycosides (*Antiaropsis*, *Streblus asper*), and striking differences in probably related taxa, e.g. in the indument (presence or absence of uncinate hairs), stamens (inflexed or straight stamens), and inflorescences (capitate or elongate, involucrate or not).

A world-wide comparative study, involving besides a wide range of morphological characters and anatomical and chemical properties, is necessary for the delimitation of the *Moreae* (at least against the *Dorstenieae*) and its genera, as well as of their subdivisions.

The generic descriptions in this treatment are only based on the characters of African species.

Several of the African *Moreae* were merged in Corner's broad genera *Streblus*, *Maclura*, and *Trophis*, or can be easily sunk in these genera. At the moment it appears wiser not to follow Corner, as expressed in the following review of the African members of the tribe. Therefore, I had to decide to leave the position of the African *Moreae* as far as possible unchanged, and consequently provisionally, also their names.

### Sloetiopsis – Bleekrodea – Fatoua

*Fatoua madagascariensis* (and possibly also *F. pilosa*) is peculiar because of the lack of latex. Although the species is reminiscent of the *Urticaceae* in some features, the characters of the pistillate flower are Moraceous. They show relationships to *Bleekrodea* and *Sloetiopsis*.

These three genera (placed in the tribe *Dorstenieae* by Bureau (1873) have in common the well-developed white pulpy dehiscent exocarp, pushing upward or (in *Fatoua* probably) ejecting the endocarp body. *Bleekrodea* and *Fatoua* have bisexual inflorescences, although in *B. madagascariensis* and in *F. madagascariensis* unisexual inflorescences may occur. *Sloetiopsis* has unisexual, or occasionally bisexual inflorescences and is mostly dioecious, but sometimes monoecious. This group of genera (to which the Asian genus *Sloetia* can be added) may be regarded as basically monoecious, and their inflorescences as basically bisexual. The genus *Fatoua* has cymose inflorescences in the Asian species *F. pilosa* and spicate-racemose inflorescences in *F. madagascariensis*. This shows that the difference in structure of the inflorescences of *Bleekrodea* (cymose inflorescences) and *Sloetiopsis* (spicate staminate or bisexual inflorescences) is not essential.

A more important difference between *Bleekrodea* and *Sloetiopsis* as well as *Fatoua* can be found in the perianth of the pistillate flower. In *Bleekrodea* it is tubular and 4-dentate and in fruit the enlarged pinkish

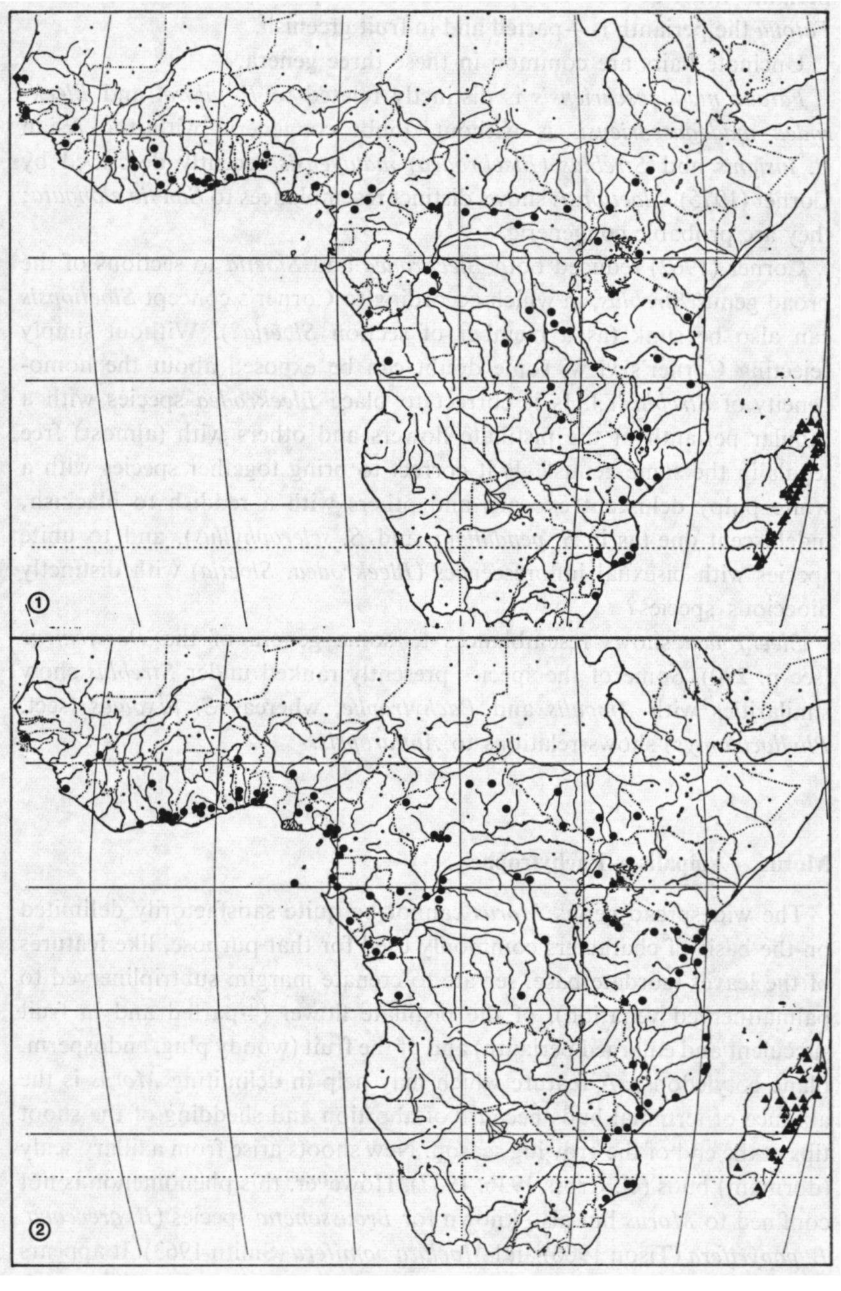

Fig. 14. — Distribution of some species of the *Moreae*: map 1, ● *Morus mesozygia*, ▲ *Pachytrophe dimepate*; map 2, ▲ *Ampalis mauritiana*, ● *Chlorophora excelsa*.

perianth must be torn to release the endocarp body. In *Sloetiopsis* and *Fatoua* the perianth is 4-parted and in fruit greenish.

Uncinate hairs are common in these three genera.

*Fatoua madagascariensis* is distinctly related to *F. pilosa*, and *Bleekrodea madagascariensis* is without doubt congeneric with the Asian *B. insignis* and *Streblus* (*Bleekrodea*) *malayensis* recently described by Corner (1975). *Sloetiopsis* shows distinct resemblances to *Sloetia elongata*; they are probable congeneric.

Corner (1962) reduced both *Bleekrodea* and *Sloetia* to sections of the broad genus *Streblus*, in which according to Corner's concept *Sloetiopsis* can also be sunk (as a member of section *Sloetia*?). Without simply rejecting Corner's view, some doubt can be exposed about the homogeneity of *Streblus* s.l. Is it correct to place *Bleekrodea* species with a tubular perianth of the pistillate flowers and others with (almost) free tepals in the same genus? Is it correct to bring together species with a white pulpy dehiscent exocarp and others with a reddish to blackish, indehiscent one (as in *S. pendulinus* and *S. sclerophyllus*), and to unite species with bisexual inflorescences (*Bleekrodea, Sloetia*) with distinctly dioecious species?

*Bleekrodea* shows resemblances to some genera of the *Dorstenieae* (see p. 290). Some of the species presently ranked under *Streblus* show similarities with *Ampalis* and *Pachytrophe*, whereas *S. taxoides* (sect. *Phyllochlamys*) shows relations to *Antiaropsis*.

### Morus – Ampalis – Pachytrophe

The widespread genus *Morus* cannot be quite satisfactorily delimited on the basis of characters commonly used for that purpose, like features of the leaves (cordate base, serrate to crenate margin, subtriplinerved to palmatinerved venation), of the pistillate flower (4-parted and in fruit succulent and enlarged perianth) and of the fruit (woody plug, endosperm, plane cotyledons). A feature which may help in delimiting *Morus* is the absence of terminal buds because of abortion and shedding of the shoot tips at the end of the growing season. New shoots arise from axillary scaly (dormant) buds (cf. Cross 1936, 1937). However, this phenomenon is not confined to *Morus* but also known for *Broussonetia* species (*B. greveana*, *B. papyrifera* (Tison 1906) and *Maclura pomifera* (Smith 1963). It appears to be correlated with occurrence in temperate regions (cf. Millington & Chaney, in Kozlowski 1973).

*Ampalis* and *Pachytrophe* are closely related and probably congeneric. If compared with *Morus*, *Pachytrophe* especially in its pistillate flowers and fruit is very similar, most distinctly so to *Morus mesozygia.* The two genera differ from *Morus* in the leaves, in the lack of well-developed scaly axillary buds, and in the absence of shedding of shoot tips. The two genera resemble several species of the genus *Streblus* sensu Corner, like *S. ascendens*, *S. pendulinus*, *S. solomonensis*, *S. sclerophyllus* (cf. Corner 1970). These *Streblus* species might prove to be more closely related to *Ampalis* and *Pachytrophe* (and through them linked to *Morus*) than to the *Bleekrodea* – *Sloetia* group. The leaves of *S. ascendens* are reminiscent of those of *Morus* species.

**Cardiogyne – Chlorophora (excelsa & regia) – Broussonetia (greveana)**

a. Corner (1962) reduced *Cardiogyne* to a section of *Maclura*, which also comprises the former genera *Cudrania* (Asia) and *Chlorophora* (Africa and America). After excluding *Chlorophora excelsa*, *C. regia*, and *C.*(= *Broussonetia*) *greveana*, and including the Asian genus *Plecospermum*, there remains a group of climbers or trees whose short-shoots often end in a spine. Alle species of this group have globose pistillate inflorescences mostly developing into yellow to orange infructescences, the outer and protective layer of which is formed by the thickened upper parts of the perianths (and sometimes also of the bracts). The perianth and/or bracts mostly contain immersed yellow glands (accumulations of the copious yellow dye present in the plants) except for those of *Plecospermum.* The stipules are very small and scale-like, except in *Chlorophora tinctoria.* The petioles are thin and leave small scars, the leaves are thin and brittle when dried, one of the style branches is mostly more or less strongly reduced. Most species have short thin brown hairs on the vegetative parts. The staminate inflorescences are capitate, spicate, or racemose. *Cudrania* and *Plecospermum* differ from the other "genera" in their straight stamens.

On the basis of the similarities one may treat this group of taxa as rather distinct, but it appears premature to assign it the rank of genus.

The closest relatives of *Cardiogyne africana* appear to be *Maclura brasiliensis* (cf. Kaastra 1973) and *Plecospermum spinosum.*

b. The two very closely related species *Chlorophora excelsa* and *C. regia* differ in several characters from the above-mentioned group, for example in the lack of spines, the long stipules, the firm leaves, the spicate

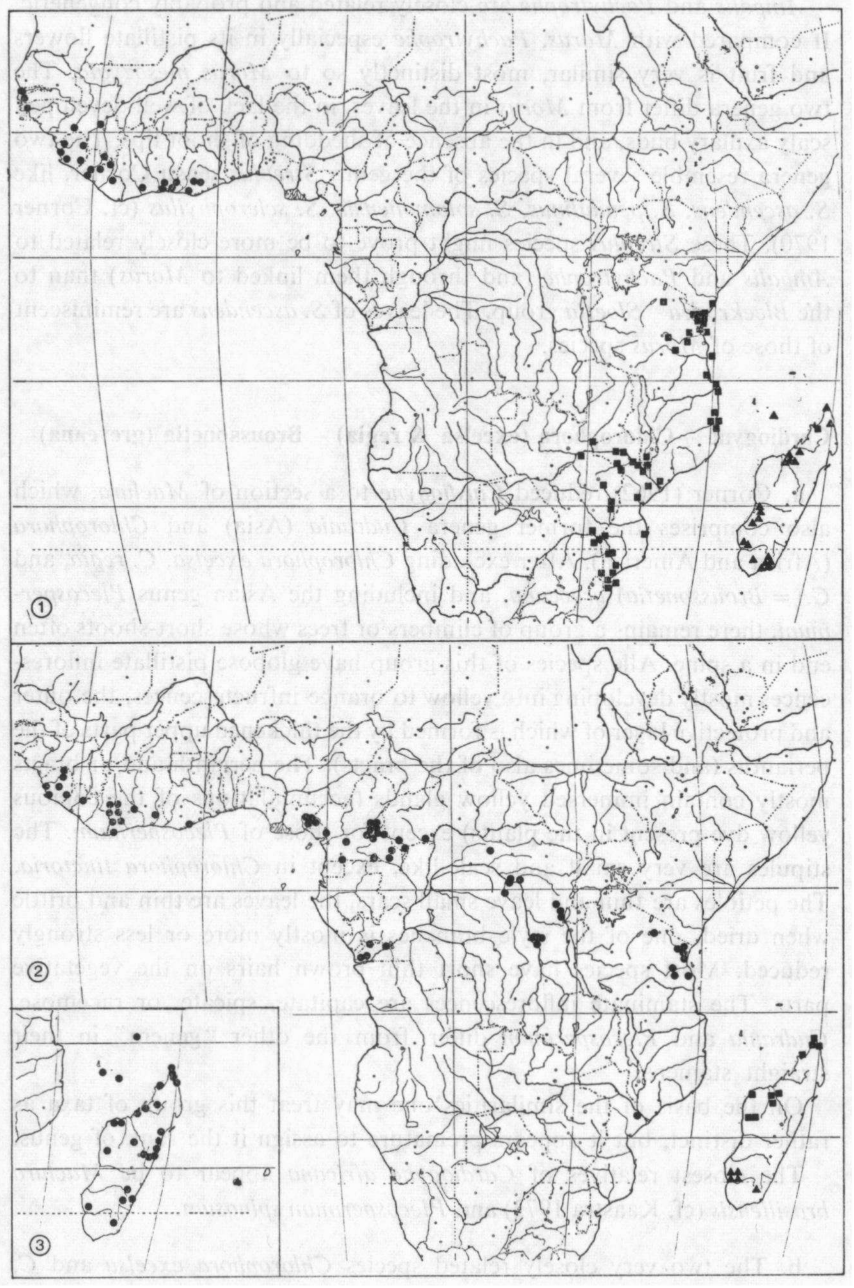

**Fig. 15. — Distribution of some species of the *Moreae*: map 1, ● *Chlorophora regia*, ■ *Cardiogyne africana*, ▲ *Broussonetia greveana*; map 2, ● *Sloetiopsis usambarensis*, ■ *Bleekrodea madagascariensis*, ▲ *Fatoua madagascariensis*; map 3, ▲ *Maillardia borbonica*, ● *M. montana*.**

pistillate inflorescences, the green infructescences, and the thin white pulpy exocarp. On the other hand there are also resemblances, but they are no more pronounced than those to *Broussonetia* or *Morus*. The closest relative of these two species might prove to be the neotropical *Bagassa guianensis*, sharing characters of habit, the conspicuously lenticellate bark, the striking differences between leaves of juvenile and adult specimens, the structure of the infructescences (globose in *Bagassa*), the pistillate flower, and the fruit. But *Bagassa* has straight stamens, in contrast to *Chlorophora excelsa* and *C. regia*.

c. *Broussonetia greveana* superficially resembles *Chlorophora excelsa* in the pistillate inflorescences. However, there are two important differences. In *Broussonetia greveana* the perianth of the pistillate flower is tubular and more or less irregularly lobed to dentate, in *C. excelsa* regularly 4-parted with distinct decussate-imbricate tepals. In *Broussonetia* the outer and protective layer of the infructescence is formed by the upper thickened parts of the bracts, but in *C. excelsa* chiefly by the thickened upper parts of the tepals. The genus *Broussonetia* can be dilimited by the two features mentioned for *B. greveana*. The fruits of *C. excelsa* and *B. greveana* are very similar. These, as well as those of the other *Broussonetia* species (as far as examined), *C. regia*, and *Bagassa guianensis* are small and have a thin white pulpy exocarp forming a short basal stipe. The seeds contain endosperm, the cotyledons are thin and the radicle is long. According to a plate in Seringa's work on *Morus* (1855), the fruit of *Broussonetia papyrifera* may have rather thick fleshy and dehiscent exocarps. This suggests that the fruits of *Broussonetia* and the other species mentioned above are morphologically related to the well-developed dehiscent pulpy exocarps of other *Moreae*. On the other hand, there are indications (cf. Corner 1962) that more or less thick (dehiscent) pulpy endocarps are widespread in *Moraceae* with free fruits.

## Maillardia

Corner reduced *Maillardia* as well as the Asian genus *Calpidochlamys* to sections of *Trophis*, thus combining the genera in which the tepals of the pistillate flowers are almost completely connate and adnate to the fruit and the staminate flowers have inflexed stamens. Corner's decision might prove to be correct. Relying on Corner's description of the endocarp of *Calpidochlamys* (1962), this genus is probably the closest relative of *Maillardia*. In further considerations about the delimitation of a genus

*Trophis* s.l. the neotropical genera *Sorocea*, *Olmedia*, and *Clarisia* should be included, also with consideration of anatomical characters.

**Treculia**

Like *Maillardia*, *Treculia* can easily be distinghuished from the other African *Moreae* by its distinct features of inflorescence and flowers. *Treculia* is very closely related to the Asian genus *Parartocarpus*. Inflorescences, infructescences, fruits, and seeds of the two genera are basically similar.

In summary one may cautiously and provisionally conclude: *Bleekrodea* is probably a good genus, related to *Fatoua*, *Sloetia*, *Sloetiopsis*, and possibly to some genera presently inserted in the *Dorstenieae*;
*Fatoua* is a good genus, related to *Bleekrodea*;
*Sloetiopsis* is probably congeneric with *Sloetia*, which may prove to include some of the species of *Streblus* sensu Corner;
*Morus* can be regarded as a distinct taxon, related to *Ampalis* and *Pachytrophe*, and through them linked to a part of the species of *Streblus* sensu Corner;
*Ampalis* and *Pachytrophe* are (probably) congeneric and show relationships (possibly below the rank of genus) to some members of *Streblus* sensu Corner, as well as to *Morus* (but possibly on the genus level);
*Cardiogyne* is closely related to and probably even congeneric with *Maclura* s. str., and besides closely related to *Plecospermum*, more distantly related to *Chlorophora tinctoria* and to *Cudrania*; *Chlorophora excelsa* and *C. regia* probably constitute a separate genus with more or less distinct relationships to *Bagassa*, *Broussonetia*, (*Chlorophora tinctora*, and *Morus*);
*Broussonetia* (with *B. greveana*) is a clear-cut genus, without very clear relationships to other genera;
*Maillardia* seems to be related to *Calpidochlamys* and possibly to *Trophis*;
*Treculia* is very closely related to *Paratocarpus*;
finally, the genera *Streblus* and *Maclura* sensu Corner (1962) appear to be too heterogenous.

**Key to the genera of the *Moreae***

1.a. Climbers, shrubs or treelets with spines; both staminate and pistillate inflorescences globose-capitate . . . . . . . . . . . . . . . 13. *Cardiogyne*
b. Trees, shrubs or herbs without spines . . . . . . . . . . . . . . . 2

2.a. Herbaceous to suffrutescent plants without latex; inflorescences normally bisexual, racemose to spicate; segments of the perianth of the staminate flower valvate; one of the style branches reduced (Madagascar) . . 16. *Fatoua*

b. Trees or shrubs with latex; inflorescences bisexual cymes or normally unisexual; segments of the staminate flower imbricate; style branches 2 and equal (one of them reduced in *Chlorophora* only) . . . . . . . . . . 3

3.a. Inflorescences bisexual, shortly branched cymes or sometimes unisexual; pistillate flower usually one, the perianth tubular and the ovary free; stamens 5 . . . . . . . . . . . . . . . . . . . . . . . . 15. *Bleekrodea*

b. Inflorescences normally unisexual (sometimes bisexual in *Treculia* but then the pistillate flower without perianth); inflorescences spicate, capitate, or the pistillate ones uniflorous, but then the perianth of the pistillate flower either with free tepals or tubular and fused with the overay; stamens 4 or less . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4.a. Often cauliflorous trees or shrubs; inflorescences globose-capitate to broadly clavate, subinvolucrate; pistillate flowers without a perianth; stamens usually less than 4 and straight; stipules fully amplexicaul . . . 18. *Treculia*

b. Ramiflorous trees or shrubs; inflorescences spicate, capitate, or the pistillate ones uniflorous, not subinvolucrate; pistillate flowers with a perianth; stamens 4, inflexed; stipules semi-amplexicaul or lateral . . . . . . . . 5

5.a. Uncinate hairs present and abundant pistillate inflorescences uniflorous; tepals of pistillate flower and the ovary free; shrubs or treelets (African continent). . . . . . . . . . . . . . . . . . . . . . . . 14. *Sloetiopsis*

b. Uncinate hairs lacking; pistillate inflorescences spicate or capitate, if uniflorous, then the perianth of the pistillate flower tubular and adnate to the ovary; trees or (in Madagascar) shrubs . . . . . . . . . . . . . . 6

6.a. Stipules subpersistent and reflexed; perianth of the pistillate flower tubular and ovary and fruit free (Madagascar) . . . . . . . . . . 12. *Broussonetia*

b. Stipules caducous; perianth of the pistillate flower not tubular, if tubular, then the ovary and fruit adnate to the perianth . . . . . . . . . . . . 7

7.a. Leaves trinerved to triplinerved, leaf margin crenate (African continent) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8. *Morus*

b. Leaves pinnately veined, leaf margin mostly entire or subentire, or (in juvenile specimens) dentate . . . . . . . . . . . . . . . . . . . . 8

8.a. Stipules connate; pistillate inflorescences with 2-15 flowers; ovary and fruit free; cotyledons unequal and conduplicate (Madagascar) . 9. *Pachytrophe*

b. Stipules free; pistillate inflorescences usually with more than 15 flowers, or with 1-2 flowers, but then the pistil and fruit adnate to the perianth; cotyledons equal or extremely unequal . . . . . . . . . . . . . . . . 9

9.a. Leaves and perianths (almost) glabrous; pistillate inflorescences with 1-2 flowers; ovary and fruit adnate to the perianth; cotyledons extremely unequal (Madagascar and other islands) . . . . . . . . . . 17. *Maillardia*

b. Leaves and perianths more or less hairy; pistillate inflorescences with many flowers; ovary and fruit free; cotyledons equal and plane . . . . . . . . 10

10.a. Stipules 0.5-5 cm long; style branches unequal or one of them lacking (African continent) . . . . . . . . . . . . . . . . . . . 11. *Chlorophora*

b. Stipules 1-3 mm long; style branches 2, equal (Madagascar) . . 10. *Ampalis*

### 8. **Morus** L., Sp. Pl.: 986 (1753). — Type species: *M. alba* L.

*Morus* L. subg. *Afromorus* A. Chev., Rev. Bot. Appl. Agr. Trop. **29**: 70 (1949), invalidly published; Leroy, Rev. Bot. Appl. Agr. Trop. **29**: 482 (1949) & Bull. Mus. Hist. Nat. Paris, ser. 2, **21**: 732 (1949).

Dioecious *trees*; shoot apices shed. *Leaves* distichous, trinerved to triplinerved; stipules free, almost lateral. *Inflorescences* usually solitary on the lower leafless nodes of new (short-)shoots arising from well developed scaly resting buds on wood of the previous season, pedunculate, bracteate; staminate inflorescences spicate, flowers many (to few), not very close together; perianth 4-parted, segments imbricate; stamens 4, inflexed, at anthesis bending outward elastically, anthers introrse; pistillode quadrangular; pistillate inflorescences capitate, with 5-15 flowers; perianth 4-parted; ovary free, style subterminal, stigmas 2. *In fruit* the lower part of the enlarged perianth more or less succulent; exocarp thin-fleshy, thicker on the seed-bearing side, indehiscent, endocarp crustaceous with a woody plug towards the hilum; testa thin, with a slightly thickened elliptic part below the hilum, with few vascular bundles, endosperm present; embryo curved, cotyledons equal and flat, not enclosing the long radicle.

It is rather surprising to meet a member of the chiefly temperate genus *Morus* in the lowlands of Africa. It was described in 1909 as *Morus mesozygia* by Stapf on material from Ivory Coast and as *Celtis lactea* by Sim on material from Moçambique. In the Flora of Tropical Africa (Rendle 1916) *Celtis lactea* was put into the synonomy of *Celtis kraussiana*. In 1922 Mildbraed recognized *C. lactea* as a species of *Morus*, which resulted in the combination *M. lactea*. Since that time *M. lactea* and *M. mesozygia* were often treated as separate species. Chevalier (1949) reduced *M. lactea* to a variety of *M. mesozygia*. He and Leroy (1949) placed the African species in *Morus* subg. *Afromorus*, thus setting it (them) apart from the other *Morus* species.

*M. mesozygia* is indeed distinct because of the attractive and conspicuous leaf venation and the infructescences. The infructescences are reminiscent, also in details, of those of *Pachytrophe* more than of *Morus* species with infructescences resembling fruits of *Rubus*, or of the elongate infructescences of the neotropical *M. insignis*. But in the characters of the leaf (base, margin, and venation) it matches the other *Morus* species, as well as in the abortion and shedding of shoot apices and the relatively large, scaly, axillary resting buds. On the other hand, *M. mesozygia* seems to be distinct from other *Morus* species in its wood anatomical characters (Normand 1950). In these features it agrees with *Chlorophora excelsa* and *C. regia* (Brazier & Franklin 1961).

Both the delimitation and the subdivision of the genus should be a subject of reconsideration when the position and relationships of *Ampalis*, *Pachytrophe* and several present members of *Streblus* s.l. (Corner 1962) are further studied (see p. 331).

8.1. **Morus mesozygia** Stapf ex A. Chev. [Végét. Ut. Afr. Trop. Fr. **5**: 263 (1909) nomen], Journ. Bot. [Paris] **22**: 99 (1909); Hauman, Fl. Congo, Ruanda-Urundi **1**: 55 (1948); A. Chev., Rev. Bot. Appl. Agr. Trop. **29**: 69 (1949). — Lectotype: *Chevalier* 16267, Ivory Coast, Zaranou (P; isotype K). — Fig. 16.

*M. mesozygia* var. *sanda* A. Chev., Rev. Bot. Appl. Agr. Trop. **29**: 71 (1949), invalidly published.

*M. mesozygia* var. *colossea* A. Chev., Rev. Bot. Appl. Agr. Trop. **29**: 71 (1949), invalidly published.

*Celtis lactea* Sim, For. Fl. Port. E. Afr.: 97, t. 96 (1909); Rendle in Prain, Fl. Trop. Afr. **6**(2): 4 (1916). — Type: *Sim* 5299, Moçambique, Quisico (K).

*Morus lactea* (Sim) Mildbr., Notizbl. Bot. Gart. Berlin **8**: 243 (1922); Leroy, Journ. Agr. Trop. Bot. Appl. **2**: 677, t. 6(1-6) (1955).

*M. mesozygia* var. *lactea* (Sim) A. Chev., Rev. Bot. Appl. Agr. Trop. **29**: 72 (1949).

*Trees* up to 35 m tall or shrubs; latex white; leafy twigs 1-3 mm thick, sparsely white-puberulous mainly on the nodes, or glabrous. *Leaves* elliptic to oblong, sometimes to lanceolate or to suborbicular, broadest in or below the middle, sometimes above the middle, (almost) equilateral, 3-13 cm long, 2-8 cm broad, chartaceous to subcoriaceous, acuminate to caudate or to subacute, at the base obtuse, truncate, emarginate, or cordate; margin crenate to serrate, at least in the upper part of the lamina; above short-pubescent at the base of the main veins, beneath on the lower part and in the axils of the main veins; veins slightly prominent to plane above, slightly prominent beneath; at the base trinervate, 3-6 smaller secondary veins arising from the upper part of the costa, tertiary veins towards the margin and the parallel ones between the main veins almost horizontal; petioles 8-20 mm long; stipules caducous, 4-5 mm long, membranous, sparsely puberulous to almost glabrous. *Staminate inflorescences* occasionally in pairs, spikes usually 1-2.5 cm long, ca. 0.8 cm in diam., sometimes interrupted; peduncle 3-20 mm long, (densely) white-puberulous; flowers many, occasionally few; perianth 2-3 mm high, membranous, ciliolate; filaments 3.5-4 mm long, anthers 1-1.2 mm long, 0.7-1 mm broad, connective rather small; pistillode ca. 0.5 mm high, apiculate; bracts differently shaped, flat, up to 1.5 mm long, membranous, ciliolate. *Pistillate inflorescences* subglobose, ca. 5 mm in diam.; peduncle 4-20 mm long, (densely) white-puberulous; flowers ca.

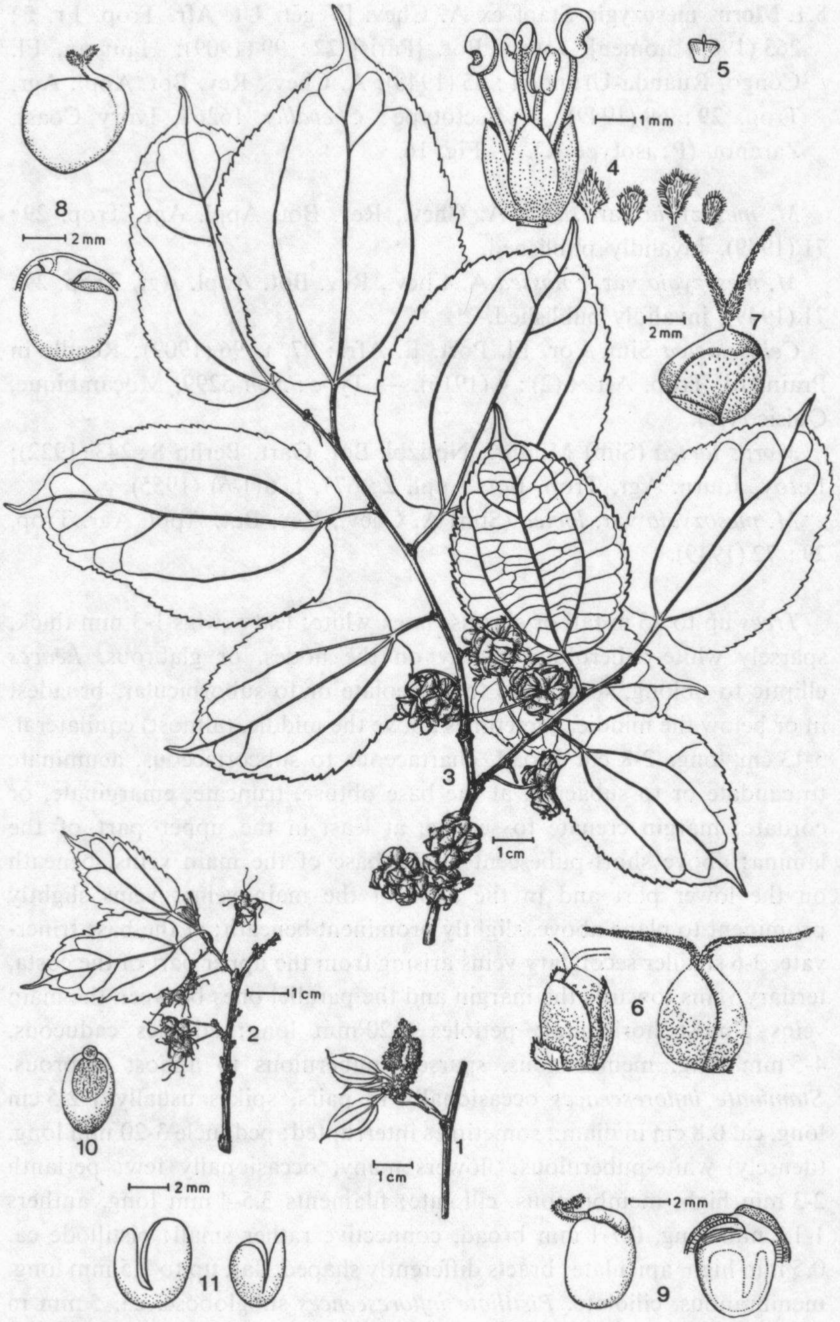

Fig. 16. — ***Morus mesozygia*: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3, leafy twig with infructescences; 4, staminate flower and bracts; 5, pistillode; 6, pistillate flowers and bracts; 7, pistillate flower in fruit; 8, fruit; 9, fruit; 10, seed; 11, embryos (1 : *Simão* 14; 2 : *Fanshawe* 9319; 3, 8-11 : *Simão* 233; 4, 5 : *Andrada* 1447; 6 : *Gomes* e *Sousa* 1862; 7 : *Esperito Santo* 1961).**

5-15, mostly ca. 10; perianth ca. 2.5 mm high, tepals ciliolate; style 0.1-0.2 mm long, stigmas filiform, 3-5 mm long, of the same or of different length, puberulous; bracts differently shaped, up to 1 mm long, ciliolate. *Infructescences* subglobose or sometimes somewhat elongate, ca. 1 cm in diam.; fruiting perianth succulent, yellowish to greenish; fruit ca. 5 mm long, 3-5 mm broad, more or less compressed; seed ca. 4.5 mm long, 2.5-4.5 mm broad, more or less compressed.

Distribution (fig. 14, map 1): In a probably discontinuous area ranging from Senegal to north-western Angola, south-western Ethiopia, and to northern Natal (Republic of South Africa); as evergreen trees in rain forests, but more usual, mostly as deciduous trees, in forests of drier regions, as in semi-deciduous forests, gallery forests, forests bordering savannas; often along streams or lakes, also in secondary forests or (left) as solitary trees after clearing of the forest; also planted (as shade tree) in villages or along streets (Ghana, Senegal); regionally rare to frequent; from sealevel to ca. 1250 m.

Number of collections examined: ca. 140.

The flowering time(s) could not be established, except for Moçambique, where the (main) flowering time seems to be from September to November. As a rule the trees flower when they come into new foliage.

The greenish to yellowish infructescences with succulent fruiting perianths and exocarps are edible. The wood is said to be a good timber; it can be confused with that of *Chlorophora excelsa*, due to strong resemblances in habit, colour of the wood (yellow), and the conspicuously lenticellate bark.

According to data gathered in Kew, *M. mesozygia* was probably published before *C. lactea.*

Infra-specific taxa, as recognized by Chevalier (1949), are untenable. *M. mesozygia* is even a rather uniform species.

9. **Pachytrophe** Bur. in DC., Prodr. **17**: 234 (1873); Benth. & Hook., Gen. Pl. **3**(1): 363 (1880); A. Richter, Term. Füzetek **18**: 294 (1895); Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 14 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 9 (1952); Corner, Gard. Bull. Singapore **19**: 214 (1962). — Lectotype species: *P. dimepate* Bur.

*Ampalis* Boj. sect. *Pachytrophe* (Bur.) Baillon, Hist. Pl. **6**: 193 (1875-1876).

Dioecious *trees*. *Leaves* distichous, pinnately veined; stipules connate, semi-amplexicaul. *Inflorescences* usually in pairs in the leaf axils, spicate, pedunculate, bracteate, some of the bracts peltate, abaxial sterile groove present, flowers sessile, close together (in longitudinal rows); staminate inflorescences with many flowers, perianth 4-parted, segments decussate-imbricate; stamens 4, inflexed, at anthesis springing back, anthers introrse; pistillode quadrangular; pistillate inflorescences with 2-14 flowers; perianth with 4 decussate-imbricate, free tepals; ovary free; style subapical; stigmas 2, of equal length. *In fruit* the perianth enlarged, more or less succulent and reddish; fruit basally adnate to the perianth, exocarp thinly fleshy, more thickly so on the seed-bearing side, indehiscent, endocarp crustaceous, with a large woody plug towards the hilum; testa thin, with an oblong to suborbicular not distinctly vascularized thickened part below the rather small hilum; embryo curved, cotyledons unequal, conduplicate, their tops inflexed, the larger enveloping the smaller; radicle rather long, enclosed by the cotyledons.

In 1873 Bureau described the genus *Pachytrophe* with two species, *P. obovata* and *P. dimepate*. Léandri (1948b) retained the two species and distinguished some varieties within the former. Material of *Pachytrophe* has been associated with and named under the Asian genus *Plecospermum* by Baillon (1895) and Richter (1895).

The two species were kept separate mainly on the basis of differences in the leaf shape and the leaf apex. Other differences than these could not be found. Although many specimens can be separated on their leaf characters, the occurrence of many intermediates and the nature of the differences do not justify separation on the specific level, and even not within one species. The differences in the leaves are probably (partly?) due to environmental conditions.

*Pachytrophe* is closely related to *Ampalis* and some species of *Streblus* sensu Corner (1962), and probably congeneric with them. These taxa are also distinctly related to *Morus* (see p. 331).

9.1. **Pachytrophe dimepate** Bur. in DC., Prodr. **17**: 234 (1873); Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 14, pl. (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 10, t. 2 (1952). — Lectotype: *Chapelier* s.n., Madagascar (P). — Fig. 17.

*P. obovata* Bur. in DC., Prodr. **17**: 235 (1873); Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 16 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 10, t. 2 (1952). — Type: *Boivin* 1717, Madagascar, Ile St. Marie (P).

*Plecospermum bureaui* A. Richter, Term. Füzetek **18**: 296 (1895), nom. nud. et superfl., with as synonym *Plecospermum obovatum* Bur., name on label of collection *Boivin* 1717.

*Plecospermum? laurifolium* Baillon in Grandidier, Hist. Madag., Bot., Atlas **3**: 294a (1895). — Type: *Hildebrandt* 3242, Madagascar, Nossi Komba (P).

*Pachytrophe obovata* var. *laurifolia* (Baillon) Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 16 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 11 (1952).

*P. obovata* var. *montana* Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 16 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 11 (1952). — Lectotype: *Ursch* 32, Madagascar, Analamazoatra Forest (P).

*Trees* to 30 m tall, or shrubs; latex white; leafy twigs 0.5-2.5 mm thick, minutely puberulous, glabrescent. *Leaves* (subrotundate to) elliptic to oblong (to lanceolate), usually broadest in or above the middle, (1-)2(-16) cm long, (0.5-)1.5-6 cm broad, coriaceous to subcoriaceous, mostly acuminate to apiculate or obtuse, sometimes subcaudate or emarginate, at the base acute to obtuse; margin entire, often somewhat revolute; above and beneath glabrous or almost so; above the costa more or less impressed, especially towards the base, the other veins slightly prominent, beneath the costa prominent, the other veins less prominent to almost plane, 5-12(-16) pairs of secondary veins, without parallel tertiary veins; petioles 3-15(-20) mm long, minutely puberulous to almost glabrous; stipules connate, 2-6(-9) mm long, sparsely to rather densely minutely puberulous. *Staminate inflorescences* 0.5-5 cm long, including the 1-5 mm long, puberulous peduncle, rather densely flowered; perianth 1-5-2 mm high, membranous, puberulous and ciliolate, tepals almost equal; filaments 2.5-3.5 mm long, anthers ca. 0.7-1.0 × 0.7-1.0 mm, connective small, more or less gland-like swollen; pistillode ca. 0.5 mm high; bracts basally attached to peltate up to ca. 1 mm long or in diameter, puberulous and ciliolate. *Pistillate inflorescences* 0.5-2.5 cm long, including the 2-15 mm long, puberulous peduncle; flowers 2-14, perianth 1.5-2 mm high, tepals distinctly decussate, rather thick, their margins membranous, ciliolate, outside sparsely and minutely puberulous to

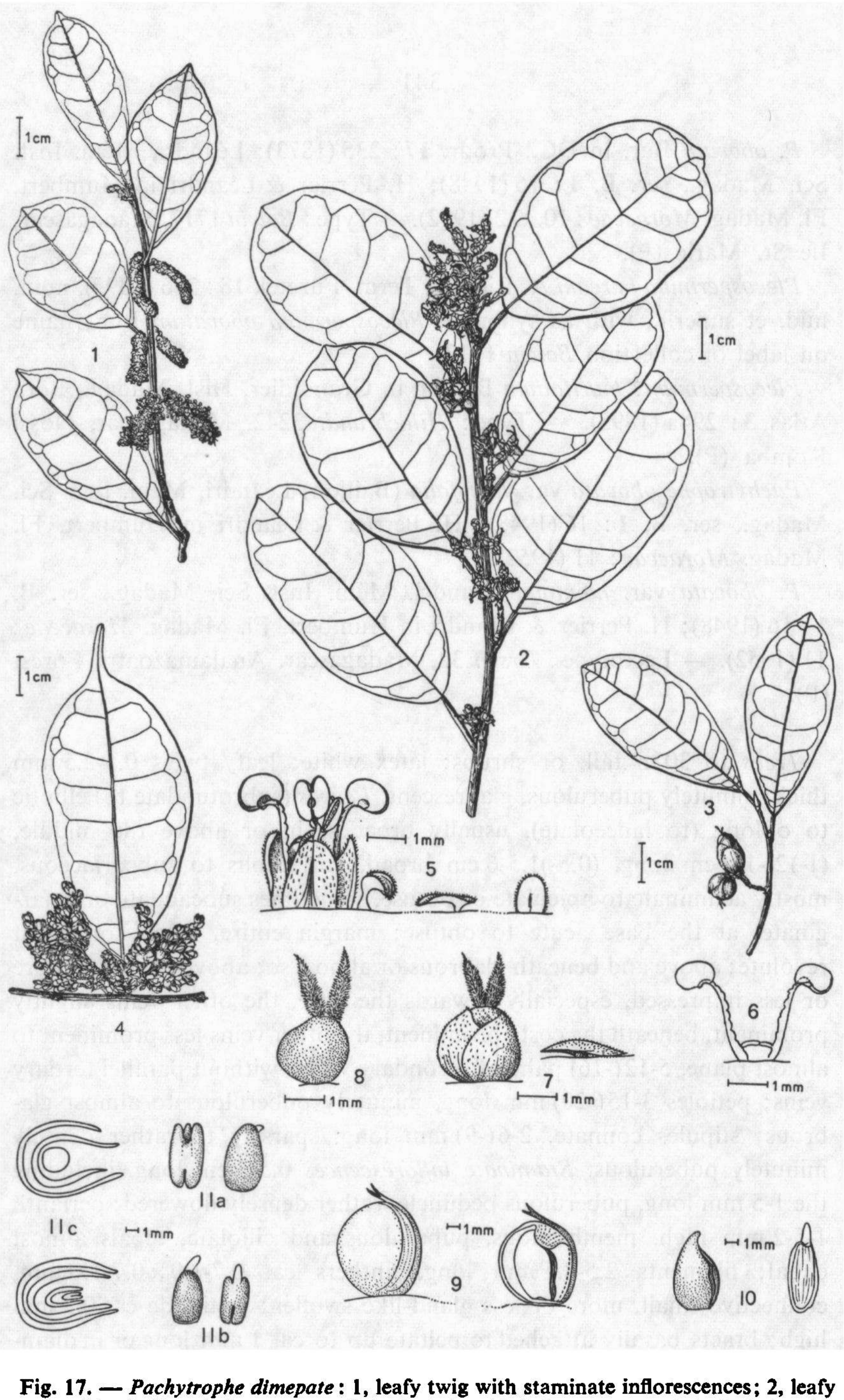

**Fig. 17.** — ***Pachytrophe dimepate*****: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3, leafy twig with infructescence; 4, leafy twig with aberrant inflorescences; 5, staminate flower and bracts; 6, stamens and pistillode; 7, pistillate flower and bract; 8, pistil; 9, fruit; 10, seed and embryo; 11, a, outer, b, inner cotyledons, c, cross sections (1 : *Ursch* 32; 2 : *Capuron* 27182; 3 : 9-11 : *Capuron* 8894; 4 : *Serv. For. Madag.* 12500; 5, 6 : *Capuron* 941; 7, 8 : *Perrier de la Bâthie* 9729).**

almost glabrous; ovary ca. 1.5 mm high, style 0-1.5 mm long, stigmas ca. 1.5-3 mm long, more or less densely puberulous; bracts crowded on the upper part of the peduncle and among the flowers, peltate (or subpeltate), up to 2.5 mm in diameter, sparsely minutely puberulous and ciliolate. *In fruit* perianth ca. 6-8 mm high, the succulent tepals striate (in herbarium material); fruit 5-8 mm high, 6-7 mm broad; seed ca. 4-5 mm long, the indistinctly vascularized part of the testa dark brown, in the spaces between the parts of the embryo membranous to mucilaginous material connected with the thickened part of the testa (probably remains of endosperm).

Distribution (fig. 14, map 1): Madagascar, confined to the eastern and north-western part of the island; as evergreen or deciduous trees or shrubs in humid to dry forests (or thickets), often by streams or the seashore; often on sand; from sealevel to 1000 m.

Number of collections examined: ca. 170.

Flowering probably throughout the year, with a peak from September to March.

The infructescence with reddish succulent perianths and exocarps are edible. The hard wood is used for carpentry.

The species may occasionally be epiphytic or liana-like.

Several specimens bear strange paniculate structures consisting of strongly branched short twigs bearing coriaceous persistent scales (probably modified stipules), among which once a seedless fruit was found. Often the ovaries do not develop into fruits.

10. **Ampalis** Boj., Hort. Maurit.: 291 (1837); Bur. in DC., Prodr. **17**: 250 (1873); Baillon, Hist. Pl. **6**: 190 (1875-1876); Benth. & Hook., Gen. Pl. **3**(1): 365 (1880); Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 9 (1948); Corner, Gard. Bull. Singapore **19**: 214 (1962). — Type species: *A. mauritiana* (Jacq.) Urb.

*Streblus* Lour. subgen. *Parastreblus* Blume, Mus. Bot. Ludg.-Bat. **2**: 80 (1956). — Type species: *S. mauritianus* (Jacq.) Blume [= *Ampalis mauritiana* (Jacq.) Urb.].

Dioecious *trees. Leaves* in spirals or mostly (almost) distichous, pinnately veined; stipules free, almost lateral. *Inflorescences* solitary or in pairs in the axils of the leaves, spicate, pedunculate, with (rather) few bracts; flowers sessile, close together in longitudinal rows, sterile groove present; perianth of the staminate flowers 4-parted, segments decussate-imbricate; stamens 4, inflexed, at anthesis springing back, anthers introrse; pistillode quadrangular; pistillate flowers with 4 free, decussate-imbricate, two by two different tepals; ovary free; stigmas 2, of equal length. *In fruit* perianth enlarged, more or less succulent (and greenish white?); exocarp thin, fleshy, thicker at the seed-bearing side, indehiscent; endocarp crustaceous, with a woody plug towards the hilum; testa rather thin, with an oblong, thickened, not distinctly vascularized part below the rather small hilum; embryo with equal, rather thick, almost plane cotyledons; radicle long.

*Ampalis mauritiana* was first described as *Morus mauritiana* by Jacquin (1791), probably on material from Mauritius, where the species was introduced long ago. Material from Mauritius also served for *Morus nitida*, described by Willemet (1796). Under the genus *Morus* the species has also been described as *M. ampalis* [by Poiret (1797) on material from Madagascar] and as *M. rigida* [by Hasskarl (1844) on material grown in the botanical garden of Bogor]. The species has been associated with *Trophis* (cf. Roxburgh 1832) and with *Streblus* (Blume 1856). The genus *Ampalis* was established by Bojer (1837) by separating *M. mauritiana* and *M. ampalis* from *Morus* and uniting them under *A. madagascariensis.*

*Ampalis* is very closely related to *Pachytrophe.* The only difference of some importance is to be found in the stipules: fused in *Pachytrophe,* free in *Ampalis.* The flowers and fruits are similar to those of *Morus mesozygia*; in the elongate inflorescences it is reminiscent of the neotropical *Morus insignis.* Furthermore, *A. mauritiana* shows distinct resemblances to species of *Streblus* sensu Corner (1962) (see p. 330).

The cotyledons apparently lie in a plane transverse to those of *Pachytrophe.* But observation of the attachment of the cotyledons shows the position of the embryo to be similar in the two taxa.

10.1. **Ampalis mauritiana** (Jacq.) Urb., Symb. Antill. **8**: 165 (1920). — Type: Jacquin, Ic. Pl. Rar. **3**: t. 617 (1789). — Fig. 18.

*Morus mauritiana* Jacq., Collect. **3**: 206 ("1789", 1791); Poir. in Lam., Encyl. Bot. **4**: 381 (1797); Willd., Sp. Pl. **4**: 371 (1805); Spreng., Syst. Veg. **1**: 492 (1825).

*Streblus mauritianus* (Jacq.) Blume, Mus. Bot. Lugd.-Bat. **2**: 80 (1856).

*S. maritimus* Palacky, Catal. Pl. Madag. **2**: 31 (1907), probably a mistake in writing or printing *S. mauritianus* Bl.

*Morus nitida* Willem. in Usteri, Ann. Bot. **18**: 56 (1796). — Type: not yet traced.

*M. ampalis* Poir. in Lam., Encycl. Bot. **4**: 380 (1797); Willd., Sp. Pl. **4**: 371 (1805); Spreng., Syst. Veg. **1**: 492 (1825). — Syntypes: ex herb. *Poiret* s.n., Madagascar and Réunion (P).

*Trophis cylindrica* Roxb. in MSS, as synonym of *Morus mauritiana* cited in Roxb., Fl. Indica **3**: 599 (1832).

*Ampalis madagascariensis* Boj., Hort. Maurit.: 291 (1837), based on and as synonym of *Morus mauritiana* and *M. ampalis*; Bur. in DC., Prodr. **17**: 251 (1873); Baillon in Grandidier, Hist. Madag., Bot., Atlas **3**: t. 293 (1895); Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 9, with plate (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 8, t. 2 (1952).

*A. madagascariensis* var. *occidentalis* Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 12, pl. (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 9 (1952). — Lectotype: *Perrier de la Bâthie* 17402, Madagascar, Manambolo River, affluent of the Upper Betsiboka River (P; isotype K).

*Morus rigida* Hassk., Cat. Hort. Bog.: 74 (1844) & Pl. Jav. Rar.: 198 (1848). — Type: *M. rigida* was possibly described from living material in the botanical garden of Bogor; several collections of the plants in Bogor have been made after the date of publication (e.g., several collections made by *Teysmann*).

Dioecious *trees* up to 15(-20) m tall, or *shrubs*; latex white; leafy twigs 1-6 mm thick, (in herbarium material the younger parts often more or less compressed and sulcate), rather conspicuously lenticellate, puberulous to hispidulous to scabrous. *Leaves* elliptic to oblong (to lanceolate), broadest in or mostly above the middle, 2-16 cm long, 1-8 cm broad, coriaceous to subcoriaceous, acuminate to obtuse, sometimes to emarginate, at the base acute to obtuse; margin callose and often somewhat revolute, entire, probably only in juvenile specimens pinnately lobed to parted; both surfaces scabrous (with short rigid hairs) to smooth and glabrous; above veins slightly prominent or the main veins more or less impressed, beneath veins prominent, 5-10 pairs of secondary veins, without parallel tertiary veins; petioles 3-15(-22) mm long, puberulous to hispidulous to scabrous or glabrous; stipules 1-3 mm long, chartaceous, minutely puberulous. *Staminate inflorescences* often on the leafless basal

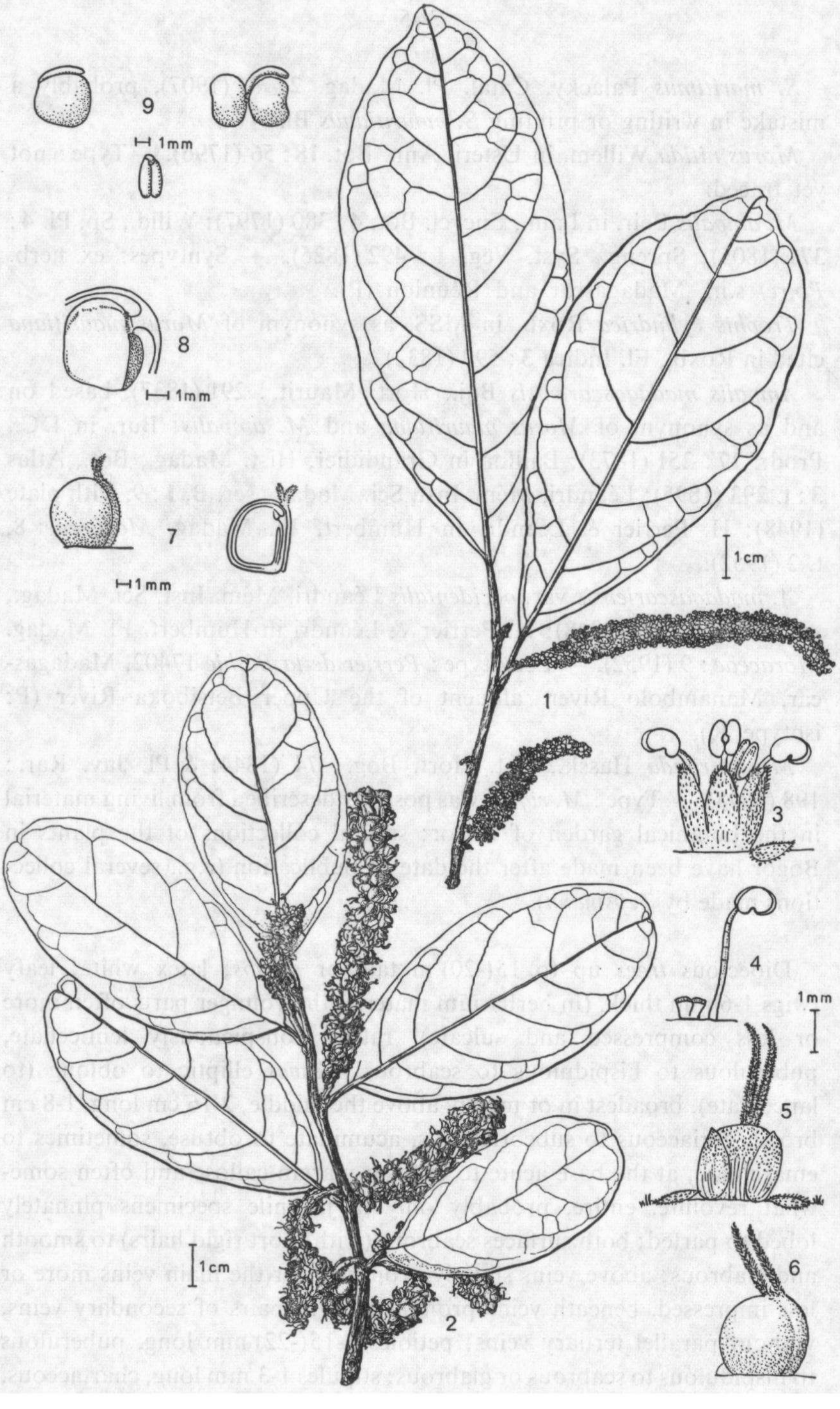

**Fig. 18. — *Ampalis mauritiana*: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3, staminate flower and bract; 4, stamen and pistillode; 5, pistillate flower and bracts; 6, pistil; 7, fruit; 8, seed; 9, embryo (1: *Capuron* 18494; 2: *Capuron* 234; 3, 4: *Humblot* 367; 5, 6: *Capuron* 27147; 7-9: *Serv. For. Madag.* 6615).**

part of new shoots, ca. 2-9 cm long including the 2-10 mm long, usually bracteate, puberulous to hirtellous peduncle; rachis puberulous; perianth 1.5-2 mm high, membranous, sparsely to rather densely puberulous with short rigid hairs with a broadened base, at the apex usually rather densely ciliolate with softer white hairs; filaments 2.5-3.5 mm long, anthers ca. 0.8-1.2 × ca. 0.8-1.2 mm; pistillode ca. 0.5 mm high, quadrangular; bracts basally attached to subpeltate, elliptic to oblong, up to 1.5 mm long, thicker than the perianth, sparsely puberulous and/or ciliolate to almost glabrous. *Pistillate inflorescences* usually solitary, sometimes paired, often on the leafless basal part of new shoots, (1-)1.5-12 cm long including the 5-20 mm long, usually bracteate, puberulous to hirtellous peduncle; rachis puberulous to hirtellous; flowers in the basal part of the rachis usually in one row and sometimes reduced, higher usually in 3 rows; perianth 1.5-2.5 mm high, tepals distinctly decussate, the inner ones often somewhat larger than the outer ones, rather thick but with a membranous margin, sparsely puberulous; ovary ca. 2 mm high, stigmas 1.5-3 mm long, rather densely puberulous; bracts rather few, scattered on the peduncle and the rachis, (sub)peltate, up to ca. 1 mm in diam., almost glabrous. *Fruiting perianth* ca. 5 mm high, the more or less succulent tepals (in herbarium material) striate; fruit ca. 4.5-5 × 5-6 mm; seed ca. 4 × 4 mm; the thickened, not distinctly vascularised part of the testa dark brown.

Distribution (fig. 14, map 2): Madagascar, mainly in the eastern part of the island, also in Mayotte (Comoro Islands); as evergreen much-branched shrubs or trees in dry to humid forests, mostly along streams, by sea coasts or lake sides, often on sandy soils, from sealevel to ca. 1500 m altitude; also cultivated. Introduced in Mauritius, Java (Bot. Gard. Bogor), India (Bot. Gard. Calcutta), Martinique, and Trinidad.

Number of collections examined: ca. 105.

Flowering probably throughout the year, but mainly from October to February.

The infructescences with succulent fruiting perianths and exocarps are edible.

11. **Chlorophora** Gaudich. in Freyc., Voy. Monde Bot.: 508 (1830); Benth. & Hook., Gen. Pl. 3(1): 363 (1880); Kaastra, Acta Bot.

Neerl. **21**: 657 (1972) & **22**: 69 (1973). — Type species: *C. tinctoria* (L.) Gaudich. ex Benth. & Hook.

*Maclura* Nutt. sect. *Chlorophora* (Gaudich.) Baillon, Hist. Pl. **6**: 193 (1875-1876); Corner, Gard. Bull. Singapore **19**: 236 (1962).

Dioecious *trees*. *Leaves* distichous, pinnately veined; stipules free, not fully amplexicaul. *Inflorescences* usually solitary in the axils of the leaves or on leafless nodes at the base of fertile twigs, spicate, pedunculate; flowers numerous in close longitudinal rows alternating with rows of basally attached bracts, abaxial sterile groove present; perianth of the staminate flower 4-parted, segments imbricate; stamens 4, inflexed, at anthesis bending outward elastically, anthers introrse; pistillode quadrangular or applanate and bidentate; perianth of the pistillate flowers 4-parted, segments decussate-imbricate, two by two differently shaped; ovary free, stigmas 2, usually one of them more or less reduced or lacking. *In fruit* the perianth enlarged and somewhat thickened; fruit stipitate and slightly compressed; exocarp thin, white, fleshy, thicker at the narrowed base and at the seed-bearing side, indehiscent; endocarp crustaceous with a small woody plug towards the hilum; testa thin with a slightly thickened ovate vascularized part below the hilum; endosperm present; embryo curved, cotyledons small, flat, equal, not enclosing the long radicle.

In 1869 Welwitsch described *Morus excelsa*. This species was referred to *Maclura* by Bureau (1873) and to *Chlorophora* by Bentham & Hooker (1880). Under *Chlorophora* some additional African species were described: *C. tenuifolia* (Engler 1898), *C. alba* (Chevalier 1912) and *C. regia* (Chevalier 1912). The first two proved to be synonyms of *C. excelsa* (cf. Rendle 1916). The same species was also described as *Milicia africana* by Sim (1909) and thus associated with *Cardiogyne africana* (= *Milicia spinosa* Sim). *Chlorophora*, composed of African and American species, was reduced to a section of *Maclura* by Corner (1962).

As discussed above (p. 331, 333), the broad genus *Maclura* has to be accepted with much reserve. A definite conclusion about the position of the two African species can only be reached after further study of *Maclura* s.l. and comparison with *Bagassa*, *Batocarpus*, *Morus*, and *Broussonetia*. At first sight the two species resemble the Madagascan *Broussonetia greveana* (formerly *Chlorophora greveana*), but they differ distinctly in the perianth of the pistillate flower and the infructescences (see p. 333).

*C. excelsa* and *C. regia* are very closely related, as shown by the fact that the initial doubt about the existence of two species faded only gradually. They are very similar in most morphological characters and also in their wood anatomy (Brazier & Franklin 1961). In adult specimens the only differences can be found in the leaf venation and the indument. Juvenile specimens of both species can be told apart by differences in the indument of the leaves and in the colour of the costa beneath which is usually red in *C. regia* and yellow in *C. excelsa.* The leaves of juvenile specimens differ in shape, margin, venation, texture, and indument from those of adult specimens. Another difference between juvenile specimens of the two species can be found in the growth habit. *C. excelsa* shows sympodial growth and bears its leaves biserially even on the stem. *C. regia* shows monopodial growth. The stem bears spirally arranged leaves. Branches with distichous leaves are horizontal and arise in continuous order (cf. Hallé & Oldeman 1970). When becoming adult, *C. regia* probably attains the same growth habit as *C. excelsa.* In West Africa the species are sympatric. There they may occur side by side in the same habitats and flower (almost) simultaneously. Both are light demanders (cf. Aubréville 1959; Voorhoeve 1965). When young both *Chlorophora* species are attacked by the parasite *Phytoloma,* but probably not by the same species (cf. White 1966).

**Key to the species of *Chlorophora***

1.a. The areoles on the lower leaf surface covered by short white hairs; 10-20 pairs of secondary veins . . . . . . . . . . . . . . . . . . . . . . 1. *C. excelsa*
b. The areoles on the lower leaf surface not covered by hairs; 7-11(-14) pairs of secondary veins . . . . . . . . . . . . . . . . . . . . . . . 2. *C. regia*

11.1. **Chlorophora excelsa** (Welw.) Benth. & Hook., Gen. Pl. **3**(1): 363 (1880); Rendle in Prain, Fl. Trop. Afr. **6**(2): 22 (1916); De Wild., Ann. Mus. Congo, Bot., ser. 5, **3**: 63 (1909); Andrews, Flow. Pl. Anglo-Egyptian Sudan **2**: 257, t. 90 (1952); Aubrév., Fl. For. Côte d'Ivoire **1**: 49, t. 4 (1959). — Type: *Welwitsch* 1559 ♀, Angola, Golungo Alta, Dembos, Cazengo (LISU; isotypes B, BM, G, K, P; the collection also contains ♂ and juvenile material). — Fig. 19.

*Morus excelsa* Welw., Trans. Linn. Soc. Lond. (Bot.) **27**: 69, t. 23 (1869).

*Maclura excelsa* (Welw.) Bur. in DC., Prodr. **17**: 231 (1873); Corner, Gard. Bull. Singapore **19**: 237 (1962).

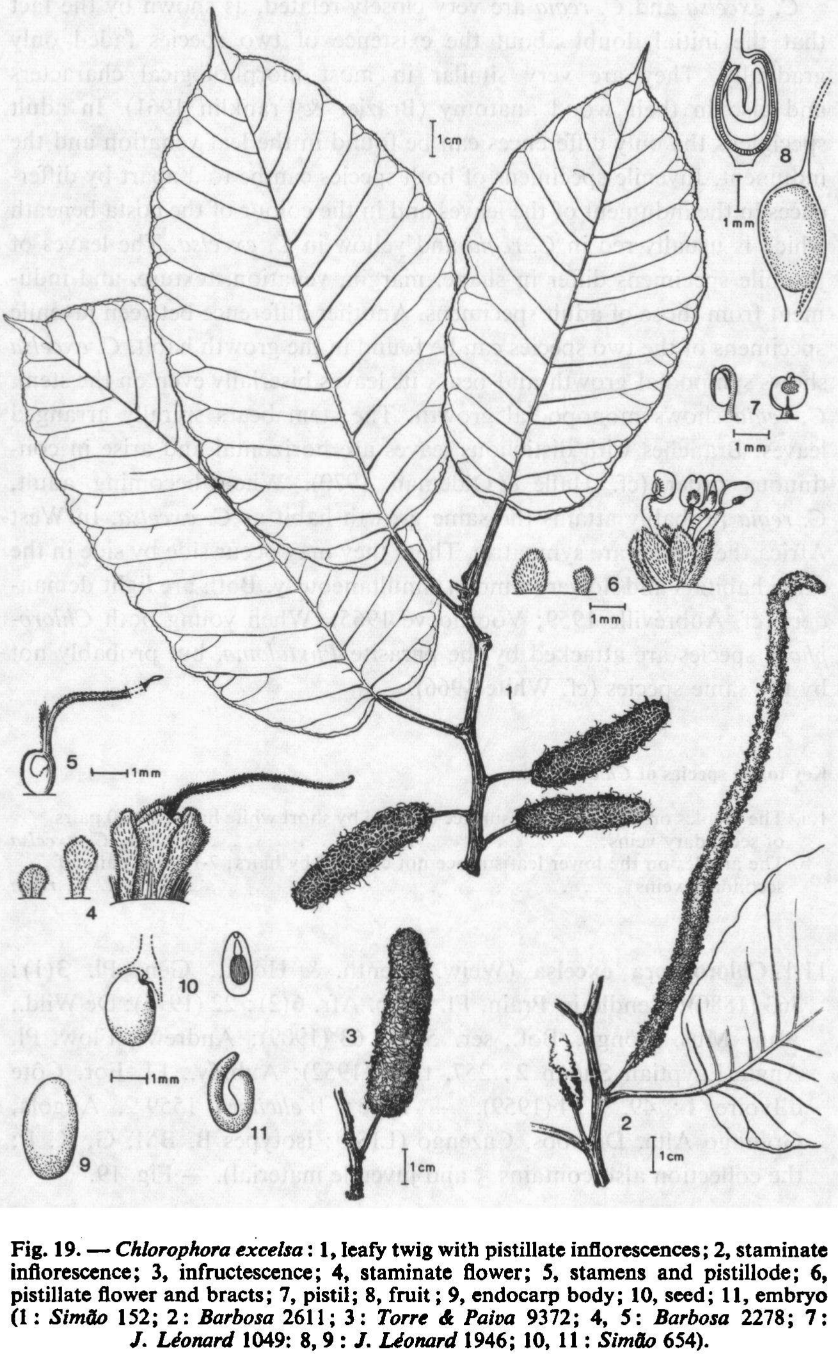

**Fig. 19.** — ***Chlorophora excelsa*: 1, leafy twig with pistillate inflorescences; 2, staminate inflorescence; 3, infructescence; 4, staminate flower; 5, stamens and pistillode; 6, pistillate flower and bracts; 7, pistil; 8, fruit; 9, endocarp body; 10, seed; 11, embryo (1 : *Simão* 152; 2 : *Barbosa* 2611; 3 : *Torre & Paiva* 9372; 4, 5 : *Barbosa* 2278; 7 : *J. Léonard* 1049: 8, 9 : *J. Léonard* 1946; 10, 11 : *Simão* 654).**

*Chlorophora tenuifolia* Engl., Bot. Jahrb. **20**: 139 (1894); Engl., Monogr. Afr. Pfl. **1**(*Moraceae*): 4 (1898); Engl., Pflanzenw. Afr. **3**(1): 21 (1915). — Type: *Quintas* 154, São Tomé (COI; isotype LISU).

*Milicia africana* Sim, For. Fl. Port. E. Afr.: 97, t. 122 (1909). — Type: *Sim* 5386, Moçambique (not yet traced).

*Chlorophora alba* A. Chev., Bull. Soc. Bot. Fr. **58**(Mém. 8d): 209 (1912). — Type: *Chevalier* 24236, Dahomey, Kouandé (P; isotype K).

Dioecious (or sometimes monoecious?) *trees* up to 35(-50) m tall; latex white or yellowish; leafy twigs 0.5-6 mm thick, white-puberulous, pubescent or almost glabrous, the lower part of new shoots with short internodes and often only scale-leaves. *Leaves* elliptic to oblong (to lanceolate), 6-20(32) cm long, 3.5-10(-12) cm broad, usually broadest in or below the middle, chartaceous to coriaceous, mostly distinctly inequilateral, mostly short-acuminate to mucronate, sometimes subacute or subcaudate, at the base obtuse to cordate, occasionally acute; margin entire to faintly repand or crenate; above puberulous or scabridulous and then often pubescent on the main costa veins and the proximal parts of the secondary veins, or (almost) glabrous, beneath on the main veins puberulous, pubescent, or almost glabrous, the areoles covered with short weak hairs inserted on the lateral sides of the veinlets; veins nearly plane above, more or less prominent beneath, 10-22 pairs of secondary veins, with parallel tertiary veins; petioles 1-5 cm long; stipules 0.5-5 cm long, (membranous to) chartaceous to subcoriaceous, those forming the buds coriaceous, rather sparsely white-puberulous to pubescent, usually leaving conspicuous white hairy scars. *Staminate inflorescences* 8-20 cm long, ca. 5 mm in diam.; peduncle 8-23 mm long, white-puberulous to pubescent to subtomentose, often with some large bracts on the upper part; perianth ca. 1.5 mm high, tepals almost equal, convex, puberulous to pubescent or to tomentellous; filaments 1.5-2 mm long, anthers 0.7-0.9 mm long, ca. 0.6 mm broad, connective rather small; pistillode membranous, 0.3-0.5 mm high; bracts ovate to spathulate, up to 1 mm long, puberulous. *Pistillate inflorescences* 2-3 cm long, 5-6 mm in diam.; peduncle 7-20 mm long, white-puberulous to pubescent to subtomentose; perianth 2-2.5 mm high, the inner tepals flat, the outer ones subconduplicate-cucullate, puberulous to pubescent or to tomentellous; ovary ca. 1 mm high, one stigma 3-7 mm long, the other 0.1-1 mm long; bracts (sub)spathulate, membranous, 0.5-1.5 mm long, puberulous. *Infructescences* 3-5 cm long, 1.5 cm in diam.; fruiting perianth 6-7 mm high, tepals somewhat thickened; fruit 2.5-3 mm long; seed ca. 2 mm long.

*Juvenile specimens*: Leafy twigs white-hirtellous to pubescent to (sub) tomentose; the leaves lanceolate to oblong, chartaceous, the apex long-acuminate to subcaudate or to subacute, the base obtuse to subcordate or to cordate, the margin serrato-dentate to crenato-dentate, above strigillose to puberulous or to hispidulous, often more or less scabrous, on the main veins often pubescent to tomentose, beneath hirtellous to sparsely or densely tomentose; the stipules puberulous to pubescent.

Distribution (fig. 14, map 2): From Guinea-Bissau to Moçambique; in deciduous, semi-deciduous, or evergreen (primary and secondary) forests, apparently with preference for the drier types of forests, often in gallery forests, in forest islands in savanna regions, or there as lone trees: occasional to predominant; from sealevel to ca. 1300 m. Trees of *C. excelsa* can often be found as lone trees in cultivated areas. For some regions (with mixed forests) the trees are reported to be deciduous for a short period, due to dry seasons (cf. Vigne 1931; Hutchinson & Dalziel 1937; Aubréville 1959).

Number of collections examined: ca. 220.

From West Africa to the Sudan (and Uganda) flowering from January to March; in East Africa (from Moçambique to Uganda) from July to December, with a peak in August and September, which also holds for some parts of Zaire, Gabon, and São Tomé. Deciduousness is correlated with flowering time.

The species is a valued timber; bark and latex are used for several purposes. A survey of the use of the species is given in the Useful Plants of West Tropical Africa, Hutchinson & Dalziel (1937) (see also Vigne 1931).

Young trees (often attacked by the gall-forming *Phytolyma lata*) have a continuous growth. The growth of adult trees is periodical, but apparently not quite synchronous and not strictly related to season and flowering time. Osmaton (1965) reported the occurrence of monoecious trees in Uganda. He contradicted the statement of Lawton (1955) that male and female trees are different in habit.

Bats and birds seem to play an important part in the dispersal (Osmaston 1965; Dale & Greenway 1961). The fallen infructescences attract small antelopes and rodents (Vigne 1931).

11.2. **Chlorophora regia** A. Chev., Bull. Soc. Bot. Fr. 58(Mém. 8d): 209 (1912); Rendle in Prain, Fl. Trop. Afr. 6(2): 23 (1916); Gomes & Sousa, Mem. Soc. Brot. 1: 74, t. 37 (1930) & Ess. Florestais Guiné Port. 4: 1-14, pl. (1956); Aubrév., Fl. For. Côte d'Ivoire 1: 49, t. 4 (1959); Voorhoeve, Liberian High Forest Trees: 285, t. 54, phot. 23 (1965). — Type: *Chevalier* 12505bis, Guinea, Fouta-Djalon, between Mamou and Timbo (P, not seen). — Fig. 20.

*Maclura regia* (A. Chev.) Corner, Gard. Bull. Singapore 19: 237 (1962).

*Trees* up to 35 m tall; latex white; leafy twigs 1-4 mm thick, sparsely white-puberulous, the lower part of new shoots with short internodes and often leafless (only stipules). *Leaves* oblong to elliptic, broadest in or below the middle, more or less inequilateral, 4-20(-28) cm long, 3-13 cm broad, chartaceous to subcoriaceous, shortly acuminate to mucronate, at the base obtuse to cordate; margin almost entire, repand or crenato-denticulate towards the apex; above glabrous or nearly so, beneath sparsely puberulous on the veins; veins slightly prominent to plane above, more or less prominent beneath; 7-11(-14) pairs of secondary veins, most tertiary veins parallel, petioles 8-36 mm long, puberulous; stipules 1-3.5 cm long, membranous to chartaceous (those forming the buds coriaceous), puberulous. *Staminate inflorescences* 8-18 cm long, 5-6 mm in diam.; peduncle 8-18 mm long, densely white-puberulous to tomentellous; perianth ca. 1.5 mm high, tepals almost free, membranous, puberulous to tomentellous; filaments ca. 3 mm long, anthers 0.8-1 cm long, 0.5-0.6 mm broad, connective rather small; pistillode ca. 0.5 mm high, membranous; some bracts 2-3 mm long and ovate to elliptic, others 1-2 mm long and oblong to (sub)spathulate, puberulous to tomentellous. *Pistillate inflorescences* 1-4.5 cm long, ca. 5 mm in diam.; peduncle 7-10 mm long, white-puberulous to tomentellous; the inner tepals flat to slightly convex, the outer ones subconduplicate-cucullate, the upper parts puberulous to tomentellous; style up to 0.5 mm long, one stigma 8-10 mm long and minutely puberulous, sometimes also the other stigma developed and up to 1 mm long; bracts 0.5-2 mm long, ovate, oblong to (sub)spathulate, puberulous to tomentellous. *Infructescences* up to 8 cm long, ca. 12 mm in diam., peduncle up to 16 mm long, perianth 5-6 mm high; fruit ca. 2.5 mm long; seed ca. 2 mm long.

*Juvenile specimens*: Leafy twigs puberulous; the leaves lanceolate to oblong, chartaceous, the apex long-acuminate, the base obtuse to cordate, the margin serrato-dentate to crenato-dentate, above puberulous to

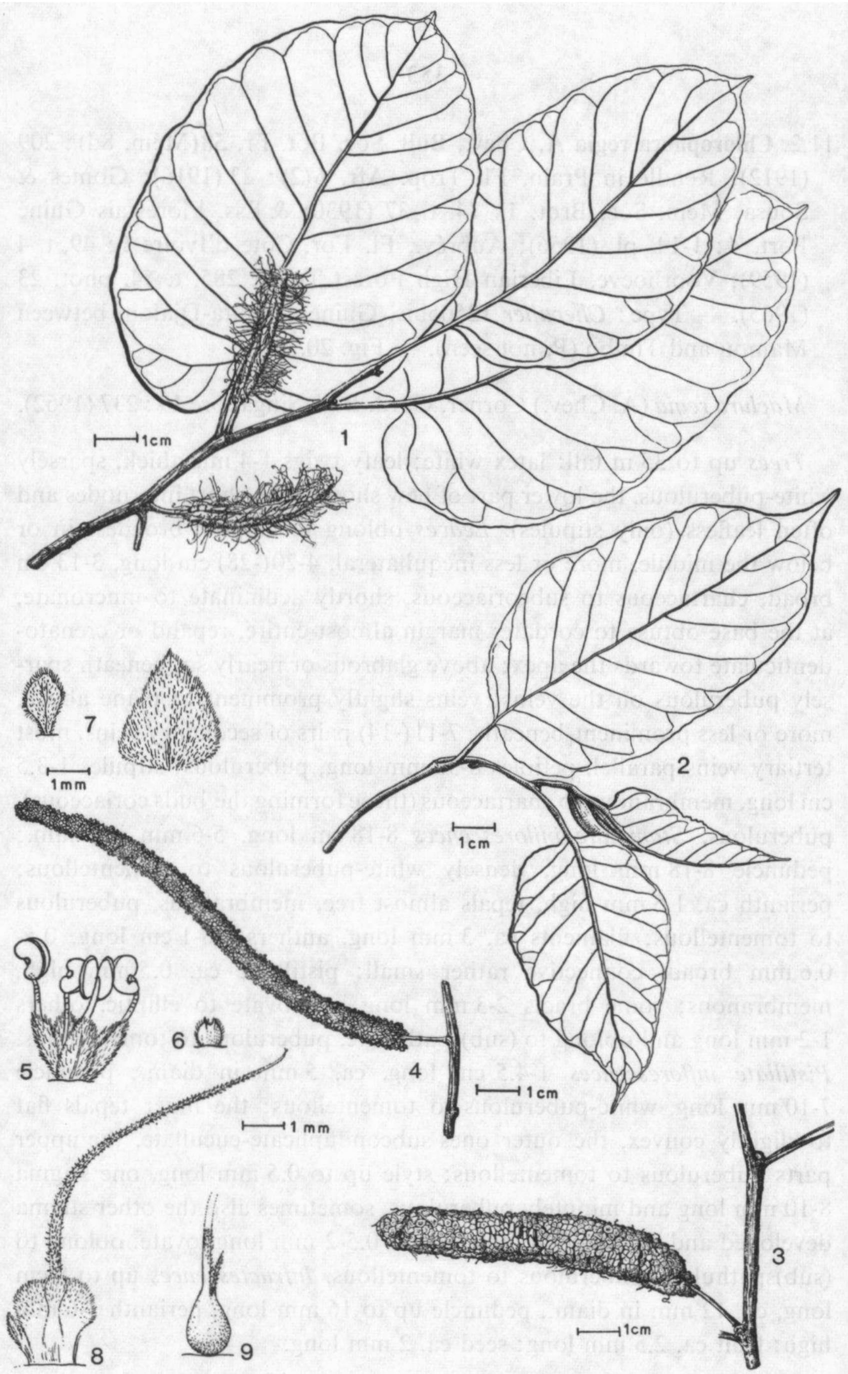

Fig. 20. — *Chlorophora regia*: 1, leafy twig with pistillate inflorescences; 2, leafy twig with long stipules; 3, infructescence; 4, staminate inflorescence; 5, staminate flower; 6, pistillode; 7, bracts of the staminate inflorescence; 8, pistillate flower and bract; 9, ovary (1, 8, 9: *Leeuwenberg* 2471; 2: *Raimbault* s.n.; 3: *de Wilde* 1044; 4: *Voorhoeve* 947; 5-7: *Voorhoeve* 180).

hirtellous to hispidulous, usually scabrous, beneath appressed-puberulous on the main veins; the stipules chartaceous, puberulous.

Distribution (fig. 15, map 1): From Gambia to western Ghana, in rain forests, or especially in the north-western part of the area in gallery forests; common or rare, at lower altitudes. Like *Chlorophora excelsa,* this species can often be found as a lone tree in cultivated areas (cf. Aubréville 1959; Voorhoeve 1965). According to Voorhoeve *C. regia* is deciduous for a short period in the dry season; according to White (1966) *C. regia* is more water-demanding and less drought-resistant than *C. excelsa.*

Number of collections: ca. 55.

Flowering from January to March, later in Guinea and Senegal (to June).

Most of what is said about the use of *C. excelsa* in the Useful Plants of West Tropical Africa, Hutchinson & Dalziel (1937) also applies to *C. regia* (see also Voorhoeve 1965).

The (fallen) sweet infructescences attract game (coll. *Cooper* 332).

In the two available collections with infructescences only a small number of the pistils had developed into fruits.

12. **Broussonetia** L'Hérit. ex Vent., Tabl. Règne **3**: 547 (1799), nom. conserv. — Type species: *B. papyrifera* (L.) Vent.

Dioecious *trees*; shoot apices shed. *Leaves* distichous, pinnately veined; stipules free, semi-amplexicaul. *Inflorescences* usually solitary in the leaf axils or on leafless nodes at the base of fertile twigs, pedunculate, bracteate; bracts basally attached; staminate inflorescences spicate, sometimes subcapitate, with a rather distinct abaxial sterile groove; flowers many; perianth 4-parted, segments valvate; stamens 4, inflexed, at anthesis bending outwards elastically, anthers introrse to latrorse; pistillode, if present, small, subulate; pistillate inflorescences capitate, sometimes elongated; flowers many; perianth unequally 2-4-lobed to 2-4-dentate; ovary free; stigmas 2, one of them strongly reduced; the upper parts of the bracts cohering by entangling hairs. *In fruit* perianth enlarged but still membranous; fruit usually short-stipitate and slightly compressed, exocarp fleshy, for the greater part rather thinly so, thicker at the base and on the seed-bearing side; endocarp crustaceous, with a thickenend crest-like part at the apex and a small woody plug towards the hilum; testa thin, with a slightly thickened oblong vascularized part below the small hilum; endosperm present; embryo curved, cotyledons unequal or almost equal, subconduplicate to almost plane, straight or the apex reflexed, not enclosing the long radicle, if unequal the larger cotyledon more or less clasping the smaller one; the bracts more or less fused at the base and hardened at the apex.

*Broussonetia greveana* was illustrated in the atlas of Grandidier's History of Madagascar (Baillon 1895) under the name *Ampalis greveana*. Léandri (1948b) transferred the species to *Chlorophora* and described *C. humbertii* as a close relative. *Chlorophora* was reduced to a section of the broad genus *Maclura* by Corner (1962), who made the combinations *M. greveana* and *M. humbertii*. Capuron (1968, 1972) united the two Madagascan species, transferred them to *Allaeanthus*, and placed them near *A. zeylanicus*. Capuron's decision was also based on anatomical studies of the wood. In 1962 Corner had reduced *Allaeanthus* to a section of the genus *Broussonetia*, but Capuron preferred to regard *Allaeanthus* as distinct. If Corner's concept is adopted, the Madagascan species should be placed in *Broussonetia*. The above description completely matches the genus description of *Broussonetia* given by Corner. By and large it also agrees with the present description of *Chlorophora*. The main differences are in the perianth of the pistillate flower and in the infructescence (see also p. 333).

*B. greveana* shows abortion and shedding of shoot apices, like *Morus mesozygia*.

12.1. **Broussonetia greveana** (Baillon) C.C. Berg comb. nov. — Type: *Grevé* 254, Madagascar, Bekopaka, near Morondava (P). — Fig. 21.

*Ampalis greveana* Baillon in Grandidier, Hist. Madag., Bot., Atlas **3**: t. 293A (1895).

*Chlorophora greveana* (Baillon) Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 18, with plates (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 12, t. 3 (1952).

*Maclura greveana* (Baillon) Corner, Gard. Bull. Singapore **19**: 237 (1962).

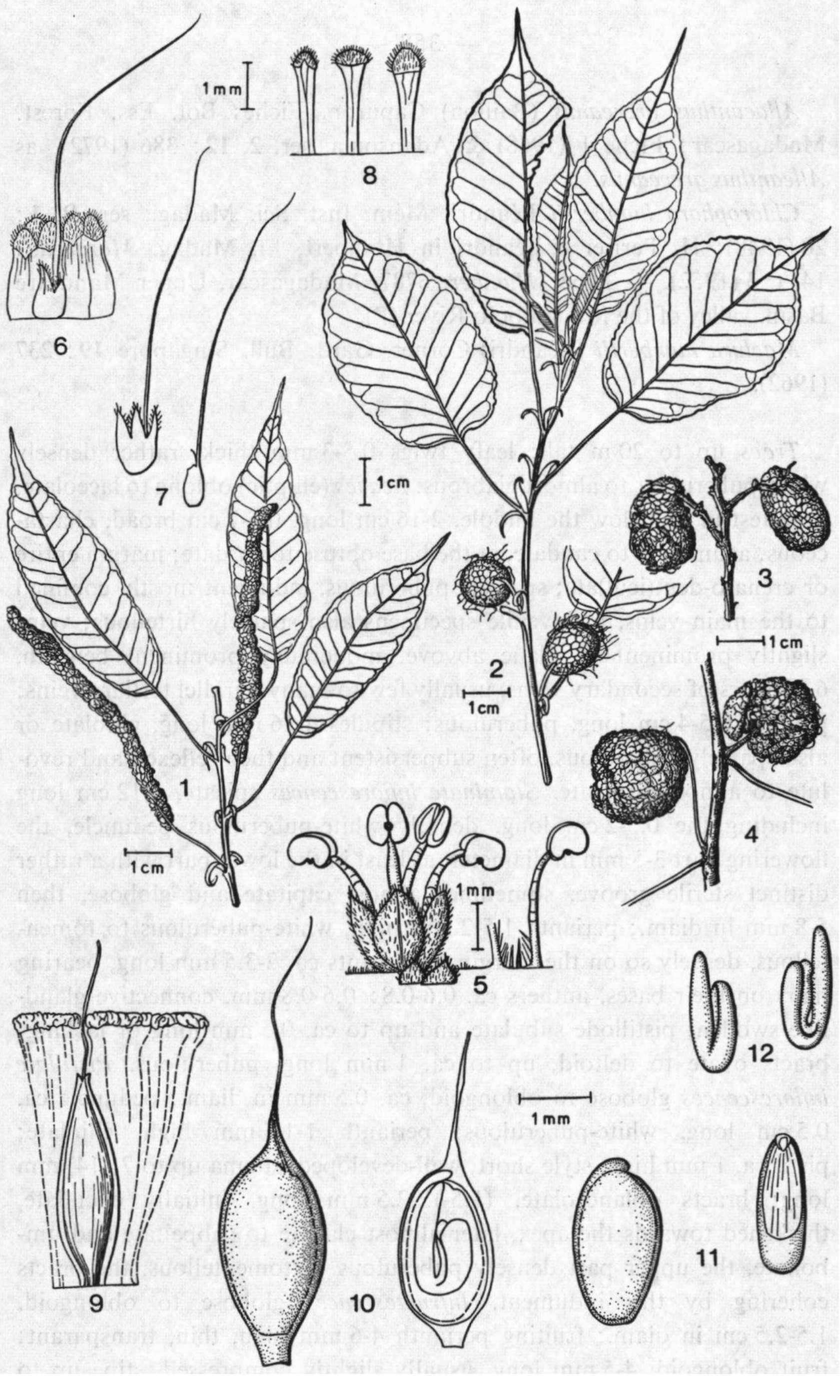

**Fig. 21.** — ***Broussonetia greveana*****: 1, leafy twigs with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3 & 4, twigs with infructescences; 5, staminate flower, bracts and pistillode; 6, pistillate flower and bracts; 7, pistillate flower and pistil; 8, bracts of pistillate flower; 9, part of the infructescence; 10, fruit; 11, seed; 12, embryo (1 : *Serv. For. Madag.* 3956; 2, 6-8 : *Serv. For. Madag.* 8373; 3 : *Humbert* 6787; 4, 9-12 : *Capuron* 6843; 5 : *Serv. For. Madag.* 15097).**

*Allaeanthus greveanus* (Baillon) Capuron, Fiches Bot. Ess. Forest. Madagascar: Fiche 1 (1968) & Adansonia, ser. 2, **12**: 386 (1972), as *Alleanthus greveanus.*

*Chlorophora humbertii* Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 20 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 14, t. 3 (1952). — Type: *Humbert* 6787, Madagascar, Upper Mandrare Basin, valley of the Manambolo River (P).

*Maclura humbertii* (Léandri) Corner, Gard. Bull. Singapore **19**: 237 (1962).

*Trees* up to 20 m tall; leafy twigs 0.5-3 mm thick, rather densely white-puberulous to almost glabrous. *Leaves* (elliptic) oblong to laceolate, broadest in or below the middle, 2-16 cm long, 0.5-7 cm broad, chartaceous, acuminate to caudate, at the base obtuse to cordate; margin entire or crenato-dent(icul)ate; sparsely puberulous, indument mostly confined to the main veins, in juvenile specimens also sparsely hirtellous; veins slightly prominent to plane abvove, moderately prominent beneath, 6-20 pairs of secondary veins, usually few to many parallel tertiary veins; petioles 0.5-4 cm long, puberulous; stipules 4-16 mm long, ciliolate or also sparsely puberulous, often subpersistent and then reflexed and revolute to almost circinate. *Staminate inflorescences* spicate, 1-12 cm long including the 0.5-2 cm long, densely white-puberulous peduncle, the flowering part 3-5 mm in diameter, at least in the lower part with a rather distinct sterile groove, sometimes almost capitate and globose, then 5-8 mm in diam.; perianth 1.5-2 mm high, white-puberulous to tomentellous, densely so on the margins; filaments ca. 2-3.5 mm long, bearing hairs on their bases, anthers ca. 0.6-0.8 × 0.6-0.8 mm, connective gland-like swollen; pistillode subulate and up to ca. 0.5 mm long or lacking; bracts ovate to deltoid, up to ca. 1 mm long, puberulous. *Pistillate inflorescences* globose to oblongoid, ca. 0.5 mm in diam.; peduncle ca. 0.5 cm long, white-puberulous; perianth 1-1.5 mm high, ciliolate; pistil ca. 1 mm high, style short, well-developed, stigma up to 7(-14) mm long; bracts oblanceolate, (1.5-)2-2.5 mm long, initially cucullate, thickened towards the apex, later almost clavate to subpeltate and umbonate, the upper part densely puberulous to tomentellous, the bracts cohering by this indument. *Infructescences* globose to oblongoid, 1.5-2.5 cm in diam.; fruiting perianth 4-6 mm high, thin, transparant; fruit oblongoid, 4-5 mm long, usually slightly compressed, stipe up to ca. 1 mm long; seed ca. 3 mm long, cotyledons up to ca. 2 mm long, radicle ca. 2.5 mm long; in fruit bracts up to 5-8 mm long, more or less flattened, the upper parts somewhat hardened, most bracts basally more or less connate.

Distribution (fig. 15, map 1): Madagascar, mainly in the western part of the island, also in the Comoro Islands (Mayotte), as deciduous or sometimes evergreen trees or shrubs, mostly in dry forests or thickets on limestone or sand, especially in the southern part of the area often along streams (cf. Capuron 1968); from sealevel to 800 m altitude.

Number of collections examined: ca. 45.

Flowering from (June) September to December, fruiting from November to January. As a rule the trees flower when coming into new foliage.

13. **Cardiogyne** Bur. in DC., Prodr. **17**: 232 (1873); Baillon, Hist. Pl. **6**: 194 (1875-1876); Benth. & Hook., Gen. Pl. **3**(1): 362 (1880); Engl. in Engl. & Prantl, Nat. Pflanzenfam. **3**(1): 76 (1889); A. Richter, Term. Füzetek **18**: 294 (1895); Kaastra, Acta Bot. Neerl. **22**: 69 (1973). — Type species: *C. africana* Bur.

*Maclura* Nutt. sect. *Cardiogyne* (Bur.) Corner, Gard. Bull. Singapore **19**: 237 (1962).

Dioecious *shrubs*, *trees*, or *climbers*, armed with short branches ending in a spine. *Leaves* in spirals, often tending to be distichous, pinnately veined; stipules free and lateral (or connate) on short-shoots. *Inflorescences* solitary or in pairs in the axils of the leaves, capitate, pedunculate, with basally attached bracts often containing immersed yellow glands; flowers numerous; perianth 4-lobed or 4-parted, segments decussate-imbricate, often with immersed yellow glands; stamens 4, inflexed, at anthesis bending outward elastically, anthers introrse to latrorse; pistillode rather small, flat; ovary free, stigma 1, occasionally 2, apical. *In fruit* perianths enlarged, fleshy and yellow to orange, sometimes basally connate; fruit free; endocarp crustaceous with a small woody plug towards the hilum; testa thin, with an orbicular to oblong thickened vascularized part below the hilum or forming an apical cap; cotyledons nearly equal, flat, strongly plicate, enclosing the long radicle.

The first account of *C. africana* was given by Kirk (1867), who recognized it as a species of *Cudrania*, partly by the yellow dye yielded by the wood. Bureau (1873) regarded *Cardiogyne* as closely related to *Plecosper-*

*mum* and as the moraceous analogue of the artocarpaceous genus *Cudrania*. Bentham & Hooker (1880) placed *Cardiogyne* under *Plecospermum*, without making a new combination. Remarks of both authors show that they saw distinct relationships between *Chlorophora*, *Maclura*, *Bagassa*, *Broussonetia*, *Allaeanthus*, *Cudrania*, *Plecospermum*, and *Cardiogyne*. Since the treatment of the *Moraceae* by Engler (1889) the genera mentioned have been regarded as distinct, until Corner (1962) united *Allaeanthus* with *Broussonetia*, and *Chlorophora*, *Cudrania* and *Cardiogyne* with *Maclura*.

As stated above (p. 348), Corner's decision with regard to *Maclura* is not very satisfactory. The relationships of *Cardiogyne* with *Plecospermum* and *Cudrania* have been the subject of a study by Richter (1895), which, however, did not lead to conclusions. By comparing members of *Maclura* sensu Corner, Kaastra (1973) concluded that *C. africana* can be regarded as congeneric with the American *M. pomifera* and *M. brasiliensis*. Further study of *Maclura* s.l. in which the genus *Plecospermum* has to be involved may prove that Kaastra's conclusion is right (see also p. 331).

The species was described as *Milicia spinosa* by Sim (1909), but was soon recognized as identical with *C. africana* (cf. Rendle 1916).

13.1. **Cardiogyne africana** Bur. in DC., Prodr. **17**: 233 (1873); Kirk, Journ. Linn. Soc. **9**: 229 (1867); Oliver in Hook., Icon. Pl.: t. 2473 (1896); Baillon in Grandidier, Hist. Madag., Bot., Atlas **3**: t. 294 (1895); Engl., Monogr. Afr. Pfl. **1**(*Moraceae*): 4 (1898); Rendle in Prain, Fl. Trop. Afr. **6**(2): 24 (1916). — Type: *Boivin* s.n. ♀, Tanzania, Zanzibar (P; isotype B). — Fig. 22.

*Maclura africana* (Bur.) Corner, Gard. Bull. Singapore **19**: 237 (1962).

*Milicia spinosa* Sim, For. Fl. Port. E. Afr.: 98, t. 74B (1909). — Type: *Sim* 6163, Moçambique (not yet traced).

*Shrubs* or *treelets* up to 7 m tall, with many long, straggling, climbing, arching, or drooping branches, these usually with up to 10 cm long, straight or slightly curved branchlets ending in a spine; leafy twigs 1-4 mm thick, white to brownish puberulous to short-velutinous. *Leaves* elliptic to lanceolate, sometimes suborbicular, 1.5-9 cm long, 1-4.5 cm broad, not or slightly inequilateral, subcoriaceous, obtuse, subacute, short-

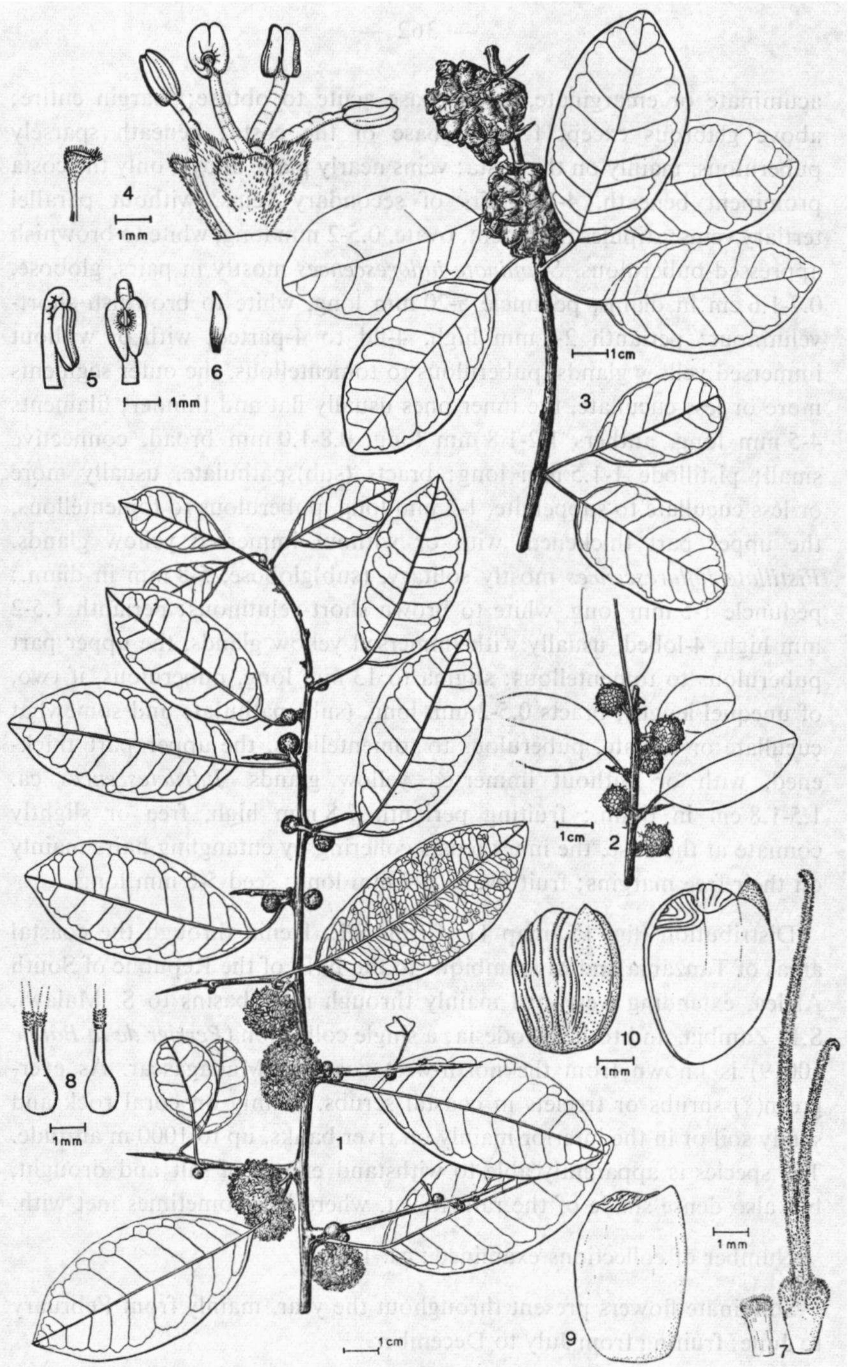

**Fig. 22.** — ***Cardiogyne africana*: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3, leafy twig with infructescences; 4, staminate flower and bracts; 5, stamens; 6, pistillode; 7, pistillate flower and bract; 8, pistil; 9, seed; 10, embryo (1: *Torre* 7142; 2: *Andrada* 1644; 3, 9, 10: *Simão* 603; 4-6: *Faulkner* 1610; 7, 8: *Drummond & Hemsley* 2391).**

acuminate or emarginate, at the base acute to obtuse; margin entire; above glabrous except for the base of the costa; beneath sparsely puberulous, mainly on the costa; veins nearly plane above, only the costa prominent beneath, 4-12 pairs of secondary veins, without parallel tertiary veins; stipules persistent, ovate, 0.5-2 mm long, white to brownish appressed-puberulous. *Staminate inflorescences* mostly in pairs, globose, 0.7-1.6 cm in diam.; peduncle 5-20 mm long, white to brownish short-velutinous; perianth 2-3 mm high, 4-fid to 4-parted, with or without immersed yellow glands, puberulous to tomentellous, the outer segments more or less cucullate, the inner ones usually flat and thinner; filaments 4-5 mm long, anthers 1.2-1.8 mm long, 0.8-1.0 mm broad, connective small; pistillode 1-1.5 mm long; bracts (sub)spathulate, usually more or less cucullate to subpeltate, 1-2 mm long, puberulous to tomentellous, the upper part thickened, with or without immersed yellow glands. *Pistillate inflorescences* mostly solitary, (sub)globose, 5-8 mm in diam.; peduncle 1-5 mm long, white to brown short-velutinous; perianth 1.5-2 mm high, 4-lobed, usually with immersed yellow glands, the upper part puberulous to tomentellous; stigma to 13 mm long, puberulous, if two, of unequel length; bracts 0.5-2 mm long, (sub)spathulate and somewhat cucullate or clavate, puberulous to tomentellous, the upper part thickened, with or without immersed yellow glands. *Infructescences* ca. 1.5-1.8 cm in diam.; fruiting perianth 7-8 mm high, free or slightly connate at the base, the inner tepals cohering by entangling hairs mainly on their free margins; fruit ovate, 6-7 mm long; seed 5-6 mm long.

Distribution (fig. 15, map 1): From S.E. Kenia through the coastal areas of Tanzania and Moçambique to the N.E. of the Republic of South Africa, extending westward mainly through river basins to S. Malawi, S.E. Zambia, and to E. Rhodesia; a single collection (*Perrier de la Bâthie* 10019) is known from the north-west coast of Madagascar. As evergreen(?) shrubs or treelets in coastal scrubs, mainly on coral rock and sandy soil or in the interior mainly on river banks, up to 1000 m altitude. The species is apparently able to withstand effects of salt and drought, but also dense shade of the rain forest, where it is sometimes met with.

Number of collections examined: ca. 120.

Staminate flowers present throughout the year, mainly from February to June; fruiting from July to December.

The yellow to orange infructescences with tasty pulp are edible. They are eaten by birds.

A remarkable feature of *C. africana* is the presence of short branchlets ending in a spine. They assist in climbing and straggling. On short branchlets or on the end of longer ones the nodes only bear (fused) stipules. These branchlets may bear inflorescences and/or side-branchlets also ending in a spine.

The immersed yellow glands occur below the thickened part of tepals and bracts. Normally two glands occur, each beside the midvein, but they are not regular in their occurrence. In some specimens they are lacking or strongly reduced. In pistillate flowers they may be absent at anthesis but then develop during maturing of the fruit.

The margins of the opposite segments of the perianth of the pistillate flower cohere by entangling hairs. This always happens with the inner tepals, with the outer tepals only if their margins approach each other. This phenomenon is especially distinct in fruiting perianths.

14. **Sloetiopsis** Engl., Bot. Jahrb. **39**: 573 (1907); Engl., Bot. Jahrb. **51**: 426 (1914); Corner, Gard. Bull. Singapore **19**: 211, 227 (1962). — Type species: *S. usambarensis* Engl.

*Neosloetiopsis* Engl., Bot. Jahrb. **51**: 426 (1914): Rendle in Prain, Fl. Trop. Afr. **6**(2): 78 (1916); Hauman, Fl. Congo, Ruanda-Urundi **1**: 82 (1948); Corner, Gard. Bull. Singapore **19**: 211, 227 (1962). — Type species: *N. kamerunensis* Engl. (= *Sloetiopsis usambarensis* Engl.).

Dioecious (or monoecious) *shrubs* or small *trees*. *Leaves* distichous, pinnately veined, stipules free, semi-amplexicaul. *Inflorescences* solitary in the axils of the leaves, (normally) unisexual, staminate ones spicate, with an abaxial sterile groove, bracteate (partly with peltate bracts); perianth 4-fid, segments imbricate; stamens 4, inflexed before anthesis, bending outward elastically at anthesis, anthers introrse; pistillode very small; pistillate inflorescences uniflorous, bracteate; perianth with 4 free, imbricate tepals; ovary free; stigmas 2, filiform. *In fruit* perianth enlarged, greenish, hardly fleshy; exocarp thick, white, fleshy, and dehiscent, pushing the endocarp body upwards; endocarp coriaceous, with a hard disc against the hilum; testa vascularized, with a thickened, more closely vascularized apical cap; cotyledons equal, thick, radicle apical and very short.

The description of the genus *Sloetiopsis* and the species *S. usambarensis* by Engler (1907) was based on a collection with for the species abnormal spicate inflorescences with both staminate and pistillate flowers. Because of the resemblance in the inflorescence, *Sloetiopsis* was associated with the Asian genus *Sloetia. Neosloetiopsis* with *N. kamerunensis*, also described by Engler (1914), was based on material with for the species normal one-flowered pistillate inflorescences.

Up to present the two genera, both still monotypic, were treated as distinct, although in 1948 Léonard only just failed to place *Neosloetiopsis* in the synonymy of *Sloetiopsis.*

Corner (1962) connected both *Sloetiopsis* and *Neosloetiopsis* with the broad genus *Streblus*, especially with sect. *Sloetia.* As stated before (p. 330), *Sloetiopsis* and *Sloetia* may prove to be congeneric and may be regarded as related to *Bleekrodea.*

14.1. **Sloetiopsis usambarensis** Engl., Bot. Jahrb. **39**: 573, pl. (1907); Engl., Pflanzenw. Afr. 3(1): 20, t. 10 (1915). — Type: *Engler* 3263, Tanzania, Usambara, Mombo (B). — Fig. 23.

*Neosloetiopsis kamerunensis* Engl., Bot. Jahrb. **51**: 426, t. 1 (1914). — Type: *Mildbraed* 4331, Cameroun, N. of Moloundou (B).

Dioecious or sometimes monoecious *shrubs* or *trees* up to 10 m tall; latex white or yellowish; leafy twigs 1-2 mm thick, sparsely to densely puberulous, some or all hairs uncinate, often the hairs distinctly different in length. *Leaves* (elliptic to) oblong (to lanceolate), usually broadest in the middle, especially towards the base inequilateral, (1-)3-16(-23) cm long, (0.5)1.5-6(-10) cm broad, chartaceous to subcoriaceous, acuminate to caudate, sometimes subacute, at the base obtuse to acute; margin entire or faintly to coarsely dentate towards the apex; on both surfaces (sub)glabrous; veins slightly prominent to plane above, prominent beneath, 4-13 pairs of secondary veins, no parallel tertiary veins; petioles 2-7 mm long, mostly puberulous (with uncinate hairs); stipules 2-8 mm long, usually with more or less distinct parallel prominent veins, sparsely puberulous, often subpersistent. *Staminate inflorescences* 0.5-5 cm long, at anthesis ca. 4 mm in diam., subsessile to pedunculate, peduncle up to 1.5 mm long; flowers not very close together; perianth ca. 1.5 mm high, 4(-6)-fid [to 4(-6)-parted], membranous, almost glabrous; filaments 2-2.5 mm long, anthers 0.6-0.8 × 0.8-1.0 mm, connective small; pistillode 0.1 mm high, conical; bracts basally attached or mostly (sub)peltate and suborbicular, up to ca. 1 mm in diameter, puberulous and ciliolate. *Pistillate inflorescences*: peduncle (including the rachis) 2-3 mm long,

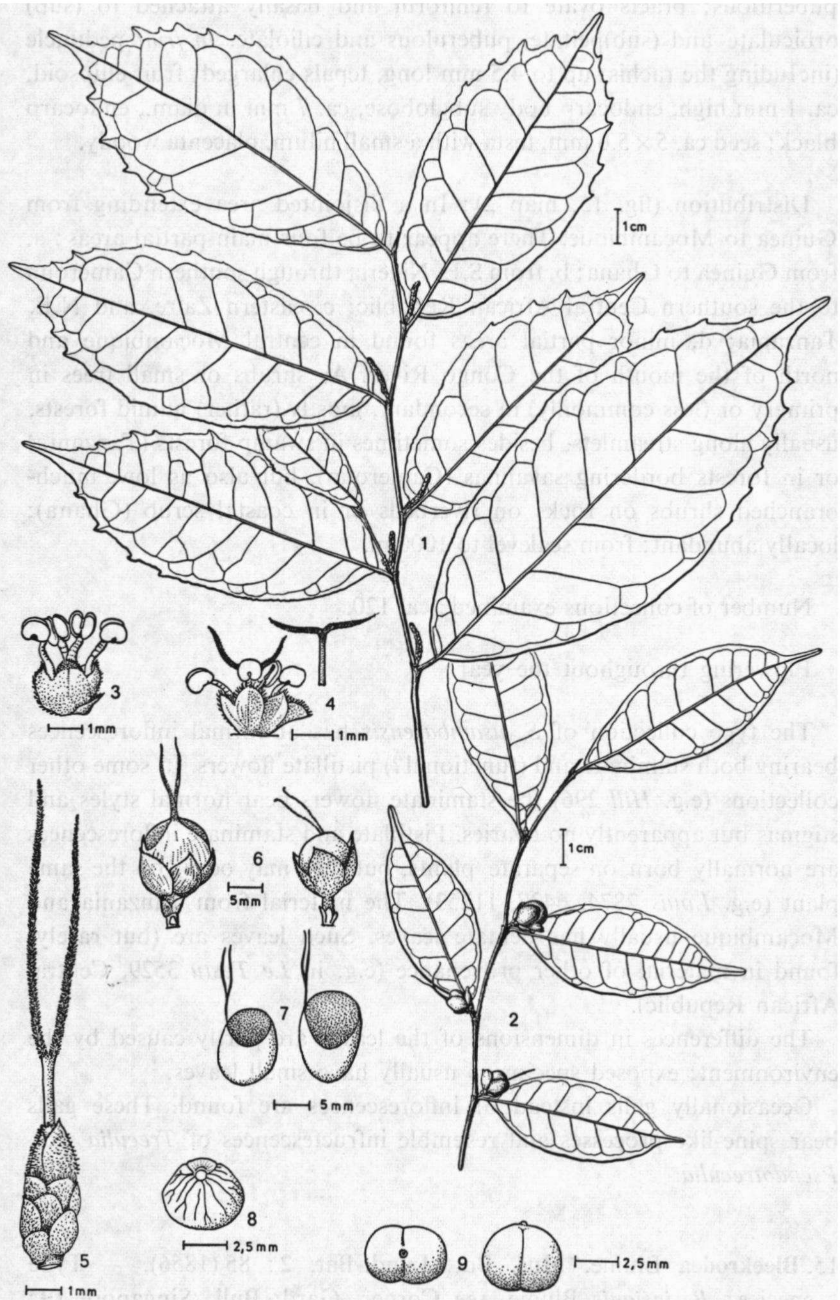

Fig. 23. — ***Sloetiopsis usambarensis*****: 1, leafy twig with young staminate inflorescences; 2, leafy twig with young infructescences; 3, staminate flower and bract; 4, staminate flower with bract and pistillode; 5, pistillate inflorescence; 6, infructescence; 7, fruit; 8, seed; 9, embryo (1 : *Simão* 336; 2 : *Gutzwiller* 2514; 3 : de *Wilde* 3542; 4 : *Hill* 296; 5 : *Breteler* 1865; 6-9 : *Breteler* 1507).**

puberulous; bracts ovate to reniform and basally attached to (sub) orbiculate and (sub)peltate, puberulous and ciliolate. *In fruit* peduncle (including the rachis) up to 4.5 mm long, tepals enlarged; fruit ellipsoid, ca. 1 mm high, endocarp body subglobose, ca. 7 mm in diam., endocarp black; seed ca. 5 × 5.6 mm, testa with a small hilum, placenta woody.

Distribution (fig. 15, map 2): In a disjointed area extending from Guinea to Moçambique. There appear to be four main partial areas: a, from Guinea to Ghana; b, from S.E. Nigeria through southern Cameroun to the southern Central African Republic; c, eastern Zaire, and N.E. Tanzania; d, minor partial areas found in central Moçambique and north of the mouth of the Congo River. As shrubs or small trees in primary or (less commonly) in secondary, mostly (rather) humid forests, usually along streamlets, besides sometimes in swamp forests (Tanzania) or in forests bordering savannas (Cameroun), but also as low, much-branched shrubs on rocks on riverbeds or in coastal scrub (Ghana); locally abundant; from sealevel to 1000 m.

Number of collections examined: ca. 120.

Flowering throughout the year.

The type collection of *S. usambarensis* has abnormal inflorescences bearing both staminate and (functional?) pistillate flowers. In some other collections (e.g. *Hill* 296) the staminate flowers bear normal styles and stigmas but apparently no ovaries. Pistillate and staminate inflorescences are normally born on separate plants, but they may occur on the same plant (e.g. *Louis* 2874, 6437, 11253). The material from Tanzania and Moçambique usually has dentate leaves. Such leaves are (but rarely) found in material of other provenance (e.g. in *Le Testu* 3529, Central African Republic).

The differences in dimensions of the leaves are partly caused by the environment; exposed specimens usually have small leaves.

Occasionally galls instead of inflorescences are found. These galls bear spine-like processes and resemble infructescences of *Treculia* sect. *Pseudotreculia*.

15. **Bleekrodea** Blume, Mus. Bot. Lugd.-Bat. **2**: 85 (1856). — Type species: *B. insignis* Blume, see Corner, Gard. Bull. Singapore **19**: 216 (1962).

*Streblus* Lour. sect. *Bleekrodea* (Blume) Corner, Gard. Bull. Singapore **19**: 216 (1962).

Monoecious *shrubs*. *Leaves* distichous, pinnately veined; stipules free, semi-amplexicaul. *Inflorescences* solitary in the leaf axils, short-branched-cymose or subcapitate, bisexual or sometimes staminate or pistillate, pedunculate, bracteate, sometimes subinvolucrate; staminate flowers one to several, sessile or short-pedicellate; perianth 5-fid to 5-parted, segments valvate; stamens 5, inflexed, at anthesis bending outward elastically, anthers introrse; pistillode small, conical; pistillate flowers 1-2 in the centre of the inflorescence; perianth tubular, 4-dentate; ovary free; stigmas 2, of equal length. *In fruit* perianth enlarged; exocarp thick, white, fleshy, and dehiscent. pushing the endocarp body upwards through the perianth; testa with a slightly thickened vascularized part below the rather small hilum; cotyledons very unequal, the smaller one in a cavity of the thick, larger cotyledon, hidden by the slightly curved, short radicle.

In 1856 Blume described *Bleekrodea* with two species, *B. madagascariensis* and *B. insignis* (from Borneo). Corner (1962) who reduced the genus to a section of the broad genus *Streblus*, described a third species, *Streblus* (*Bleekrodea*) *malayensis* from Malaya in 1975. The three species are very closely related. *Bleekrodea* and *Fatoua* show similarities in their disjunct distribution. Although *Bleekrodea* appears to be related to some members of *Streblus* s.l., it is justified to assign it the rank of genus, mainly because of the tubular perianth of the pistillate flower. The closest relatives of *Bleekrodea* appear to be *Sloetiopsis* (and *Sloetia*) and *Fatoua*. Furthermore, the inflorescences of *Bleekrodea* show resemblances to those of *Utsetela* and *Helianthostylis*, presently ranked among the *Dorstenieae* (see p. 269, 290).

15.1. **Bleekrodea madagascariensis** Blume, Mus. Bot. Lugd.-Bat. **2**: 88 (1856); Baillon in Grandidier, Hist. Madag., Bot., Atlas **3**: t. 295 (1895); Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 5, pl. (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 6, t. 1 (1952). — Type: *Pervillé* 694, Madagascar, Nossi Bé (L; isotypes B, BM, E, G, K, P). — Fig. 24.

*Streblus madagascariensis* (Blume) Corner, Gard. Bull. Singapore **19**: 220 (1962).

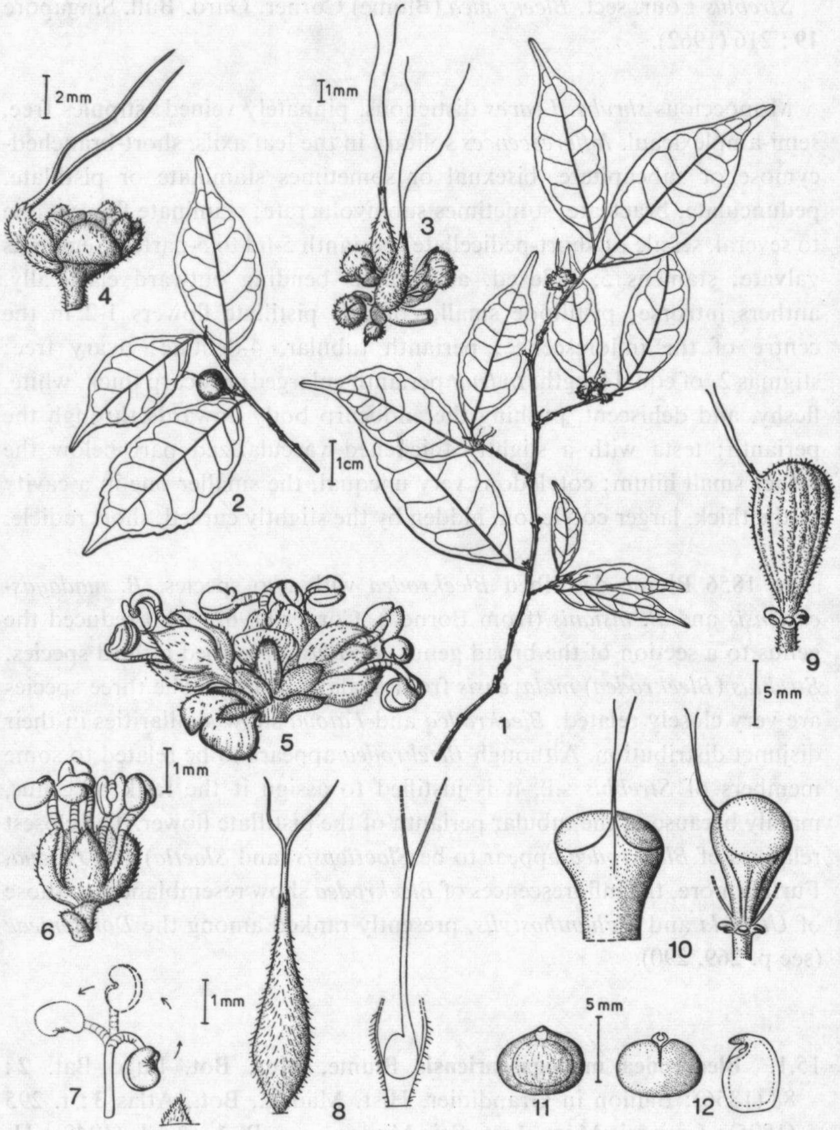

Fig. 24. — ***Bleekrodea madagascariensis*** : 1, leafy twig with inflorescences; 2, leafy twig with infructescence; 3 & 4, inflorescences; 5, staminate inflorescence; 6, staminate flower; 7, stamen and pistillode; 8, pistillate flower and pistil; 9, infructescence; 10, fruit; 11, seed; 12, embryo (1 : *Razafindrakota* 4688; 2 : *Léandri & Saboureau* 2619; 3 : *Léandri* 2817; 4-7 : *Pervillé* 694; 8 : *Léandri & Saboureau* 2817; 9-12 : *Capuron* 23287).

*Bleekrodea madagascariensis* var. *longifolia* Bur. in DC., Prodr. **17**: 255 (1873). — Type: *Boivin* 2028, Madagascar, Nossi Bé, Djabal (P).

*Shrubs* or small *trees* up to 5 m tall. Leafy twigs 0.5-2 mm thick, (sparsely) puberulous, some or all hairs retrorse and uncinate. *Leaves* elliptic to oblong to lanceolate, broadest in or above the middle, 1-8(-12) cm long, 0.5-3(-5.5) cm broad, chartaceous to subcoriaceous, acuminate to (sub)caudate, at the base acute to obtuse; margin entire, subentire, denticulate to dentate, or irregulary pinnatilobed to -parted; above with sparse hairs, glabrescent, beneath sparsely puberulous with uncinate hairs on the veins; above veins almost plane, the costa often slightly impressed, beneath veins prominent, 3-9(-12) pairs of secondary veins, no parallel tertiary veins; petioles 1-5 mm long, puberulous with uncinate hairs; stipules subpersistent, 1-7 mm long, sparsely puberulous to almost glabrous, with a prominent costa. *Inflorescences* ca. 4-12 mm in diam., shortly pedunculate to subsessile; peduncle up to 7 mm long, bracteate, puberulous to subglabrous; staminate flowers sometimes wanting or one to several, sessile or shortly pedicellate, pedicel up to 2 mm long; perianth 1.5-2 mm high, sparsely puberulous; filaments 3-4 mm long, anthers ca. 0.8-1.0 × 0.8-1.0 mm, connective rather small; pistillode ca. 0.5 mm long, hairy; perianth of the pistillate flower tubular, ca. 3-5 mm high, (2-)4-dentate, puberulous with straight and uncinate hairs; ovary ca. 1 mm high, style 3.5-5 mm long, stigmas filiform, to 9 mm long; bracts basally attached, deltoid to ovate to linear, rather thick, sparsely puberulous. *In fruit* perianth ca. 1 cm high, oblongoid to obovoid to subglobose, slightly fleshy, pink, sparsely puberulous; fruit ca. 1 cm long, endocarp body ca. 5 × 7 mm, usually broader than long, endocarp rather thin; seed ca. 5 × 6 mm, testa thin; the smaller cotyledon ligulate.

Distribution (fig. 15, map 2): North-western Madagascar, as evergreen or deciduous shrubs in the undergrowth of humid to dry forests or thickets, often (?) along streams, on various soils, from sealevel to 600 m.

Number of collections examined: ca. 40.

Flowering throughout the year.

Like *Fatoua madagascariensis*, this species may bear unisexual inflorescences, either pistillate or staminate. As far as could be deduced from the herbarium material, the endocarp body, pushed upwards by the exocarp, is exposed and/or released through a tear in the fruiting perianth. The pinkish colour of the fruiting perianth (noted by *Léandri & Saboureau* 2886) may play a part in dispersal. If so, *B. madagascariensis* is better adapted to dispersal than, e.g., *Sloetiopsis usambarensis* with its green fruiting perianth (see p. 363).

16. **Fatoua** Gaudich. in Freyc., Voy. Monde Bot.: 509 (1830). — Type species: *F. pilosa* Gaudich.

*Plants* monoecious, suffrutescent to herbaceous; latex absent. *Leaves* distichous, pinnately veined; stipules free, lateral. *Inflorescences* in pairs in the axils of the leaves, spicate, bisexual, sometimes staminate or pistillate, bracteate, pedunculate, abaxially without flowers; flowers sessile or short-pedicellate; perianth 4-parted, segments valvate; stamens 4, inflexed, at anthesis bending outward elastically, anthers introrse; pistillode minute; ovary free, style lateral, one of the stigmas strongly reduced. *In fruit* perianth enlarged, exocarp thick, white fleshy and dehiscent (probably) ejecting the endocarp body; testa thin with a slightly thickened suborbicular vascularized part near the small hilum, endosperm present; embryo curved, cotyledons equal and plane, radicle long.

The genus *Fatoua* was established by Gaudichaud (1830) when describing the new species *F. pilosa*. This species, extending from Japan to New Caledonia, was the only *Fatoua* species recognized for a long time. The second species was not collected until 1933 by Humbert (coll. 11242) and described by Léandri (1948b).

*F. madagascariensis* is distinctly related to *F. pilosa*. A remarkable difference between the two species is found in the inflorescence which is spicate to racemose in the former and cymose in the latter. The inflorescence of *F. pilosa* resembles that of *Bleekrodea*. *Fatoua* is a clear-cut genus, probably related to *Bleekrodea*, and through this genus linked with *Sloetiopsis* (and *Sloetia*) (see p. 330).

Latex seems to be absent in *F. madagascariensis*. Léandri (1948b) did not even find laticiferous elements when studying the anatomy of this species.

16.1. **Fatoua madagascariensis** Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 4, pl. (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 4, t. 1 (1952); Bosser & Léandri, Le Naturaliste Malgache **19**: 37, pl. (1957). — Type: *Humbert* 11242, Madagascar, forest of Besomaty, between the Fiherenana and Isuhaina Rivers (P). — Fig. 25.

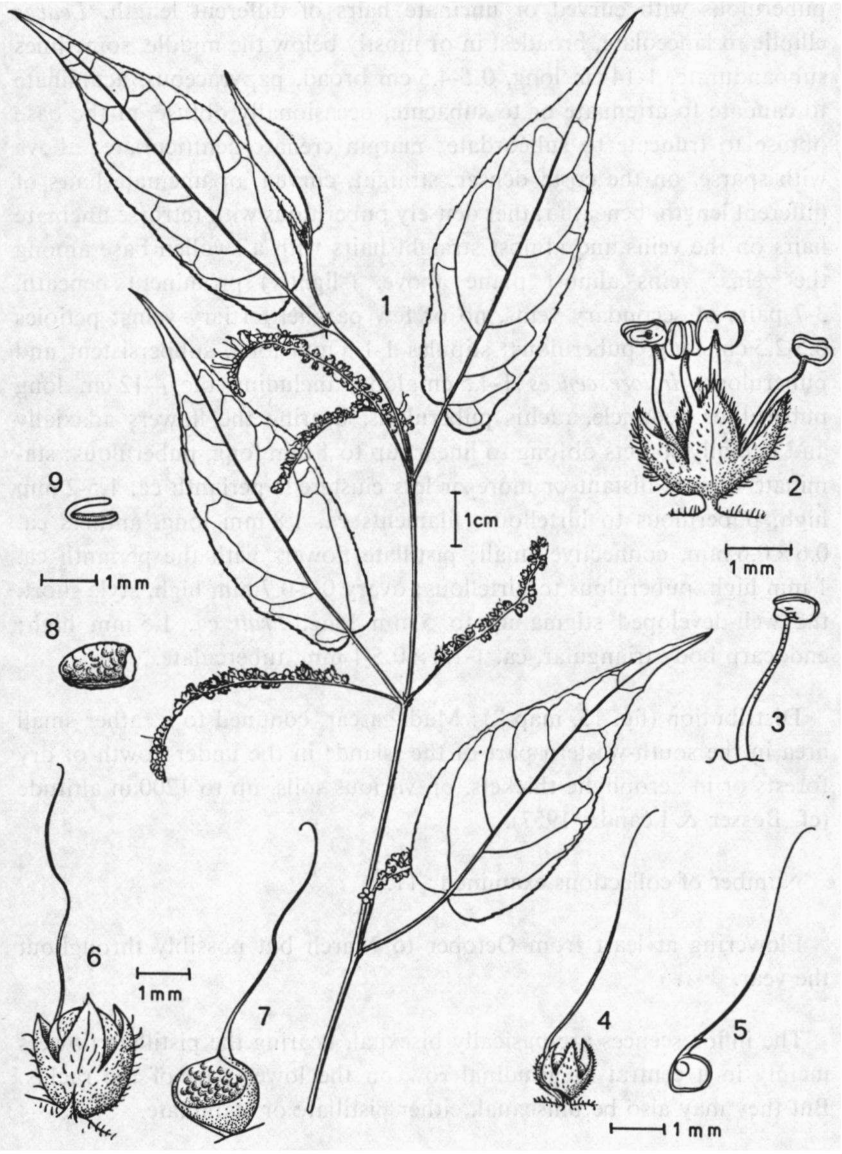

**Fig. 25.** — ***Fatoua madagascariensis*****: 1, leafy twig with inflorescences; 2, staminate flower; 3, stamen and pistillode; 4, pistillate flower; 5, pistil; 6, pistillate flower in fruit; 7, fruit; 8, seed; 9, embryo (*****Capuron*** **20602).**

*Plants* up to 1 m tall; roots yellow; leafy twigs 0.5-1.5 mm thick, puberulous with curved or uncinate hairs of different length. *Leaves* elliptic to lanceolate, broadest in or mostly below the middle, sometimes subpandurate, 1-14 cm long, 0.5-4.5 cm broad, papyraceous, acuminate to caudate to attenuate or to subacute, occasionally obtuse, at the base obtuse to truncate to subcordate; margin crenato-dent(icul)ate; above with sparse, on the costa denser, straight, curved, or uncinate hairs of different length, beneath rather densely puberulous with retrorse uncinate hairs on the veins and almost straight hairs with a swollen base among the veins; veins almost plane above, (slightly) prominent beneath, 3-7 pairs of secondary veins, no or few parallel tertiary veins; petioles 0.5-2.5 cm long, puberulous; stipules 1-1.5 mm long, subpersistent and puberulous. *Inflorescences* 1-4.5 cm long, including the 4-12 cm long puberulous peduncle, rachis puberulous, bearing the flowers adaxially and laterally; bracts oblong to linear, up to 1 mm long, puberulous; staminate flowers distant or more or less clustered; perianth ca. 1.5-2 mm high, puberulous to hirtellous; filaments ca. 1.8 mm long, anthers ca. 0.6 × 0.6 mm, connective small; pistillate flowers with the perianth ca. 1 mm high, puberulous to hirtellous; ovary 0.5-0.7 mm high, style short, the well-developed stigma up to 5 mm long. *Fruit* ca. 1.5 mm high; endocarp body triangular, ca. 1-1.3 × 0.5-1 mm, tuberculate.

Distribution (fig. 15, map 2): Madagascar, confined to a rather small area in the south-western part of the island; in the undergrowth of dry forests or in xerophytic thickets, on various soils, up to 1200 m altitude (cf. Bosser & Léandri 1957).

Number of collections examined: 11.

Flowering at least from October to March but possibly throughout the year.

The inflorescences are basically bisexual, bearing the pistillate flowers mainly in a central longitudinal row on the lower part of the rachis. But they may also be unisexual, either pistillate or staminate.

17. **Maillardia** Frapp. ex Duchartre in Maillard, Notes sur l'île de la Réunion, Annexe P.: 3 (1863?); Bur. in DC., Prodr. **17**: 220 (1873); Benth. & Hook., Gen. Pl. **3**(1): 360 (1880); Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 23 (1948); H. Perrier & Léandri in Humbert, Fl.

Madag. *Moraceae*: 15 (1952). — Type species: *M. borbonica* Duchartre.

*Trophis* P. Br. sect. *Maillardia* (Duchartre) Corner, Gard. Bull Singapore **19**: 230 (1962).

Dioecious *trees*. *Leaves* distichous, pinnately veined; stipules free, semi-amplexicaul. *Staminate inflorescences* solitary or in pairs, spicate to subcapitate, with an abaxial sterile groove, pedunculate, with (sub)peltate bracts; flowers few to many; perianth 4-parted, segments decussate-imbricate; stamens inflexed, at anthesis bending outward elastically, anthers introrse; pistillode quadrangular. *Pistillate inflorescences* solitary or in pairs (occasionally 3 together), 1 or 2 flowers sessile at the end of the peduncle with (sub)peltate bracts; perianth tubular, 4-lobed; ovary adnate to the perianth, style terminal, stigmas 2, equal. *In fruit* perianth enlarged, fleshy and red; endocarp thin-crustaceous, at the seed-bearing side with a more or less prominent longitudinal woody crest; seed with a split corresponding with the crest; testa thin, with a thickened oblong vascularized part below the small hilum, in the middle with a fold protruding into the split; embryo longitudinally aligned, cotyledons very unequal, the smaller one flat and reniform, the larger one thick and conduplicate, radicle subapical, short, straight.

The genus *Maillardia* was established by Duchartre (1863?). He used a manuscript of Frappier and adopted the genus name given by Frappier. The genus was placed in the *Artocarpeae* sensu Trécul (1847) (in spite of the presence of stamens inflexed in the bud and springing back at anthesis) and regarded as related to the neotropical genera *Olmedia* and *Pseudolmedia*. For the epitheton Duchartre did not adopt the name *lancifolia* given by Frappier. Until 1948 *M. borbonica* was the only described species. Then Léandri (1948b) described the apparently rather common Madagascan representatives of *Maillardia* under four names. However, only one Madagascan species can be distinguished. To this species also belongs the material collected on the Aldabra Atoll for which Fosberg (1974) proposed a new species.

*Maillardia* belongs to a group of chiefly Asian and American genera in which the perianth of the pistillate flower is tubular, in fruit fleshy, reddish or black, and fused with the fruit. By virtue of this it is clearly distinguished from the other African *Moreae*. Corner (1962) reduced *Maillardia* (and the Asian genus *Calpidochlamys*) to sections of *Trophis* subg. *Trophis*. The two neotropical genera (*Sorocea* and *Clarisia*) with the same type of pistillate flower were kept separate. These two genera are distinct as their stamens are not inflexed in bud and do not spring back at anthesis. As stated before (see p. 334), Corner's decision might prove to be correct, but further study of the members of *Trophis* s.l., as well as of *Sorocea*, *Clarisia*, and *Olmedia* (cf. Berg 1977) appears to be necessary before more definite decisions can be reached.

The two species of *Maillardia* are very closely interrelated. The main differences are in the leaves.

The minute warts (in young leaves) and dots (in older leaves) are caused by cystoliths (cf. Léandri 1948b).

**Key to the species of *Maillardia***

1.a. Stipules (4-)6-15 mm long; leaves with a sharp acumen . . . 1. *M. borbonica*
b. Stipules 1-3 mm long; leaves with a blunt acumen . . . . . 2. *M. montana*

17.1. **Maillardia borbonica** Duchartre, Notes sur l'île de la Réunion, Annexe P.: 3 (1863?); De Cordemoy, Flore de l'île de la Réunion: 275 (1895). — Syntypes: *Frappier* 279 and s.n. (several sterile, staminate and fruiting collections), Réunion (P). — Fig. 26.

*Trees* up to 7 m tall; leafy twigs 1-4 mm thick, glabrous. *Leaves* elliptic to oblong, broadest in or below the middle, 2-11 cm long, 0.7-4 cm broad, coriaceous, sharply acuminate to subcaudate, at the base acute to obtuse; margin entire, often slightly revolute; above and beneath glabrous, above more or less distinctly minutely tuberculate to punctate; the costa almost plane, the other veins more or less prominent above, the veins prominent beneath, 6-18 pairs of secondary veins, without parallel tertiary veins; petioles (2-)4-12 mm long, glabrous; stipules (4-)6-15 mm long, glabrous. *Staminate inflorescences* mostly solitary, 2-3.5 cm long, including the ca. 1 mm long, sparsely puberulous and bracteate peduncle; usually more flowers than in *M. montana*, the floral parts and bracts similar to those of *M. montana*, except for the sparsely puberulous perianth. *Pistillate inflorescences* solitary; peduncle 5-11 mm long, sparsely puberulous to almost glabrous; a single flower at the end of the peduncle; floral parts similar to those of *M. montana*; bracts spread or crowded at the upper end of the peduncle, (sub)peltate, suborbicular to elliptic, up to ca. 2 mm long, glabrous. *In fruit* perianth oblongoid, ca. 17 × 8 mm, apiculate; endocarp body ca. 15 × 7 mm; seed ca. 12 × 5 mm.

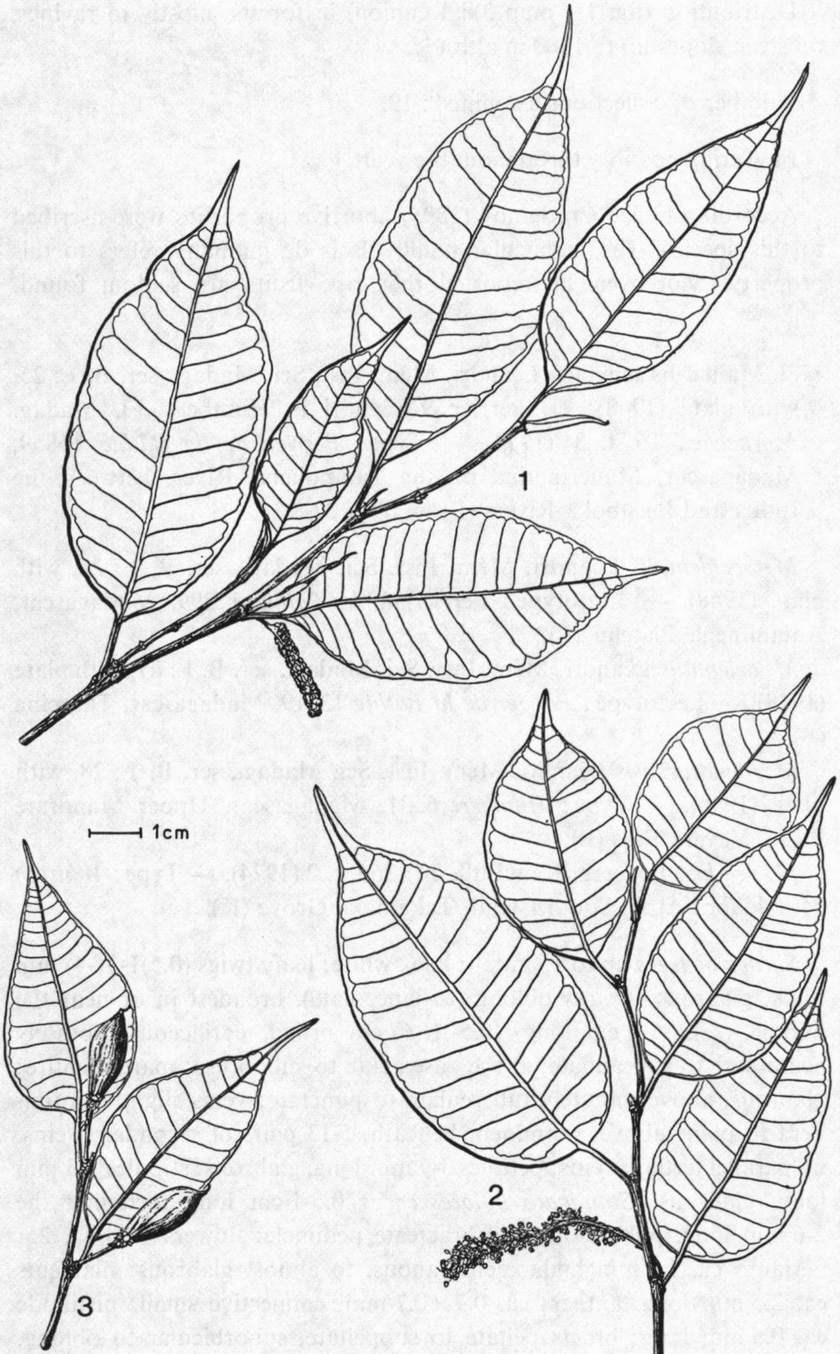

Fig. 26. — *Maillardia borbonica*: 1, leafy twig with young staminate inflorescence (*Capuron* 28237); 2, leafy twig with staminate inflorescence (*Friedmann* 1232); 3, leafy twig with young infructescences (*Friedmann* 1071).

Distribution (fig. 15, map 3): Réunion, in forests, mostly in ravines, on steep slopes up to 1300 m altitude.

Number of collections examined: 19.

Flowering possibly throughout the year.

According to De Cordemoy (1895) abortive properties were ascribed to this species. The vernacular name "Bois de maman" refers to this property. Moreover, he reported that ripe fruits are seldom found.

17.2. **Maillardia montana** Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 25, with plate (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 16, t. 3 (1952). — Type: *Perrier de la Bâthie* 16859, Madagascar, Manerinerina on the Tampoketsa River, between the Ipoka and Betsiboka Rivers (P). — Fig. 27.

*M. occidentalis* Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 26, with plate (1948). — Lectotype: *Perrier de la Bâthie* 12399, Madagascar, Antanimena Plateau (P).

*M. orientalis* Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 27, with plate (1948). — Lectotype: *Perrier de la Bâthie* 13319, Madagascar, Tampina (P).

*M. mandrarensis* Léandri, Mém. Inst. Sci. Madag., ser. B, **1**: 28, with plate (1948). — Type: *Humbert* 6531, Madagascar, Upper Mandrare Basin, Vavara Pass (P).

*M. pendula* Fosberg, Kew Bull. **29**: 266, t. 2 (1974). — Type: *Whitton* 94, Aldabra Atoll, South Island, Takamaka Grove (K).

*Shrubs* or *trees* up to 15 m tall; latex white; leafy twigs (0.5)1-3(-4) mm thick, glabrous. *Leaves* oblong (to lanceolate), broadest in or near the middle, (1-)2(-13) cm long, (0.5-)1(-6) cm broad, coriaceous, obtusely acuminate to subcaudate, at the base acute to subobtuse; margin entire; glabrous, above minutely tuberculate to punctate; veins slightly prominent to plane above, prominent beneath, 5-13 pairs of secondary veins, no parallel tertiary veins; petioles 3-9 mm long, glabrous; stipules 1-3 mm long, glabrous. *Staminate inflorescences* 0.5-1 cm long including the 2-6 mm long, puberulous and bracteate peduncle; flowers 6 to ca. 25; perianth ca. 1.5 mm high, membranous, to almost glabrous; filaments ca. 2.5 mm long, anthers ca. 0.7 × 0.7 mm, connective small; pistillode ca. 0.5 mm long; bracts peltate to subpeltate, suborbicular to oblong,

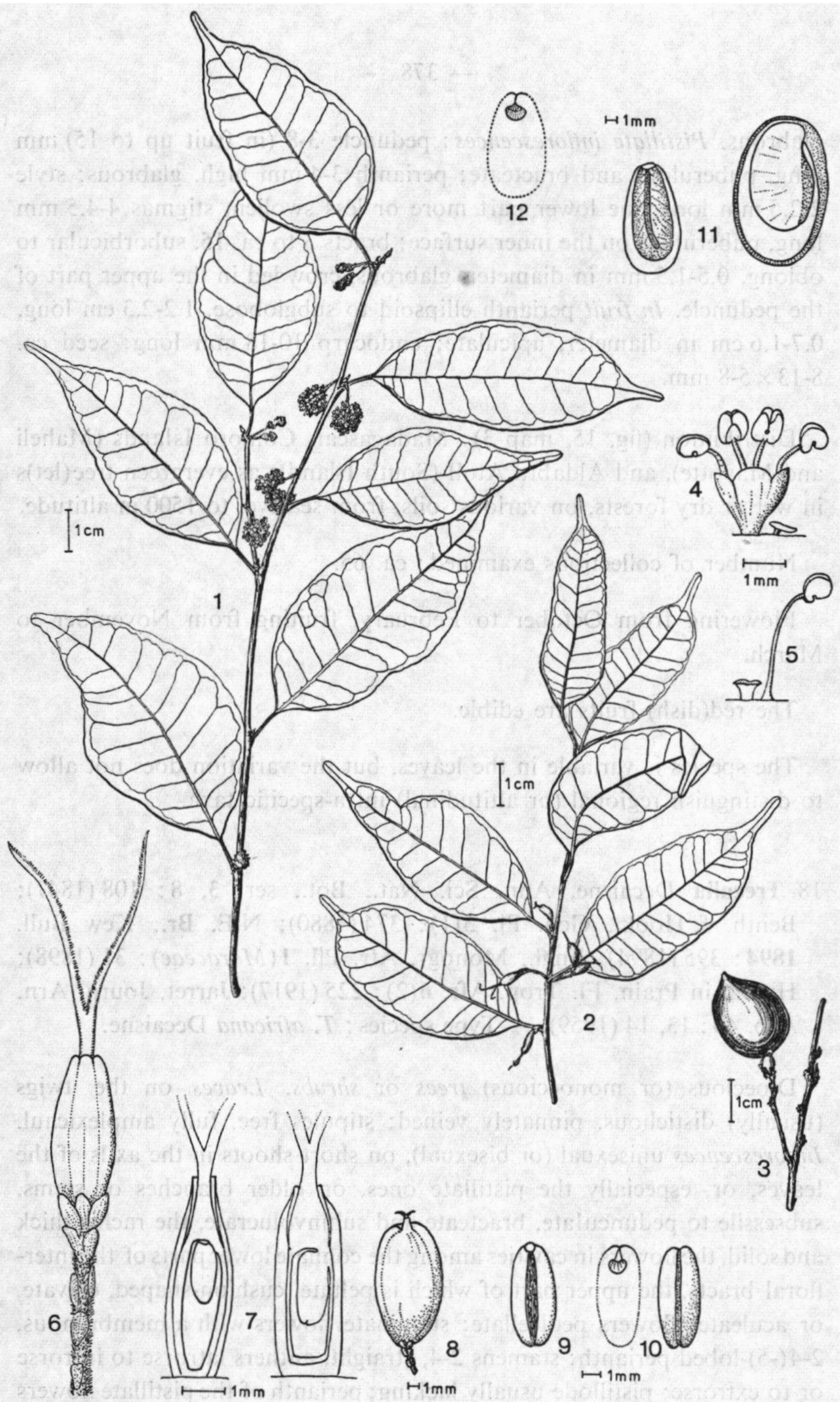

Fig. 27. — *Maillardia montana*: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate flowers; 3, infructescence; 4, staminate flower and bract; 5, pistillode and stamen; 6, pistillate inflorescence; 7, pistillate flower; 8, infructescence; 9, seed, 10, embryo; 11, seed; 12, small cotyledon (1: *Capuron* 18831; 2, 6, 7: *Perrier de la Bâthie* 17863; 3, 11, 12: *Capuron* 27407; 4, 5: *Serv. For. Madag.* 6430; 8-10: *Léandri* 555).

glabrous. *Pistillate inflorescences*: peduncle 3-8 (in fruit up to 15) mm long, puberulous and bracteate; perianth 3-4 mm high, glabrous; style 2-2.5 mm long, the lower part more or less swollen, stigmas 4-4.5 mm long, puberulous on the inner surface; bracts 3 to ca. 15, suborbicular to oblong, 0.5-1.5 mm in diameter, glabrous, crowded in the upper part of the peduncle. *In fruit* perianth ellipsoid to subglobose, 1.2-2.3 cm long, 0.7-1.6 cm in diameter, apiculate; endocarp 10-18 mm long; seed ca. 8-13 × 5-8 mm.

Distribution (fig. 15, map 3): Madagascar, Comoro Islands (Maheli and Mayotte), and Aldabra Atoll (South Island); as evergreen tree(let)s in wet or dry forests, on various soils, from sealevel to 1500 m altitude.

Number of collections examined: ca. 65.

Flowering from October to February, fruiting from November to March.

The red(dish) fruits are edible.

The species is variable in the leaves, but the variation does not allow to distinguish regional (or altitudinal) infra-specific taxa.

18. **Treculia** Decaisne, Ann. Sci. Nat., Bot., ser. 3, **8**: 108 (1847); Benth. & Hook., Gen. Pl. 3(1): 374 (1880); N.E. Br., Kew Bull. **1894**: 395 (1894); Engl., Monogr. Afr. Pfl. **1** (*Moraceae*): 31 (1898); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 225 (1917); Jarret, Journ. Arn. Arb. **40**: 13, 14 (1959). — Type species: *T. africana* Decaisne.

Dioecious (or monoecious) *trees* or *shrubs*. *Leaves* on the twigs (usually) distichous, pinnately veined; stipules free, fully amplexicaul. *Inflorescences* unisexual (or bisexual), on short shoots in the axils of the leaves, or, especially the pistillate ones, on older branches or stems, subsessile to pedunculate, bracteate and subinvolucrate, the rachis thick and solid, the flowers in cavities among the connate lower parts of the interfloral bracts, the upper part of which is peltate, cushion-shaped, clavate, or aculeate; flowers pedicellate; staminate flowers with a membranous, 2-4(-5)-lobed perianth; stamens 2-4, straight, anthers latrorse to introrse or to extrorse; pistillode usually lacking; perianth of the pistillate flowers (probably) lacking; ovary free; style with 2 filiform stigmas. *In fruit* the upper parts of the interfloral bracts hardened; the fruits in a (rather) soft layer; endocarp crustaceous, exocarp firm and coriaceous or weak and more or less fleshy; testa rather thick, with an orbicular thickened vascularized part below the small hilum; embryo curved, cotyledons unequal, the smaller one plane and enclosed by the thick larger one or strongly reduced; radicle short and apical, remains of endosperm mainly in the apical part of the seed.

The genus *Treculia*, with the only species *T. africana*, was established by Decaisne in Trécul's monographic treatment of the "Artocarpées" (1847). Baillon (1875) added a second species, *T. acuminata*, and placed it in the section *Pseudotreculia*. N.E. Brown (1894) described three *Treculia* species, *T. affona*, *T. madagascarica*, and *T. obovoidea*, which were not mentioned in Engler's monographic treatment of African *Moraceae* (1898). Later about ten more species were described in the genus by Engler (1898, 1908), De Wildeman & Durand (1899, 1900), De Wildeman (1914), Jumelle (1920), and Léandri (1948a).

In 1908 Engler described the genus *Acanthotreculia*, with *A. winkleri.* Hutchinson (1917) recognized the type of *A. winkleri* as female material of the species which Engler (1898) had previously described from male specimens as *T. staudtii* and N.E. Brown (1894) as *T. obovoidea.* In 1897 Engler named some new *Treculia* species and placed them in the section *Microtreculia*, based on differences in the anthers. He soon (1898) relalized that these species were related to *T. acuminata*, and consequently re-established Baillon's section *Pseudotreculia*, inserting in it all the species he recognized exept *T. africana.* Material of *T. africana* has been described as a species of *Ficus* (Stapf 1909) and *Artocarpus* (Sim 1909).

*Treculia* comprises three species, the widespread and (especially on Madagascar) variable *T. africana* with several infra-specific taxa, and the less variable and more restricted *T. acuminata* and *T. obovoidea.* The differences between *T. africana* and the latter two species justify retention of Engler's subdivision of the genus (Engler 1898). *T. acuminata* and *T. obovoidea* are very closely interrelated.

There is a contrast in the areas of *T. africana* and the two species of sect. *Pseudotreculia.* The former matches the large areas of the tall arborescent *Moraceae* extending more or less far outside the rain forest areas, the two other species share the small areas of many small-sized components of the humid rain forest.

As stated before (p. 334), *Treculia* shows striking morphological similarities to the Asian genus *Parartocarpus* (cf. Jarrett 1959, 1960; Corner 1962). Poisonous properties reported for latex and seeds ("fruits") of *T. africana* may also indicate close relationship to *Parartocarpus* (cf. Jarrett 1960).

*Inflorescences*: The inflorescences are borne on more or less distinct short-shoots bearing fused and modified stipules. Male specimens of *T. acuminata* usually have short-shoots up to ca. 1 mm long, which bear a large number of inflorescences appearing successively. In *T. africana* and *T. obovoidea* the pistillate inflorescences are mostly born below the leaves on older branches, in *T. africana* even on the trunk. The staminate inflorescences can often be found in the axils of the leaves. *T. acuminata* and *T. obovoidea* are dioecious. *T. africana* may be monoecious. Moreover, inflorescences of *T. africana* are sometimes bisexual, having staminate flowers in the lower part and pistillate flowers in the upper part, or staminate flowers spread over the inflorescence and preceding the pistillate flowers in flowering. In the pistillate inflorescences of *T. africana* abortive staminate flowers can usually be found. In *T. africana* the inflorescences of the two sexes are very similar. They are globose, obovoid, or broadly clavate. The short peduncle bears several to many basally attached bracts subtending the inflorescence and forming an involucre. The interfloral bracts are basically peltate. Their lower parts are fused. In pistillate inflorescences they become longer by intercalary growth in the fused parts. Cavities left among the bracts contain the pedicellate flowers. The pedicels are completely or only basally fused with the surrounding (lower part of the) bracts. Two types of interfloral bracts can be distinguished: the first formed ones as primary interfloral bracts, and those which develop later towards the cavities as secondary interfloral bracts. In *T. africana* the secondary bracts are smaller and the smallest ones are often not distinctly peltate. In *T. obovoidea* the primary bracts are (almost) cushion-shaped and gradually pass into the aculeate secondary ones. In *T. acuminata* the primary bracts are either peltate or ovoid to aculeate. As a rule they gradually pass into the aculeate (to subulate) secondary bracts, but in staminate inflorescences the secondary bracts may also be peltate. In inflorescences of *T. acuminata* bracts of all shapes from peltate to obovoid to clavate to subulate to aculeate may be found. The "spines" of the infructescences of *T. acuminata* and *T. obovoidea* are formed by the elongated and indurated aculeate bracts. The primary bracts of *T. obovoidea* also form "spines", but they are usually shorter than those formed by the secondary bracts. Peltate bracts do not appear to form "spines".

*Pistillate flowers*: The pistillate flowers lack a perianth as far as could be observed in examining the material without anatomical study. The pedicels are completely fused with the surrounding tissue of the fused lower parts of the interfloral bracts. In *T. africana* the flowers do not mature simultaneously. As the interfloral bracts still elongate during anthesis in the inflorescence, the flowers are situated at different distances from the rachis and have pedicels of different length. This results in sufficient room being available for the numerous fruits in the infructescence. Elongation of the bracts also leads to shedding of the style, the infructescence then being covered by loose styles. In *T. acuminata* and *T. obovoidea* the pistillate flowers of each inflorescence flower almost simultaneously.

*Staminate flowers*: The staminate flowers have a membranous perianth. The number of stamens varies from (1-)2 to 4. Flowers of the same inflorescence may differ in the number of stamens. The anthers of *T. africana* are relatively long and narrow and introrse; they are attached to the filament in the upper half and sometimes near the top. The anthers of *T. acuminata* and *T. obovoidea* are relatively short and broad, latrorse to introrse (in *T. obovoidea*) or to extrorse (in *T. acuminata*). Pistillodes may be present. Abortive staminate flowers occur in most pistillate inflorescences of *T. africana*; their pedicels are almost completely fused with the bracts.

In *T. africana* before anhesis the flowers are enclosed in the cavities among the bracts, but they are raised on their long pedicels; in the other two species the pedicels are very short or almost lacking.

*Infructescences*: The fruits are imbedded in a layer formed by the fused parts of the interfloral bracts. This layer is rather soft and more or less mucilaginous in *T. africana*, more solid in *T. acuminata* and *T. obovoidea*. The basal part of the fruit is fused with the surrounding tissue. The more or less indurated free parts of the bracts form a protective layer consisting of "spines" in *T. acuminata* and *T. obovoidea*.

The fruits of *T. africana* differ from those of *T. acuminata* and *T. obovoidea*. The exocarp is thinly fleshy (—when dry membranous—) in *T. africana*, but coriaceous in the latter two species. In these two species the endocarp bears dense hair-like structures (probably remains of cell-walls) in a more or less gelatinous layer between endocarp and exocarp. The endocarp is crustaceous. The seed contains remains of endosperm, especially in its apical part, around the radicle and below the thickened vascularized part of the testa, and also between the cotyledons, especially in *T. africana*. The embryo occupies a longitudinal position.

In *T. africana* the smaller cotyledon varies in length considerably. In *T. acuminata* and *T. obovoidea* one of the cotyledons is strongly reduced and completely enclosed by the larger cotyledon.

**Key to the species of *Treculia***

1.a. Lamina usually more or less inequilateral; inflorescences only with peltate interfloral bracts, the staminate ones at least 5 mm in diam.; anthers long and narrow . . . . . . . . . . . . . . . . . . . . . . . . . . 1. *T. africana*
  b. Lamina not or hardly inequilateral; inflorescences usually with aculeate interfloral bracts; if only peltate bracts present, the staminate inflorescences at most 5 mm in diam.; anthers short and broad . . . . . . . . . . . . 2
2.a. Shrubs; the costa beneath with sparse uncinate hairs; "spines" of the infructescence up to 0.5 cm long . . . . . . . . . . . . . . . . . 2. *T. acuminata*
  b. Trees; the costa beneath only with appressed straight hairs; "spines" of the infructescence up to 2 cm long . . . . . . . . . . . . . . 3. *T. obovoidea*

## 18. A. **Treculia** Decaisne sect. **Treculia**

Dioecious or (often?) monoecious *trees*. *Inflorescences* sometimes bisexual, the pistillate ones usually with abortive staminate flowers; interfloral bracts peltate; anthers long, narrow, and introrse. *Fruit* with a thinly fleshy exocarp.

18.1. **Treculia africana** Decaisne, Ann. Sci. Nat., Bot., ser. 3, **8**: 109, t. 3 (1847); Hook., Bot. Mag.: t. 5986 (1872); Engl., Monogr. Afr. Pfl. 1(*Moraceae*): 32, t. 12, 13 (1898); De Wild. & Th. Dur., Ann. Mus. Congo, Bot., ser. 1, **1**: 139 (1900); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 227 (1917); Andrews, Fl. Pl. Anglo-Egyptian Sudan **2**: 273, t. 97 (1952); Aubrév., Fl. For. Côte d'Ivoire **1**: 58, t. 7 (1959). — Type: *Heudelot* s.n., "Senegambia" (P).

The variation of *T. africana* in the African continent is rather continuous; the hairy form presently still distinguished as var. *mollis* may prove not to be taxonomically distinct. In Madagascar the representatives show more and discontinuous variation, but as a whole they do not show important morphological differences if compared with the continental ones. Some of the Madagascan specimens can hardly be distinguished from continental ones. Distinction of a continental and a Madagascan subspecies is mainly based on the different variation patterns in connection with geographical aspects, and because of the fact that discontinuities in variation allow subdivision of the Madagascan segregate. Each of the subspecies is fully described below.

### 18.1.a. **Treculia africana** Decaisne ssp. **africana**

Dioecious or sometimes monoecious *trees*, up to 30(-50) m tall; latex white, turning brownish; leafy twigs 2-6 mm thick, (rather) sparsely puberulous to almost glabrous or hirtellous to (sub)tomentose. *Leaves* oblong to lanceolate, sometimes elliptic, broadest in or below the middle, more or less inequilateral (distinctly inequilateral at the base), (5-)10-25(-50) cm long, (2.5-)4-12(-20) cm broad, coriaceous (to subcoriaceous), acuminate to apiculate, sometimes subacute, at the base obtuse to cordate, or sometimes one half (sub)acute and the other half obtuse, occasionally both halves acute; margin entire or faintly repand (dentate in saplings); above glabrous or nearly so, beneath often sparse uncinate hairs on the secondary veins or beneath hirtellous to subtomentose; veins slightly prominent to plane above, more or less prominent beneath, (8-)10-(-18) pairs of secondary veins, no or some parallel tertiary veins; petioles 2-14 mm long, glabrous, sparsely appressed-puberulous or substrigose (often the periderm peeling off); stipules 10-18 mm long, almost glabrous or puberulous to hirtellous, caducous. *Staminate inflorescences* mostly solitary, sometimes paired on short-shoots in the axils of the leaves or on older (already leafless) twigs or branches, globose to ellipsoid or to obovoid, 2.5-10 cm in diam., subsessile to pedunculate; peduncle up to 4 mm long, bearing several rows of (sub)reniform to elliptic, basally attached, outside glabrous or sparsely appressed-puberulous, ciliolate bracts; flowers numerous, solitary in the cavities of the inflorescence; pedicel 1-20 mm long; perianth 3-6 mm high, membranous, 2(-3)-lobed to -fid, (almost) glabrous; stamens 2, often 3, or sometimes 4, filaments 5-12 mm long, anthers 2-4.5 mm long, 0.4-0.7 mm broad, attached to the filament about 1/3-1/4 from the apex, (versatile?), connective narrow, often with a puberulous apiculus; interfloral bracts with a 2-6 mm long, more or less clavate, sparsely puberulous to glabrous stipe, narrowed towards the insertion of the peltate part, peltate part 0.2-5 mm in diam., ciliolate and often appressed-puberulous. *Pistillate inflorescences* solitary or in pairs on distinct short-shoots, usually below the leaves on older branches or on the trunk, globose to obovoid (rather variable in dimensions, probably at least 2.5 cm in diam.); peduncle short, bearing in 4-6 series many basally attached, depressed-semicircular to elliptic, coriaceous, ciliolate, outside sparsely puberulous to glabrous bracts; flowers numerous; ovary ca. 1-1.5 cm high, style up to10 mm long, puberulous, stigmas 3-5(-10) mm long; interfloral bracts 4-5 mm long, similar to those of the staminate inflorescence; the cavities containing the pistillate flowers invested with short hairs; among the bracts usually up to 1 mm long, shortly pedicellate, abortive staminate flowers which may have a subulate pistillode. *Infructescences* (sub)globose, up to 30 cm in diam., the rachis surrounded by a 7-8 cm broad layer of elongate lower parts of the interfloral bracts, the outer part of this layer for the greater part consisting of the indurated free upper parts of the bracts sometimes having lost their peltate parts, the inner part of the layer soft and more or less mucilaginous containing (more or less scattered) the fruits; fruits 10-15 mm long, the exocarp thinly fleshy, the endocarp often with an apical dent.

18.1.a′. **Treculia africana** Decaisne ssp. **africana** var. **africana**. — Fig. 28 & 30.

*T. affona* N.E. Br., Kew Bull. **1894**: 360 (1894); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 227 (1917). — Type: *Millson* s.n., Nigeria, Yorubaland (K; isotypes B, E).

*T. africana* var. *nitida* Engl., Monogr. Afr. Pfl. **1** (*Moraceae*): 33 (1898); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 227 (1917). — Type: *Lehmbach* 3a, Cameroun (B).

*T. dewevrei* De Wild. & Th. Dur., Ann. Mus. Congo, Bot., ser. 2, **1**: 54 (1899); De Wild. & Th. Dur., Ann. Mus. Congo, Bot., ser. 1, **1**: 139, t. 70 (1900); De Wild. & Th. Dur., Ann. Mus. Congo, Bot., ser. 3, **1**: 217 (1901). — Type: *Dewèvre* s.n., Zaire, near Umangi (BR).

*T. engleriana* De Wild. & Th. Dur., Ann. Mus. Congo, Bot., ser. 1, **1**: 140 (1900). — Type: *Gillet* s.n., Zaire, Kisantu (BR).

*T. africana* var. *engleriana* (De Wild. & Th. Dur.) Engl., Pflanzenw. Afr. **3**(1): 30, t. 8 (1915).

*Ficus whytei* Stapf in Johnston, Liberia **2**: 650 (1906). — Type: *Whyte* 21, Liberia, Sinoe Basin, near Kuvu (K; isotype BM).

*Artocarpus? africanus* Sim, For. Fl. Port. E. Afr.: 102, t. 32 (1909). — Type: *Sim* 3999, Moçambique (not yet traced).

*Treculia centralis* A. Chev., Etud. Fl. Afr. Centr. Fr. **1**: 292 (1913), nom. (sub)nud.

*T. erinacea* A. Chev., Etud. Fl. Afr. Centr. Fr. **1**: 292 (1913), nom. (sub)nud.

*Myriopeltis edulis* Welw. (MSS) mentioned by Hook., Bot. Mag.: t. 5986 (1872), nomen.

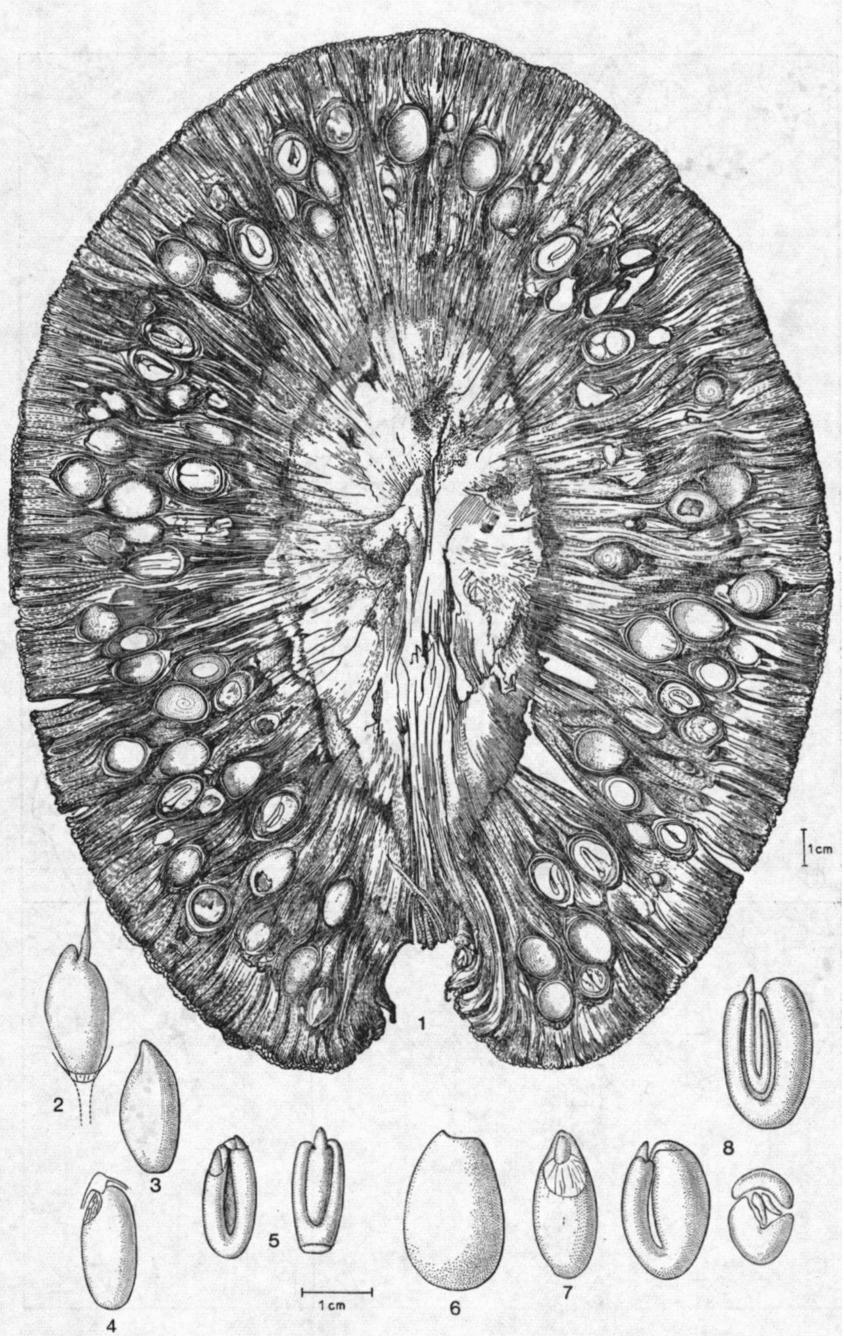

Fig. 28. — *Treculia africana* ssp. *madagascarica* var. *ilicifolia*: 1, infructescence (*Capuron* 6894). — *Treculia africana* ssp. *africana* var. *africana*: 2, fruit; 3, endocarp body; 4, seed; 5, embryo; 6, endocarp body; 7, seed; 8, embryo (2-5: *Leeuwenberg* 10217; 6-8: *Esperito Santo* 5).

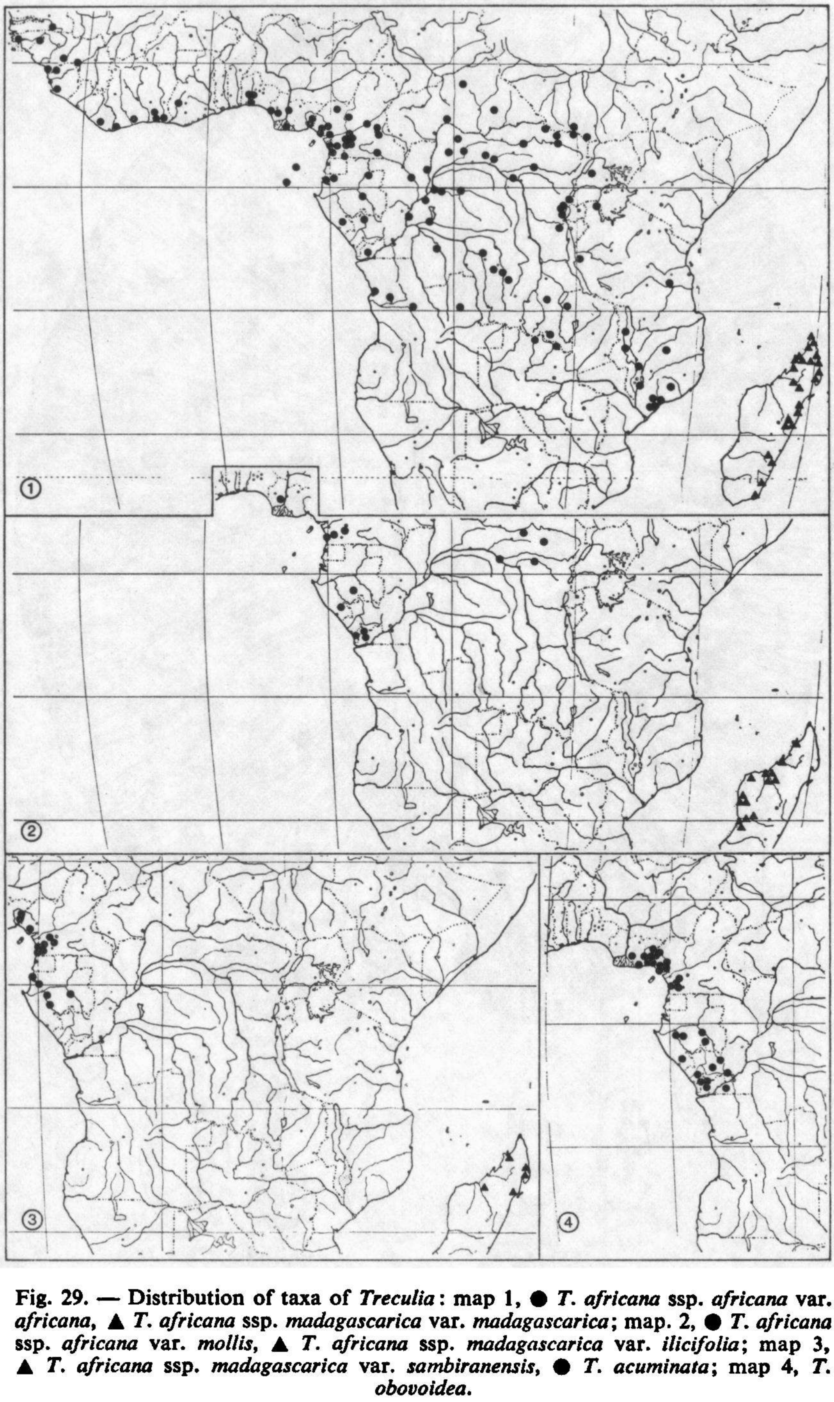

Fig. 29. — Distribution of taxa of *Treculia*: map 1, ● *T. africana* ssp. *africana* var. *africana*, ▲ *T. africana* ssp. *madagascarica* var. *madagascarica*; map. 2, ● *T. africana* ssp. *africana* var. *mollis*, ▲ *T. africana* ssp. *madagascarica* var. *ilicifolia*; map 3, ▲ *T. africana* ssp. *madagascarica* var. *sambiranensis*, ● *T. acuminata*; map 4, *T. obovoidea*.

*Ficus welwitschii* Miq. (MSS) mentioned by Hook., Bot. Mag.: t. 5986 (1872), nomen.

Leafy *twigs* sparsely puberulous to almost glabrous. *Leaves* with lower surface glabrous or nearly so, the secondary veins often with a few uncinate hairs; stipules almost glabrous.

Distribution (fig. 29, map 1): From Senegal to southern Sudan, southward to Angola and to central Moçambique, also on São Tomé; as evergreen (or sometimes deciduous?) trees in humid to dry primary forest, preferring riversides or regionally almost confined to them, also on rocks in riverbeds, in swamp forests, in secondary forests, or cultivated; regionally abundant to rare; from sealevel to 1300 m.

Number of collections examined: ca. 250.

The flowering times could not be established, There may be regionally different (main) flowering times, but the material is too scarce for establishing them.

The wood is said to be a good timber. The oil-containing seeds are consumed; they can be ground to meal and the oil can be extracted. The infructescences are eaten by various animals: elephants (cf. Brown 1894), antelopes, and large forest snails (Hutchinson & Dalziel 1937). Fruits are said to be poisonous for horses, sheep, and goats (cf. Hutchinson 1917).

Corner (1962) associated the infructescences of *Treculia africana* with those of *Artocarpus* species, and with the analogous Durian fruit. Because of the structure of the infructescence and the properties of the fruits *T. africana* may be also be brought into connection with the Durian fruit with regard to dispersal (cf. van der Pijl 1972). It is often reported on labels that the staminate inflorescences are highly scented. The sweet odour may be pleasant, but as a rule it is reported as unpleasant to disgusting and reminiscent of aceton, rotten apples, etc. It is uncertain whether the unpleasant odour is produced in all stages or only when the inflorescence is old. Germain (coll. 303) reported that the bad smell is released after cutting the staminate inflorescences. According to Leeuwenberg (coll. 2435) the inflorescences may be inhabited by beetles and grubs. This suggests that the staminate inflorescences may function as broodplaces and, moreover, that *T. africana* resembles the cauliflorous *Artocarpus heterophyllus* in the way of pollination (cf. van der Pijl 1953).

Seedlings of *T. africana* show a distichous arrangement of the leaves from the youngest stages; the first pair of normal leaves are opposite, the following ones distichous.

Young staminate and pistillate inflorescences cannot be distinguished. In these inflorescences several primary interfloral peltate bracts are conspicuous by their dimensions and in dried material by their darker colour; the largest is usually at the top of the inflorescence. In fruit the interfloral bracts sometimes shed their peltate upper parts. In staminate inflorescences the whole perianth of the staminate flower may exceed the bracts or only their upper parts.

The variation in the number of stamens, used to distinguish separate species (De Wildeman & Th. Durand 1900) proved not to be taxonomically significant. Variation in the number of stamens can even occur in the same inflorescence, as already stated by Engler (1915) and Hutchinson (1917).

18.1.a′. **Treculia africana** Decaisne ssp. **africana** var. **mollis** (Engl.) J. Léonard. — Type: *Zenker* 3333, Cameroun, near Bipinde (B; isotypes E, G). — Fig. 30.

*T. mollis* Engl., Bot. Jahrb. **40**: 546 (1908); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 229 (1917).

*T. africana* var. *mollis* (Engl.) J. Léonard, Bull. Jard. Bot. Etat Brux. **18**: 145 (1947); Hauman, Fl. Congo, Ruanda-Urundi **1**: 91 (1948).

Leafy *twigs* hirtellous to (sub)tomentose. *Leaves* with lower surface hirtellous to (sub)tomentose; stipules puberulous to hirtellous.

Distribution (fig. 29, map 2): Known from some more or less isolated localities in Zaire, Gabon, Cameroun, and Nigeria.

Number of collections examined: ca. 25.

*T. mollis* was distinguished on the basis of a dense tomentose to hirtellous indument on leaves, twigs, and stipules (Engler 1908). This species was reduced to a variety of *T. africana* by J. Léonard (1947). The present material is too scanty to establish if there are also constant differences in inflorescences and flowers between this variety and the typical variety. But it does not seem likely. This as well as the distribution of var. *mollis* suggest that the taxonomical value of the differences in the indument is small and that the form hardly merits recognition.

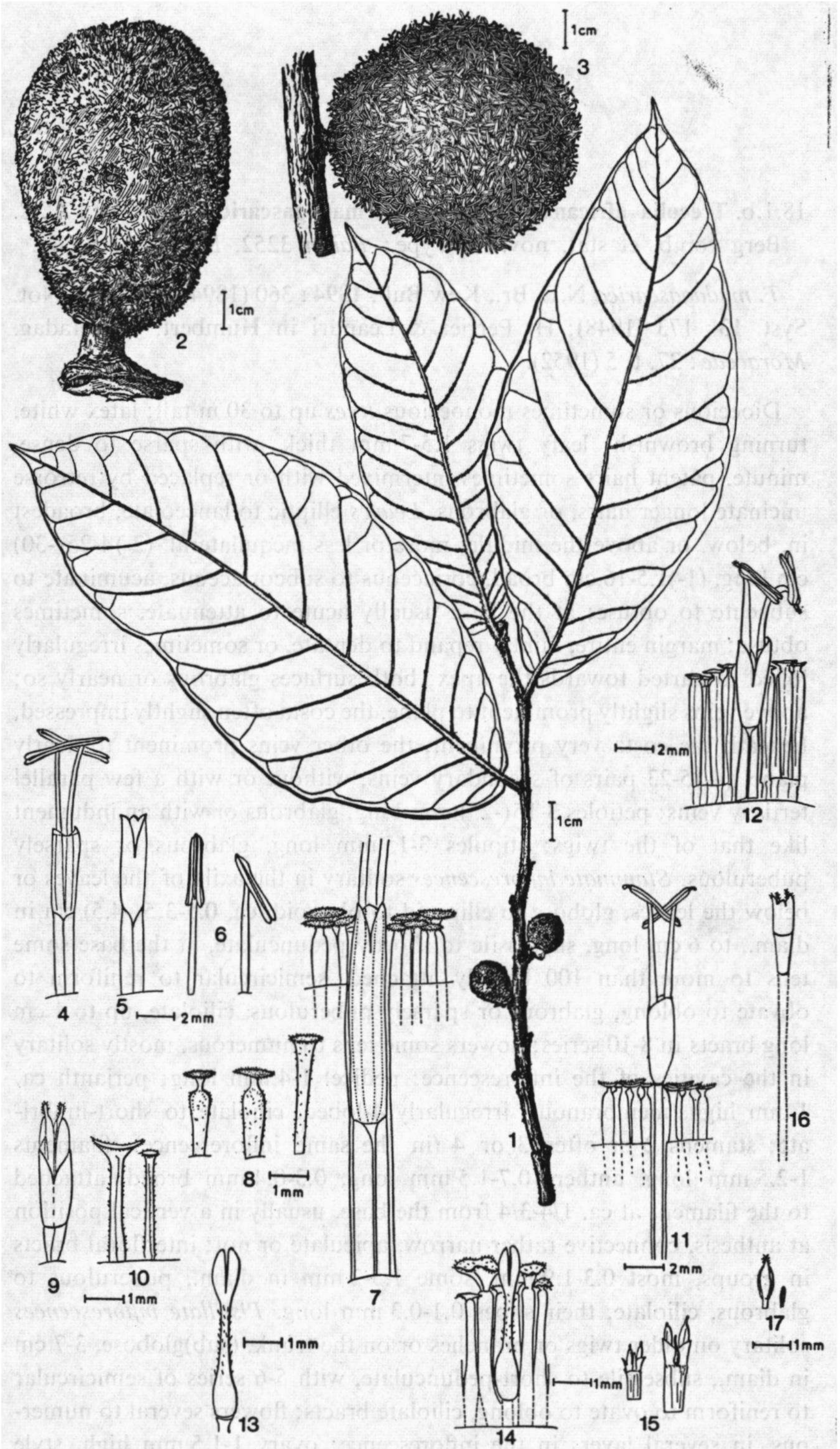

Fig. 30. — ***Treculia africana*** **ssp.** ***africana*** **var.** ***mollis*****: 1, leafy twig with inflorescences (*Benoit Mpom* 134). — *Treculia africana* ssp. *africana* var. *africana*: 2 & 3, staminate inflorescences; 4, staminate flower; 5, perianth; 6, stamens; 7 & 8, bracts of staminate flower; 9, staminate flower; 10, id., bracts; 11 & 12, staminate flowers and bracts; 13, young pistillate flower; 14, id., bract; 15, abortive staminate flower; 16, abortive staminate flower (in pistillate inflorescence); 17, stamen and pistillode of abortive flower (2: *Le Testu* 3848; 3, 11: *de Wilde* 2605; 4-8: *de Wilde* 2662; 9, 10: *Callens* 2886; 12: *Zenker* 2525; 13-15: *Le Testu* 3831; 16, 17: *Leeuwenberg* 10217).**

18.1.b. **Treculia africana** Decaisne ssp. **madagascarica** (N.E. Br.) C.C. Berg comb. et stat. nov. — Type: *Baron* 3252, Madagascar (K).

*T. madagascarica* N.E. Br., Kew Bull. **1894**: 360 (1894); Léandri, Not. Syst. **13**: 173 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 27, t. 5 (1952).

Dioecious or sometimes monoecious *trees* up to 30 m tall; latex white, turning brownish; leafy twigs 1.5-7 mm thick, with sparse to dense, minute, patent hairs sometimes intermixed with or replaced by retrorse uncinate longer hairs, or glabrous. *Leaves* elliptic to lanceolate, broadest in, below, or above the middle, more or less inequilateral, (2-)4-25(-30) cm long, (1-)1.5-16 cm broad, coriaceous to subcoriaceous, acuminate to subacute to obtuse; at the base usually acute to attenuate, sometimes obtuse; margin entire, faintly repand to dentate, or sometimes irregularly lobed to parted towards the apex; both surfaces glabrous or nearly so; above veins slightly prominent to plane, the costa often slightly impressed, beneath the costa very prominent, the other veins prominent to nearly plane, (4-)5-23 pairs of secondary veins, without or with a few parallel tertiary veins; petioles 3-15(-25) mm long, glabrous or with an indument like that of the twigs; stipules 3-15 mm long, glabrous or sparsely puberulous. *Staminate inflorescences* solitary in the axils of the leaves or below the leaves, globose to ellipsoid to obovoid, ca. 0.5-3.5(-4.5) cm in diam., to 6 cm long, subsessile to shortly pedunculate, at the base some tens to more than 100 basally attached, semicircular to reniform to obvate to oblong, glabrous or sparsely puberulous, ciliolate, up to 1 cm long bracts in 8-10 series; flowers some tens to numerous, mostly solitary in the cavities of the inflorescence; pedicel 1-4 mm long; perianth ca. 1 mm high, membranous, irregularly 4-lobed, ciliolate to short-fimbriate; stamens 2 or often 3 or 4 (in the same inflorescence), filaments 1-2.5 mm long, anthers 0.7-1.5 mm long, 0.3-0.4 mm broad, attached to the filament at ca. 1/4-3/4 from the base, usually in a vertical position at anthesis, connective rather narrow, apiculate or not; interfloral bracts in groups, most 0.3-1.9 mm, some 1.5-2 mm in diam., puberulous to glabrous, ciliolate, their stipes 0.1-0.3 mm long. *Pistillate inflorescences* solitary on older twigs or branches or on the trunk, (sub)globose, 3-7 cm in diam., subsessile to short-pedunculate, with 5-6 series of semicircular to reniform to ovate to oblong, ciliolate bracts; flowers several to numerous, in several layers in the inflorescence; ovary 1-1.5 mm high, style to 6-13 mm long, usually sparsely hairy, stigmas up to 18 mm long, of equal or unequal length, sometimes one of the stigmas strongly reduced;

interfloral bracts with 1-2 mm long puberulous stipes narrowed towards the insertion of the peltate part of the bract, which is ca. 0.5-1.5 mm in diam. or in a few bracts up to 3 mm in diam., puberulous. *Infructescences* globose to oblongoid or ovoid, up to 40 cm long, up to 40 cm in diam., sometimes irregularly furrowed, the layer containing the fruits up to 8 cm broad; fruits ellipsoid, 15-18 mm long, seed similar to that of ssp. *africana*; the peltate parts of the bracts persisting in fruit.

Distribution (fig. 29, maps 1-3): Madagascar, as evergreen or caducous trees in humid to dry forests (or thickets), mainly along streams, also in sublittoral forests, on various soils, but probably not on calcareous soils; from sealevel to 1300 m.

Number of collections examined: ca. 75.

According to Perrier de la Bâthie (coll. 9996) the latex is poisonous.

Three varieties can be distinguished, mainly on differences of the leaves. In northern Madagascar the three varieties occur together. Var. *madagascarica*, in the northern part of the island also occurring on the western side, extends southward along the eastern side of the island to near Fort Dauphin. Var. *ilicifolia*, confined to the western part of Madagascar, extends southward to the region between the Tsiribihina and Mangoky Rivers. Var. *sambiranensis* is confined to northern Madagascar and occurs there both on the eastern and the western side.

### 18.1.b′. **Treculia africana** Decaisne ssp. **madagascarica** (N.E. Br.) C.C. Berg var. **madagascarica**. — Fig. 31.

*Leaves* variously shaped, mostly oblong, sometimes lanceolate or elliptic, mostly 1.5-5 cm broad, with up to 15 pairs of secondary veins; margin mostly entire, sometimes lobed, sometimes more or less undulate; apex acute to acuminate, often abruptly acuminate, sometimes lobed towards the apex. *Twigs* glabrous, with only retrorse uncinate hairs, or also with minute patent hairs. *Staminate inflorescences* 0.5-2 cm in diam.

Distribution: see p. 386.

Number of specimens examined: ca. 45.

This variety is less homogenous in the leaf characters than the other two varieties and comprises forms passing into them.

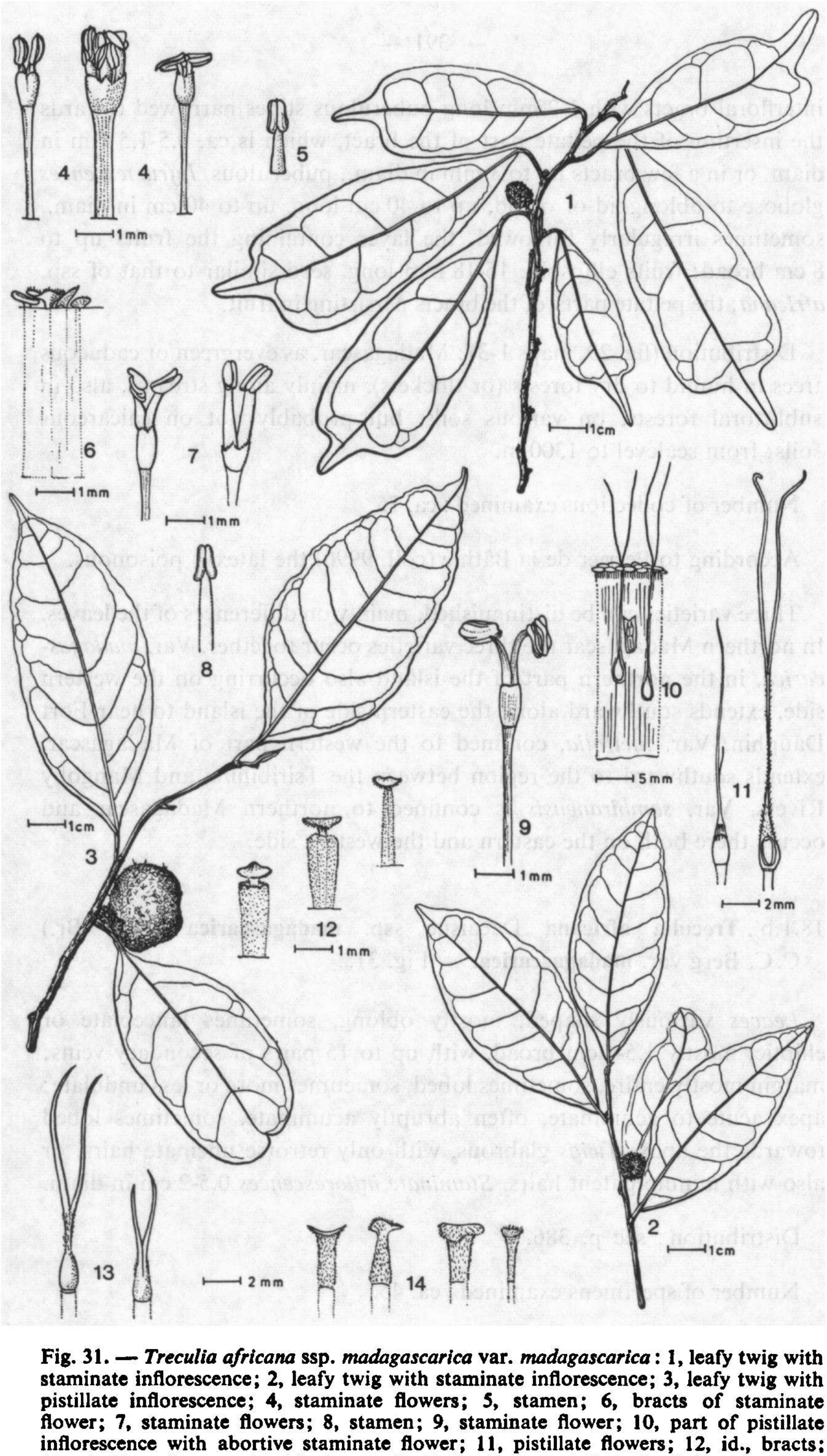

**Fig. 31. —** ***Treculia africana*** **ssp.** ***madagascarica*** **var.** ***madagascarica*****: 1, leafy twig with staminate inflorescence; 2, leafy twig with staminate inflorescence; 3, leafy twig with pistillate inflorescence; 4, staminate flowers; 5, stamen; 6, bracts of staminate flower; 7, staminate flowers; 8, stamen; 9, staminate flower; 10, part of pistillate inflorescence with abortive staminate flower; 11, pistillate flowers; 12, id., bracts; 13, pistillate flowers; 14, id., bracts (1, 7, 8:** ***Capuron*** **24858; 2:** ***Saboureau*** **4406; 3:** ***Capuron*** **11455; 4-6:** ***Serv. For. Madag.*** **7891; 9:** ***Decary*** **14728; 10-12:** ***Capuron*** **8676; 13, 14:** ***Perrier de la Bâthie*** **10063).**

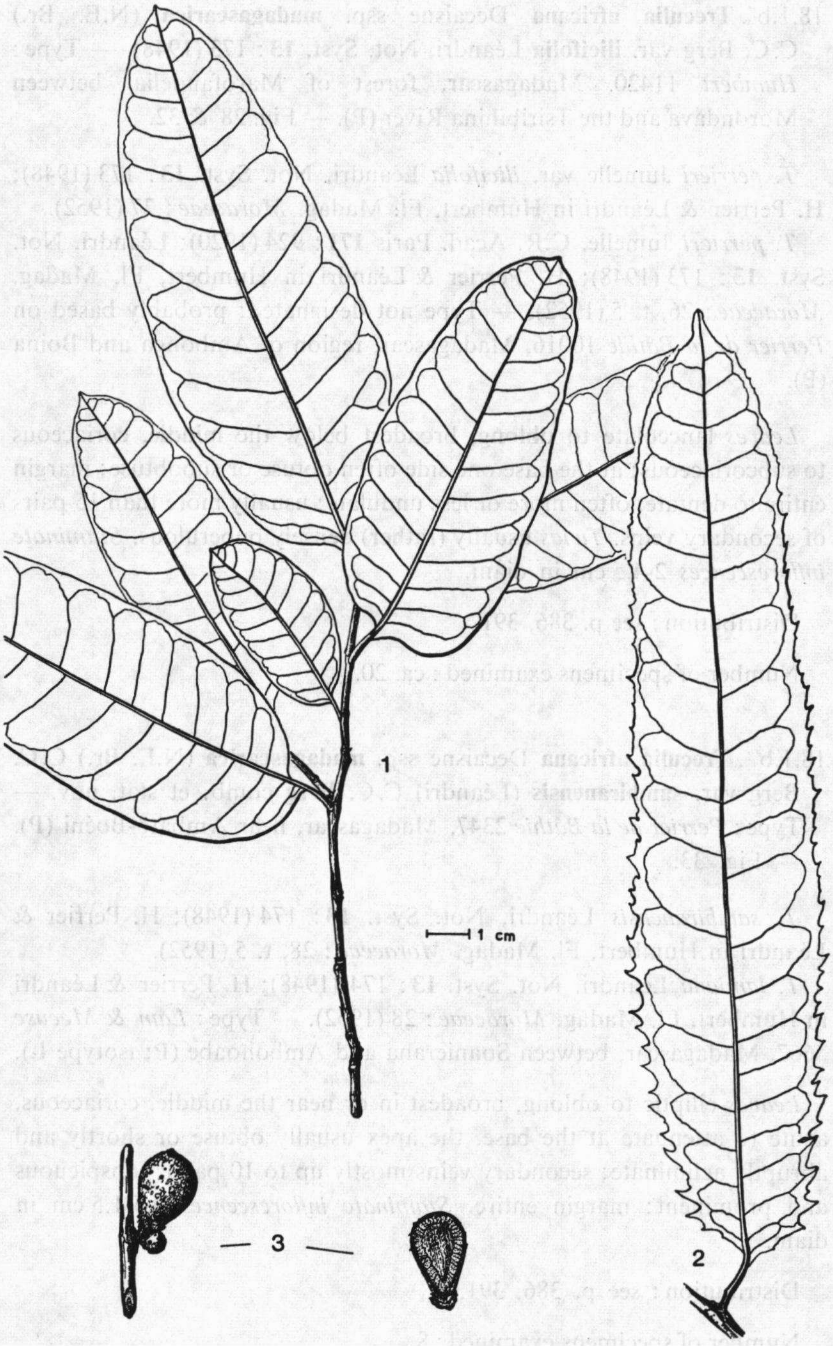

Fig. 32. — ***Treculia africana*** **ssp.** ***madagascarica*** **var.** ***ilicifolia*****: 1, leaves (*****Capuron*** **6894); 2, leaf (*****Perrier de la Bâthie*** **13899); 3, staminate inflorescences (*****Humbert*** **11420).**
)

**18.1.b″. Treculia africana** Decaisne ssp. **madagascarica** (N.E. Br.) C.C. Berg var. **ilicifolia** Léandri, Not. Syst. **13**: 173 (1948). — Type: *Humbert* 11420, Madagascar, forest of Marofandelia, between Morondava and the Tsiribihina River (P). — Fig. 28 & 32.

*T. perrieri* Jumelle var. *ilicifolia* Léandri, Not. Syst. **13**: 173 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 27 (1952).

*T. perrieri* Jumelle, C.R. Acad. Paris **171**: 924 (1920); Léandri, Not. Syst. **13**: 173 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 26, t. 5 (1952). — Type not designated; probably based on *Perrier de la Bâthie* 10016, Madagascar, region of Ambonga and Boina (P).

*Leaves* lanceolate to oblong, broadest below the middle, coriaceous to subcoriaceous; at the base one side often obtuse or subobtuse; margin entire to dentate, often more or less undulate; usually more than 15 pairs of secondary veins. *Twigs* usually (rather) densely puberulous. *Staminate inflorescences* 2-4.5 cm in diam.

Distribution: see p. 386, 391.

Number of specimens examined: ca. 20.

**18.1.b‴. Treculia africana** Decaisne ssp. **madagascarica** (N.E. Br.) C.C. Berg var. **sambiranensis** (Léandri) C.C. Berg comb. et stat. nov. — Type: *Perrier de la Bâthie* 2347, Madagascar, near Ambato-Boéni (P). — Fig. 33.

*T. sambiranensis* Léandri, Not. Syst. **13**: 174 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 28, t. 5 (1952).

*T. lamiana* Léandri, Not. Syst. **13**: 174 (1948); H. Perrier & Léandri in Humbert, Fl. Madag. *Moraceae*: 28 (1952). — Type: *Lam & Meeuse* 5667, Madagascar, between Soanierana and Ambohoabe (P; isotype L).

*Leaves* elliptic to oblong, broadest in or near the middle, coriaceous, acute to attenuate at the base, the apex usually obtuse or shortly and abruptly acuminate; secondary veins mostly up to 10 pairs, conspicuous and prominent; margin entire. *Staminate inflorescences* 0.5-1.5 cm in diam.

Distribution: see p. 386, 391.

Number of specimens examined: 8.

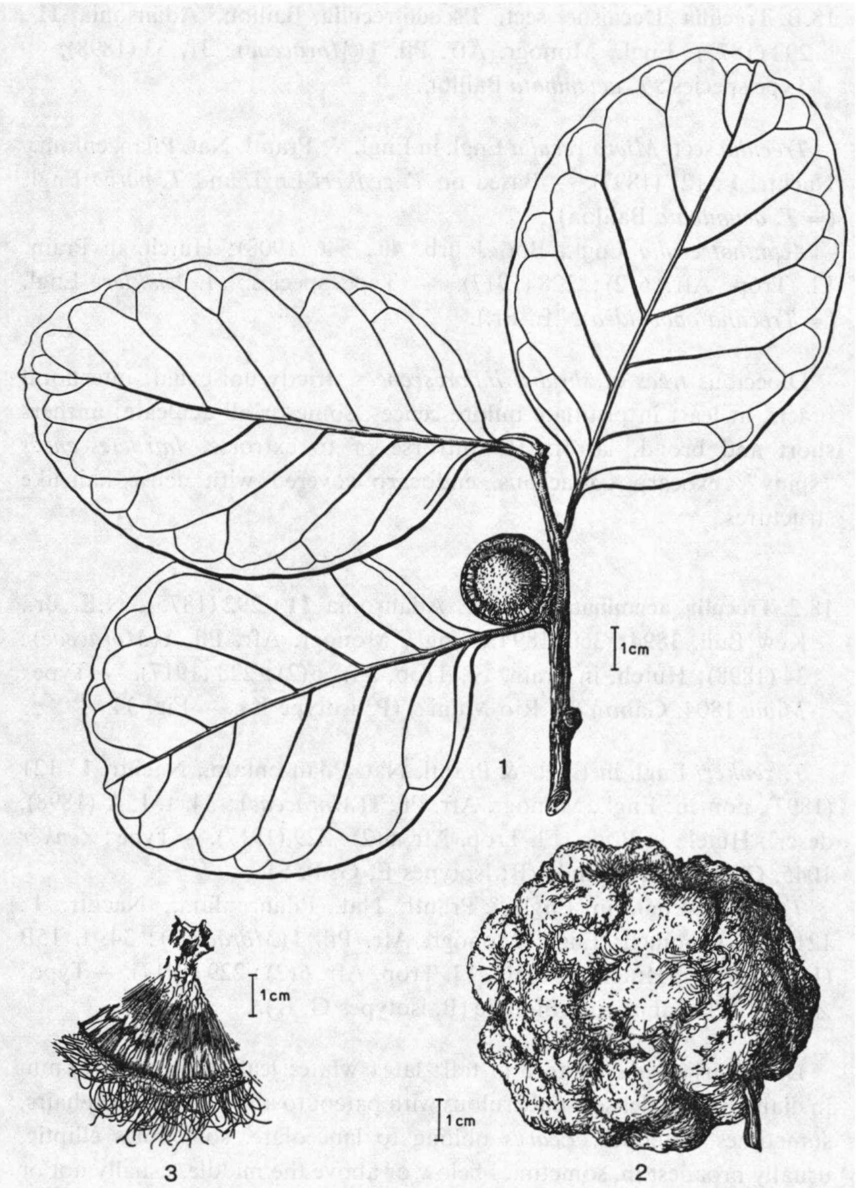

Fig. 33. — ***Treculia africana*** **ssp.** ***madagascarica*** **var.** ***sambiranensis*****: 1, leafy twig with pistillate inflorescence (*Capuron* 8676); 2, infructescence (*Humbert & Capuron* 22394); 3, part of inflorescence (*Capuron* 8676).**

18.B. **Treculia** Decaisne sect. **Pseudotreculia** Baillon, Adansonia **11**: 292 (1875); Engl., Monogr. Afr. Pfl. 1(*Moraceae*): 31, 33 (1898). — Type species: *T. acuminata* Baillon.

*Treculia* sect. *Microtreculia* Engl. in Engl. & Prantl, Nat. Pflanzenfam., Nachtr. **1**: 121 (1897). — Based on *T. zenkeri* Engl. and *T. parva* Engl. (= *T. acuminata* Baillon).

*Acanthotreculia* Engl., Bot. Jahrb. **40**: 546 (1908); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 228 (1917). — Type species: *A. winkleri* Engl. (= *Treculia obovoidea* N.E. Br.).

Dioecious *trees* or *shrubs*. *Inflorescences* strictly unisexual; interfloral bracts, at least in pistillate inflorescences, some or all aculeate; anthers short and broad, latrorse to introrse or to extrorse. *Infructescences* "spiny"; exocarp coriaceous, endocarp covered with dense hair-like structures.

18.2. **Treculia acuminata** Baillon, Adansonia **11**: 292 (1875); N.E. Br., Kew Bull. **1894**: 360 (1894); Engl., Monogr. Afr. Pfl. 1(*Moraceae*): 34 (1898); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 228 (1917). — Type: *Mann* 1804, Gabon (or Rio Muni?) (P; isotype K). — Fig. 34.

*T. zenkeri* Engl. in Engl. & Prantl, Nat. Pflanzenfam., Nachtr. **1**: 121 (1897), nomen; Engl., Monogr. Afr. Pfl. 1(*Moraceae*): 34, t. 15A (1898), descr.; Hutch. in Prain, Fl. Trop. Afr. **6**(2): 229 (1917). — Type: *Zenker* 1045, Cameroun, Bipinde (B; isotypes E, G, P, S).

*T. parva* Engl. in Engl. & Prantl, Nat. Pflanzenfam., Nachtr. **1**: 121 (1897), nomen; Engl., Monogr. Afr. Pfl. 1(*Moraceae*): 34, t. 15B (1898), descr.; Hutch. in Prain, Fl. Trop. Afr. **6**(2): 229 (1917). — Type: *Zenker* 983, Cameroun, Bipinde (B, isotypes G, K).

Dioecious *shrubs* up to 3 m tall; latex white; leafy twigs 1-3(-6) mm in diam., rather densely puberulous with patent to almost appressed hairs, sometimes hirtellous. *Leaves* oblong to lanceolate, sometimes elliptic, usually broadest in, sometimes below or above the middle, usually not or hardly inequilateral, (3.5-)6-24 cm long, (1.5-)2.5-8 cm broad, chartaceous (to subcoriaceous), acuminate to caudate, at the base acute to obtuse; margin entire; above glabrous, beneath on the costa and the secondary veins sparsely puberulous, partly with uncinate hairs, glabrescent; veins plane to slightly prominent above, prominent beneath,

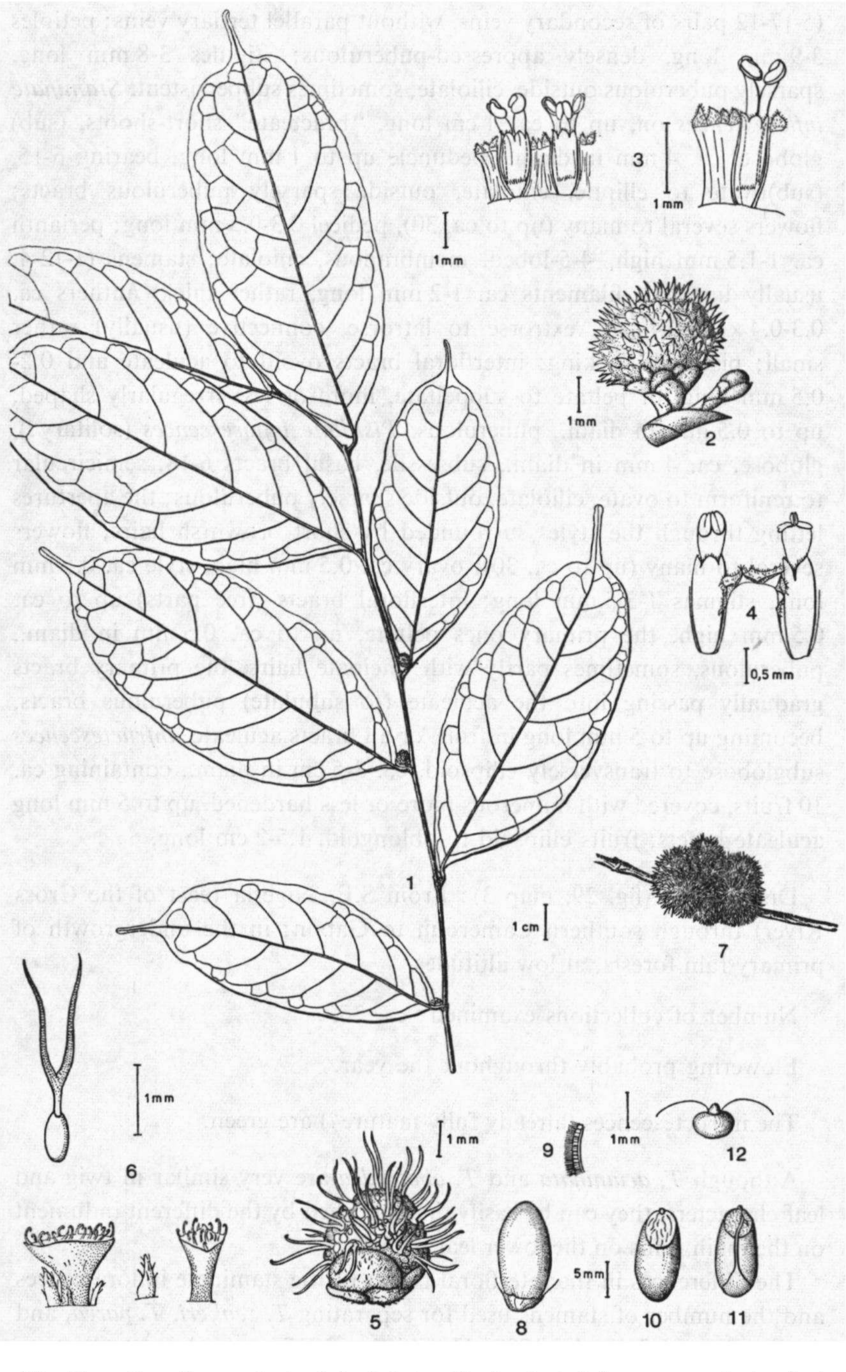

Fig. 34. — ***Treculia acuminata*** **: 1, leafy twig with staminate inflorescences; 2, staminate inflorescences, one very young, the other just before anthesis; 3 & 4, staminate flowers and bracts; 5, pistillate inflorescence; 6, pistil and bracts; 7, infructescence; 8, fruit; 9, testa, endocarp and layer with hair-like structures; 10, seed, 11, embryo; 12, small cotyledon (1 :** ***Klaine*** **2174; 2 :** ***Klaine*** **966; 3 :** ***Breteler*** **5724; 4 :** ***de Wilde*** **1448; 5, 6 :** ***Letouzey*** **12357; 7 :** ***Klaine*** **3004; 8-12 :** ***Walker*** **s.n.).**

(5-)7-12 pairs of secondary veins, without parallel tertiary veins; petioles 3-9 mm long, densely appressed-puberulous; stipules 3-8 mm long, sparsely puberulous outside, ciliolate, sometimes subpersistent. *Staminate inflorescences* on, up to ca. 1 cm long, "bracteate" short-shoots, (sub) globose, ca. 4 mm in diam.; peduncle up to 1 mm long, bearing 6-15, (sub)ovate to elliptic, ciliolate, outside sparsely puberulous bracts; flowers several to many (up to ca. 30), pedicel 0.3-0.5 mm long; perianth ca. 1-1.5 mm high, 4-5-lobed, membranous, ciliolate; stamens (1-)2-4, usually unequal, filaments ca. 1-2 mm long, rather thick, anthers ca. 0.3-0.4 × 0.3-0.4 mm, extrorse to latrorse, connective (usually) rather small; pistillode lacking; interfloral bracts ovoid to aculeate and 0.2-0.5 mm long, or peltate to subpeltate, more or less irregularly shaped, up to 0.5 mm in diam., puberulous. *Pistillate inflorescences* (solitary?), globose, ca. 4 mm in diam., subsessile, basal bracts 6-18, semicircular to reniform to ovate, ciliolate, outside sparsely puberulous; the apertures letting through the styles surrounded by short brownish hairs; flowers several to many (up to ca. 30); ovary ca. 0.5 mm high, style ca. 0.5 mm long, stigmas 1-3.5 mm long; interfloral bracts (free parts) up to ca. 0.5 mm high, the primary ones peltate, up to ca. 0.5 mm in diam., puberulous, sometimes partly with uncinate hairs, the primary bracts gradually passing into the aculeate (to subulate) puberulous bracts, becoming up to 5 mm long in fruit, or all bracts aculeate. *Infructescences* subglobose to transversely ellipsoid, ca. 3-5 cm in diam., containing ca. 10 fruits, covered with numerous more or less hardened, up to 5 mm long aculeate bracts; fruits ellipsoid to oblongoid, 1.5-2 cm long.

Distribution (fig. 29, map 3): From S.E. Nigeria (east of the Cross River) through southern Cameroun to Gabon; in the undergrowth of primary rain forests, at low altitudes.

Number of collections examined: ca. 35.

Flowering probably throughout the year.

The infructescences (already fully mature?) are green.

Although *T. acuminata* and *T. obovoidea* are very similar in twig and leaf characters, they can be easily distinguished by the different indument on the main veins on the lower leaf surface.

The differences in the interfloral bracts of the staminate inflorescences and the number of stamens used for separating *T. zenkeri*, *T. parva*, and *T. acuminata* (cf. Engler 1898; Hutchinson 1917) proved not to be consistent. The staminate inflorescences may bear only peltate interfloral bracts, only obovoid to aculeate interfloral bracts, or a mixture of peltate and obovoid to aculeate interfloral bracts. In several specimens a series of transitions from peltate to aculeate bracts was found.

18.3. **Treculia obovoidea** N.E. Br., Kew Bull. **1894**: 361 (1894); Benth. & Hook., Gen. Pl. **3**(1): 375 (1880); Hauman, Fl. Congo, Ruanda-Urundi **1**: 92 (1948). — Lectotype: *Mann* 2303, Nigeria, (Old) Calabar River (K). — Fig. 35.

*T. staudtii* Engl. in Engl. & Prantl, Nat. Pflanzenfam., Nachtr. **1**: 120 (1897), nomen; Engl., Monogr. Afr. Pfl. **1**(*Moraceae*): 33, t. 14B (1898), descr.; Hutch. in Prain, Fl. Trop. Afr. **6**(2): 228 (1917). — Type: *Staudt* 633, Cameroun, (Johan-Albrechtshöhe =) Kumba (B, not seen; isotypes COI, G).

*T. staudtii* var. *augustifolia* Engl., Monogr. Afr. Pfl. **1**(*Moraceae*): 34 (1898). — Type: *Staudt* 270, Cameroun, Lolodorf, Mount Mbanga (B; isotypes COI, E, G, K, P, S).

*Acanthotreculia winkleri* Engl., Bot. Jahrb. **40**: 548, t. 2 (1908); Engl., Pflanzenw. Afr. **3**(1): 30, t. 19 (1915); Hutch. in Prain, Fl. Trop. Afr. **6**(2): 228 (1917). — Lectotype: *Zenker* 2295, Cameroun, Bipinde (B; isotypes BR, COI, K, L, P).

*Treculia brieyi* De Wild., Repert. Sp. Nov. **13**: 374 (1914), erroneously published as *Trichilia brieyi*; De Wild., Mission de Briey: 24 (1920); Hauman, Fl. Congo, Ruanda-Urundi **1**: 91 (1948). — Type: *de Briey* 133, Zaire, Mayumbe, Ganda-Sundi (BR).

Dioecious *trees* up to 20 m tall; latex white turning brown or pinkish; leafy twigs 1.5-5 mm thick, (rather) sparsely appressed puberulous. *Leaves* oblong to lanceolate, broadest in or near the middle, not or slightly inequilateral, (3-)6-25 cm long, (1-)2-9 cm broad, chartaceous to subcoriaceous, acuminate to caudate, at the base acute to obtuse; margin (sub)entire; above glabrous, beneath sparsely appressed-puberulous on the costa and the secondary veins, glabrescent; veins plane to slightly prominent above, more or less prominent beneath, 7-16 pairs of secondary veins, without parallel tertiary veins; petioles 3-9 mm long; stipules 4-10 mm long, sparsely appressed puberulous and short-ciliate. *Staminate inflorescences* usually solitary, sometimes in pairs, occasionally several together in the leaf axils or below the leaves, obovoid, often almost oblongoid or ellipsoid, sometimes almost globose, 1-2.5 cm long,

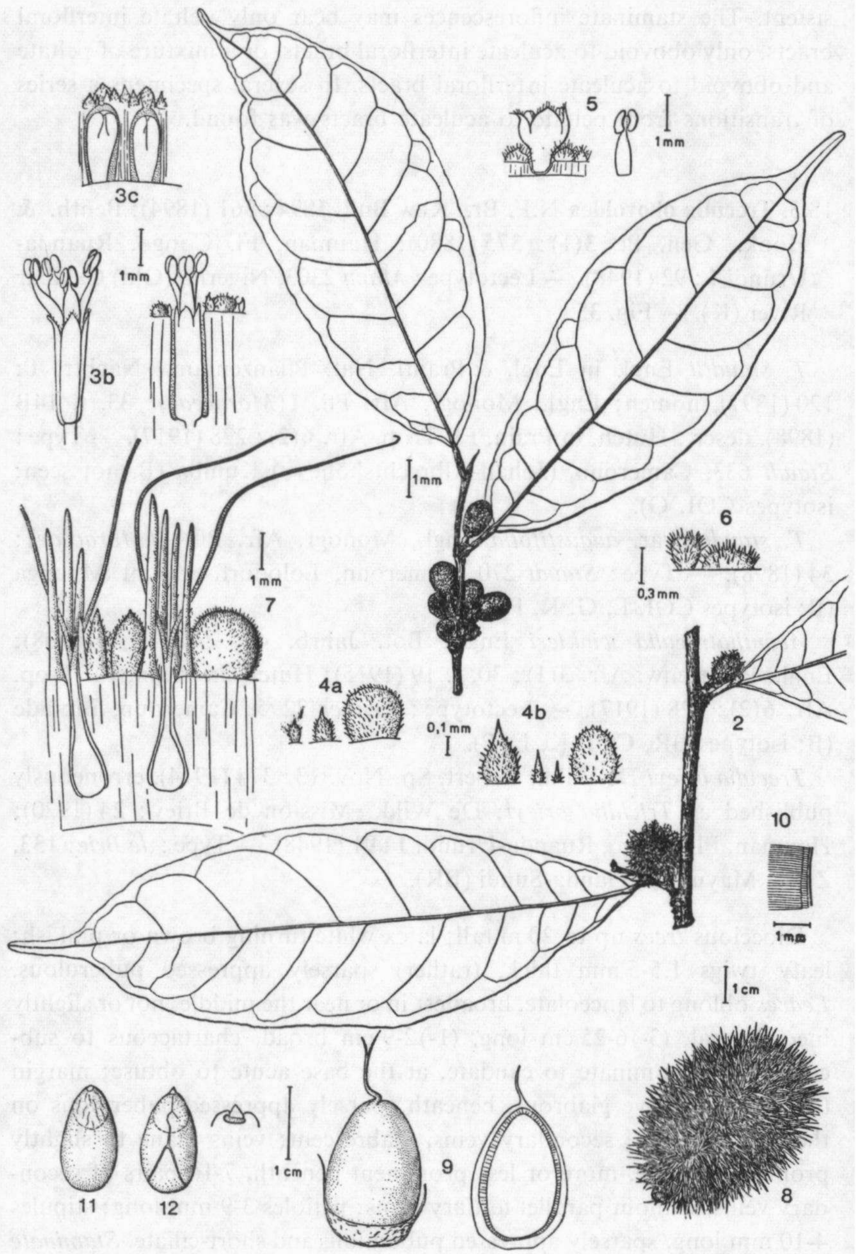

Fig. 35. — ***Treculia obovoidea*: 1, leafy twig with staminate inflorescences; 2, leafy twig with pistillate inflorescences; 3a & b, staminate flowers; 4a & b, id., bracts; 5, staminate flowers and stamen; 6, bracts of staminate flower; 7, pistillate flowers and bracts; 8, infructescence; 9, fruit; 10, testa, endocarp and layer of hair-like structures; 11, seed; 12 embryo (1, 3, 4 : *Zenker* 3776; 2, 7 : *Monteiro, Santos & Murta* 285; 5, 6 : *Staudt* 633; 8-12 : *Leeuwenberg & Berg* 9719).**

0.8-1.5 cm in diam., subsessile to pedunculate; peduncle up to 7 mm long, bearing 10-12, ovate, puberulous bracts; flowers numerous, sessile or subsessile; perianth 2.5-3 mm high, 3(-4)-lobed to 3(-4)-fid, membranous, glabrous except for the margin; stamens 3-4, usually unequal, filaments usually 3-4 mm long, anthers ca. 0.3-0.4 × 0.3-0.4 mm, latrorse (to introrse), connective narrow; pistillode subulate, 0.1-0.5 mm long or almost lacking; interfloral bracts numerous, up to 0.3 mm long, the primary ones more or less cushion-shaped and more or less densely puberulous, with or without an aculeate apex, the secondary ones, surrounding the apertures of the cavities, aculeate and only basally puberulous. *Pistillate inflorescences* solitary, sometimes in pairs behind the leaves, often on old branches or on the stem, (sub)globose, ca. 10 mm in diam.; peduncle up to 5 mm long; the apertures letting through the styles surrounded by hairs; flowers several to numerous; ovary ca. 1.5 mm long, style ca. 2 mm long, stigmas filiform, 6-9 mm long; the primary bracts cushion-shaped to subclavate, initially with or without an aculeate apex, up to 2 mm long, puberulous, passing gradually into the aculeate, up to 6 mm long, almost glabrous secondary bracts which surround the apertures letting through the styles. *Infructescences* globose to ellipsoid, 5-6.5 cm in diam., covered by the up to ca. 2 cm long indurated aculeate bracts, the primary bracts usually shorter than the secondary bracts and sometimes (sub)clavate; fruits ellipsoid to oblongoid, 15-20 mm long.

Distribution (fig. 29, map 4): From S.E. Nigeria (east of the Cross River) through southern Cameroun, Gabon, and western Congo to Angola-Cabinda and the adjacent part of Zaire; in primary or sometimes secondary rain forests, often (or mostly?) along streams, locally common, at low altitudes.

Number of collections examined: ca. 85.

Flowering probably throughout the year.

The infructescences are pale yellow. The seeds are edible.

The species is uniform; variation of some importance is only found in the shape and dimensions of the staminate inflorescences and in the staminate flowers.

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## INDEX OF NAMES OF THE SYSTEMATIC PART

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