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THE GENERA OF CHRYSOBALANACEAE: A STUDY IN PRACTICAL AND THEORETICAL TAXONOMY AND ITS RELEVANCE TO EVOLUTIONARY BIOLOGY

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[Plate 1]

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This account is a generic monograph of a medium-sized (494 species) pantropical plant family. Its rank, circumscription and relationships to other families are examined. An attempt is made to provide an objective and repeatable taxonomy and to formulate evolutionary hypotheses consistent with the facts presented. The monograph is also used to test the general application of certain relatively new and still controversial theoretical approaches to descriptive and evolutionary biology, notably numerical taxonomy, cladistics and vicariance biogeography. The practical value of some potentially useful sources of taxonomic information, especially electron

microscopy and phytochemical analysis, is also examined. This is possibly the first time that non-traditional approaches to taxonomy have been so comprehensively evaluated within the framework of a worldwide monograph.

Based mainly on original investigations, the morphology, anatomy, reproductive biology, distribution and ecology of each of the 17 genera are described and illustrated. Published works by others on chemistry, embryology and chromosome cytology are summarized. The delimitation and arrangement of the genera included here depart somewhat from those of earlier systems. Most of the new taxa have been formally published elsewhere but the following are proposed here for the first time: tribus Chrysobalaneae, tribus Parinarieae Prance & F. White, tribus Couepieae Prance & F. White, tribus Hirtelleae Prance & F. White, *Licania* subgenus *Angelesia* (Korth.) Prance & F. White and *Atuna latifrons* (Kosterm.) Prance & F. White.

All Chrysobalanaceae are woody. They vary greatly in size but are uniform in their vegetative architecture. By contrast, the structure of the inflorescence, flower and fruit is much more diverse; detailed examination has revealed a multitude of previously overlooked characters of classificatory importance. Individually these characters are small, but they are well correlated and belong to character complexes of high diagnostic value which are also functional syndromes related to pollination, dispersal and germination.

Each genus is unique in the precise way in which its stigmatic and polliniferous surfaces are presented to pollen vectors and in the structure of its fruit, although within a genus there may be more than one principal pollinator or disperser. Except for a few anomalous species, each genus is distinct in its general appearance. Membership of a genus can be detected by intuitive perception, based on rapid inspection 'by eye' of herbarium specimens with flowers. This is possible because of the underlying structural uniformity of the inflorescence and the similar proportions of the flower in all congeneric species. For two genera, *Couepia* and *Hirtella*, their objectivity and ease of identification by rapid visual means was demonstrated by simple experiments involving colleagues with little experience of taxonomy and no previous knowledge of the group. The characteristics these 'subjects' had subconsciously used were then explicitly formulated in taxonomic terms and their individual diagnostic values calculated.

Some methods of numerical taxonomy were found to be useful, although less so than their advocates frequently claim. This is because of problems associated with the detection, selection and weighting of characters.

Attempts to apply cladistic analysis to the Chrysobalanaceae were largely unsuccessful because of parallelism and the difficulty of identifying sister groups. The occurrence and extent of parallelism was shown by using a 'principle of discordant characters', which is defined and discussed. The ideas underlying it are widely known but the principle itself does not seem to have been previously used as an analytical tool in taxonomic research. In the Chrysobalanaceae, parallelism is so rife that convincing cladograms cannot be constructed; for this reason, among others, the methods of vicariance biogeography are inappropriate. Aspects of evolution other than branching patterns, however, are more relevant to general biology, and monographic studies should help to identify them. Examples from Chrysobalanaceae include: (*a*) the response in growth-form to geomorphological and climatic change; (*b*) the biological consequences of dispersal across faunistic barriers; and (*c*) the evolution of ocean-dispersed, obligate strand plants.

It is concluded that monographers cannot afford to ignore fine structure and chemistry, though there is no evidence that they are more fundamental in practical taxonomy than other sources of information. The Chrysobalanaceae and other families show that parallelism is as likely to occur in fine structure and chemistry (at least of secondary compounds) as in gross morphology, and it is much more expensive to detect. At present, for tropical plants, some currently fashionable approaches to taxonomy are of limited relevance. It is much more important to develop objective methods of visual analysis for dealing with the copious material that monographic work entails. It is equally necessary to understand the central role of ecology in biology. Without ecological understanding taxonomy is lifeless and dull, and taxonomically important information and interesting evolutionary situations go undetected.

1. INTRODUCTION

This work is a generic monograph of a medium-sized, pantropical plant family, the Chrysobalanaceae. Use is made of as many fields of evidence as possible in an attempt to provide an objective and repeatable taxonomic framework, and to formulate evolutionary hypotheses which are consistent with the empirical knowledge we have acquired.

The Chrysobalanaceae is particularly suitable for such a study. It is one of the few plant families which (i) occurs throughout the tropics in sufficient structural and ecological diversity to provide material for a wide range of evolutionary studies; and (ii) is sufficiently small to be tackled comprehensively by a small group of workers in a relatively short time.

We recognize 17 genera and nearly 500 species. The Neotropics are overwhelmingly richer in species than the tropics of the Old World, although the latter provide more diversity of structure. All Chrysobalanaceae are woody plants; there are no true herbs, although the smallest members are easily mistaken for them until their woody underground parts are examined. Despite a wide range in stature, from 10 cm to more than 40 m, the vegetative architecture of the plants is essentially uniform. The flower, by contrast, is comparatively diverse, although nearly every genus is characterized by an underlying uniformity of inflorescence and floral structure, which is clearly related to pollen transfer.

At first sight the drupaceous fruit shows little structural modification; but this is a false impression, belied by living material, which, when examined in relation to the requirements of dispersal and germination, shows a multitude of structural and physiological differences. These are useful in taxonomy.

Our work on Chrysobalanaceae began more than 25 years ago, when one of us embarked on a study of generic delimitation in the group and its relationships to Rosaceae and other families (Prance 1963). This was probably the first botanical study of its kind, in that non-traditional approaches to taxonomy, mainly blastogeny, palynology and various aspects of anatomy, were comprehensively used in a relatively large but tightly knit group, and that various numerical methods, which had only recently been developed, were applied in a genuinely monographic context.

Three main conclusions were drawn from this investigation. First, that the Chrysobalanaceae is so different from Rosaceae that family rank is justified; second, that two genera, *Rhabdodendron* and *Stylobasium*, formerly placed in it, should be removed; and third, that some drastic reorganization at the generic level was called for, especially concerning the genus *Parinari*; the latter was dismembered into no fewer than eight segregate genera.

This last step, it was felt, might require some explanation to the general scientific public, in view of the latter's justifiable reluctance to accept newly proposed name changes without good cause. It was therefore decided that the second author should test the new generic classification as rigorously as possible. This was done more extensively and independently than was originally thought possible, largely owing to the availability of new material, much of it representing species (some of them new to science) not included in the original study. The second study was based on more than twice as much material as the first. It abundantly confirmed the conclusions based on the original work, especially concerning *Parinari*; only a few relatively minor changes were found to be necessary, elsewhere in the family.

Our continuing work on the group, partly done in the field, has shown that the genera are more distinct than we originally supposed. Detailed examination of the inflorescence, flower and fruit has brought to light a wealth of previously overlooked characters of classificatory importance. Individually, many of them are small, but they have high diagnostic value. Most of them are tightly correlated among themselves and are part of character complexes which are also functional syndromes related to pollination, dispersal and germination.

During the period of our study some radical changes in taxonomic procedure have been proposed, sometimes by people with little practical experience of taxonomy. In the course of our work we have sought opportunities to apply the new ideas and methods, and to test their usefulness. In the following pages we have described this at some length, because we firmly believe that examples of the application of controversial or insufficiently tested methods are worth much more than volumes of theorizing.

Our own approach throughout has been empirical and objective in intent. We have found, not surprisingly, that some of the new methodologies and sources of information have proved useful, although only in some situations, and less generally than some of their advocates would have us believe. By contrast, and again in the context of the Chrysobalanaceae, for reasons given, we were unable to apply, except to a very limited degree, some theoretical methodologies, notably those of cladistics and vicariance biogeography. Other workers, including Cain (1983), have had a similar experience, based on a more epistemological approach and examples derived from the animal kingdom.

In the course of a study lasting 25 years we have failed to discover any evidence that points unequivocally to a close evolutionary relationship between the Chrysobalanaceae and any other family. Similarly, because of widespread parallelism, we have been unable to construct a convincing cladogram or other type of family tree which reflects generic and specific relationships. In common with Gilbert-Carter (1936), Davis (1978) and others, we believe that speculation along such lines, without fossil evidence, is of limited value and should have a low priority in publicly financed scientific research. We do believe, however, that aspects of evolution other than branching patterns are of more interest to the general biologist, and that monographic studies of families such as the Chrysobalanaceae can help to identify them.

All known neotropical species of Chrysobalanaceae have been described by Prance (1972, *et seq.*). The African and, to a lesser extent, the Asiatic species have been studied in comparable detail, but publications about them are scattered and, for the most part, not readily accessible. We have therefore given brief synopses of the Old World species. In the general chapters, authorities for plant names are cited only where they assist in understanding. For all species they are given in the index.

Grammatically, 'Chrysobalanaceae' is a collective noun. We have treated it as singular or plural according to the context, not consistently one or the other as some grammarians recommend.

PART I. GENERALITIES

2. Taxonomic history

(*a*) *Introduction*

The taxonomic history of the Chrysobalanaceae is more confused and complex than that of most flowering plant families. There appear to be four main reasons for this.

(i) A superficial resemblance in the floral structure of certain Rosaceae and Chrysobalanaceae has led several authors to unite them.

(ii) The dispersal of Aublet's herbarium after his death in 1778 (Stafleu 1971; Stafleu & Cowan 1976) led to persistent confusion of some of his genera, especially *Acioa*, *Couepia*, *Licania* and *Moquilea*, both among themselves and with others such as the subsequently described *Dactyladenia*.

(iii) A serious error of judgement in 1849 by Bentham, who greatly enlarged the concept of *Parinari* by defining it on an artificial character, the false dissepiment dividing the ovary, led to that genus becoming an unwieldy heterogeneous assemblage.

(iv) There is a lack of thorough and comprehensive studies. Before the onset of the present study in 1960, the group had last been monographed at the species level in 1825, by de Candolle in his *Prodromus*, and at the generic level by Focke in 1891 in Engler & Prantl's *Die natürlichen Pflanzenfamilien*; Focke's account is rather superficial, and all subsequent work had been undertaken on a restricted basis. In the absence of monographic studies several extraneous genera became associated with the family, most notably and persistently *Lecostemon* and *Stylobasium*, whose relationships were not finally cleared up until after the present study began (Prance 1963, 1965, 1968*a*).

In this section the way in which our own work has developed in the past 20 years is briefly told in the context of a succinct taxonomic history. Historical aspects of four major topics are included elsewhere:

(i) rank and circumscription of the group and its relationships to other families (§5);
(ii) generic delimitation (§6);
(iii) grouping of the genera within the family (§7);
(iv) the use of anatomical characters (§4).

(*b*) 1753–1891; *Linnaeus to Engler & Prantl*

The first edition of the *Species plantarum* (1753) contains two members of the Chrysobalanaceae, *Chysobalanus icaco*, which Linnaeus placed in Polyandria Monogynia, and *Hirtella americana*, which he included in Triandria Monogynia. Their generic names for purposes of valid publication are associated with the subsequent descriptions given in the fifth edition of the *Genera plantarum* (1754), although both genera had been described in earlier editions of that work, and *Hirtella* was described in the *Hortus cliffortianus* (1737*b*).

In 1775 Aublet described seven South American genera which have subsequently been assigned to Chrysobalanaceae, namely *Licania* in Pentandria Monogynia, *Tachibota* in Pentandria Trigynia, *Parinari*, *Couepia* and *Moquilea* in Icosandria Polygynia and *Acioa* in Monadelphia Decandra. Aublet misinterpreted the floral structure of *Moquilea*, which is now considered to be a synonym of *Licania*. He regarded the seventh genus, *Ferolia*, which was based on a sterile specimen and Barrère's (1741) pre-Linnean description, as imperfectly known.

Most subsequent authors have merged it with *Parinari*, but it is a synonym of *Brosimum* in the Moraceae (Standley 1929; Berg 1968).

Owing to the dispersal of Aublet's herbarium after his death, some of his genera were misinterpreted for nearly a hundred years (§6).

In Jussieu's *Genera plantarum* (1789), the first comprehensive, modern natural classification of flowering plants, and the starting point for the nomenclature of families, the above-mentioned genera were brought together for the first time. Jussieu placed them in two of his seven tribes of Rosaceae, where they were associated with the chrysobalanaceous *Grangeria* as well as some other genera that are now excluded from the group (§5*b*). *Grangeria*, based on a Commerson specimen from Réunion, was described by Jussieu for the first time.

Robert Brown (1818) was the first author to give family status to this group as 'Chrysobalaneae'. The reliability of Brown's taxonomic judgement is clearly shown by the fact that, unlike all previous and nearly all subsequent specialists on the group, he only included genera which correctly belong to Chrysobalanaceae: *Chrysobalanus*, *Moquilea*, *Grangeria*, *Couepia*, *Acioa*, *Licania*, *Hirtella*, *Thelira* and *Parinari*. *Thelira* had been described by Du Petit-Thouars (1806) but no species was assigned to it. It is, in fact, a Malagasy *Hirtella*. Brown characterized the family by its basal style, erect embryo and ovule and a tendency to zygomorphy.

In 1819 Desfontaines described a new genus, *Stylobasium*, which he placed in the order Terebinthales. It has been included in Chrysobalanaceae by many subsequent authors but in our opinion it belongs to a distinct family (Prance 1965).

de Candolle in his *Prodromus* (1825) treated the Chrysobalaneae of Robert Brown as the first tribe of his Rosaceae. He included *Chrysobalanus*, *Moquilea*, *Couepia*, *Acioa*, *Parinari*, *Grangeria*, *Licania*, *Thelira* ('*Thelyra*') and *Hirtella*. He also described a new genus, *Lecostemon*, from a drawing by Mociño & Sesse and placed it in 'Genera Rosaceis affinia' together with the genus *Trilepisium*. The identity of *Lecostemon* has been the subject of much uncertainty and is fully discussed in a separate paper (Prance 1968*a*), where it is shown to be congeneric with *Sloanea* L. (Elaeocarpaceae). *Trilepisium* had been earlier described by Du Petit-Thouars (1806) who did not provide a name for the type species. de Candolle met this deficiency by publishing the binomial *T. madagascariense*. The true relationship of *Trilepisium* remained unknown until relatively recently when Capuron (1968) showed that it is an earlier name for the well-known *Bosqueia* (Moraceae).

Lindley (1836) accepted the Chrysobalanaceae as a family and placed it between the Rosaceae and Leguminosae. The genera he included are *Chrysobalanus*, *Moquilea*, *Couepia*, *Acioa*, *Parinari*, *Grangeria*, *Licania*, *Thelira*, *Hirtella*, *Stylobasium* and *Prinsepia*. *Prinsepia* was later removed to the Prunoideae by Hooker (in Bentham & Hooker 1865; see also Sterling 1963).

Meisner (1837–8) was the first to make a key to the genera of the Chrysobalanaceae ('Chrysobalaneae'), which he treated as the first tribe of his Rosaceae. As it includes several misplaced genera it sheds little light on relationships. His genera are *Roydsia* Roxb. (now placed in Capparidaceae), *Trilepisium* Thou., *Lecostemon*, *Stylobasium*, *Licania*, *Parinari*, *Chrysobalanus*, *Grangeria*, *Bartlingia* Brongn. (= *Pultenaea* Sm., Leguminosae: Papilionoideae), *Hirtella*, *Moquilea* sensu Martius (see §6*b*), *Balantium* Desv. ex Ham. and *Thelyra*. *Balantium* is a *Parinari*. The first four of these were only doubtfully included. In 1838 Rafinesque described *Atuna*, which was disregarded by other botanists for more than a hundred years (see §16.13).

Endlicher (1840, 1842) treated the Chrysobalanaceae ('Chrysobalaneae') as a family in the order Rosiflorae and included in it *Chrysobalanus*, *Hirtella*, *Licania*, *Moquilea*, *Parinari*, *Thelyra*, *Grangeria* and *Prinsepia* Royle as well as three 'genera dubiae', *Lecostemon*, *Trilepisium* and *Stylobasium*. Like Meisner, he followed Martius in citing *Acioa* and *Couepia* as synonyms of *Moquilea* (see §6*b*).

In an account of the South American genera, Bentham (1840) restored to generic rank Aublet's *Couepia*, which had been confused with *Acioa* and *Moquilea* (see §6*b*). Nine years later in Hooker's *Niger Flora* (1849) he greatly extended the concept of *Parinari*, an error of judgement which has had serious repercussions up to the present time (see §6*d*). Welwitsch, in 1859, published the genus *Dactyladenia*, which subsequent authors overlooked or confused with *Acioa* (see §16.14).

The account of the group (as Rosaceae: Chrysobalaneae) by J. D. Hooker, in the *Genera plantarum* of Bentham & Hooker (1865) was much more comprehensive and accurate than all previous accounts. Hooker included *Chrysobalanus*, *Licania*, *Moquilea*, *Grangeria*, *Parinari*, *Trichocarya*, *Parastemon*, *Hirtella*, *Couepia*, *Griffonia*, *Lecostemon* and *Stylobasium*. *Prinsepia* was correctly placed in the Prunoideae ('Pruneae') in spite of its basal style. *Acioa* was still treated as part of *Couepia*, but a new genus, *Griffonia*, was based on an African species now placed in *Dactyladenia*.

Parastemon had been described by de Candolle (1842) to accommodate his *Embelia urophylla*, which he had placed in Myrsinaceae a few years previously (1837). de Candolle remained in some doubt as to the relationships of this new genus and had tentatively transferred it to Olacineae. *Trichocarya* was published by Miquel (1855) and based on two species which Korthals had recently published in other genera as *Angelesia splendens* and *Diemenia racemosa*. In our opinion *Angelesia* is best regarded as a subgenus of *Licania*, and *Diemenia* is a *Parastemon*. *Thelira* was mistakenly reduced to synonymy under *Parinari*, an error which has been revived in the seventh and eighth editions of Willis's *Dictionary of flowering plants and ferns* (1966, 1973).

Baillon (1868) showed that *Thelira* is a *Hirtella* and also commented on the difficulty of subdividing the Chrysobalanaceae which, in his *Histoire* (1869), he included in the Rosaceae. He is the first author to arrange the genera into groups based on the symmetry of the flower. 'Group a' contains *Chrysobalanus*, *Licania* (including *Moquilea*), *Lecostemon* and *Stylobasium*. 'Group b' comprises *Grangeria*, *Hirtella*, *Couepia*, *Parinari*, *Acioa* and *Parastemon*. He did not see material of *Trichocarya*. Baillon, following Grisebach (1857), was the first author of a comprehensive account of the family to unite *Moquilea* with *Licania*. He also reduced *Griffonia* Hook.f. (non Baillon) to synonymy under *Acioa*, in our opinion mistakenly (see §16.10). His other views have been largely accepted by later workers, although there are some errors, particularly concerning the illustrations.

Fritsch (1889*a*) considered the Chrysobalanaceae to be a well-defined family, clearly separable from its nearest allies, the Rosaceae and Leguminosae. He made three subfamilies:

(i) 'Chrysobalaneae', including *Chrysobalanus*, *Licania*, *Grangeria*, *Hirtella*, *Couepia*, *Acioa*, *Parinari*, *Angelesia*, *Diemenia* and *Parastemon*;

(ii) 'Lecostemoneae', containing *Lecostemon*;

(iii) 'Stylobasieae', containing *Stylobasium*.

The following year he published a valuable conspectus of all known species of *Licania* and gave reasons for uniting *Licania* and *Moquilea* (Fritsch 1889*b*).

Focke (1891) in Engler & Prantl's *Die natürlichen Pflanzenfamilien* treated the group as a subfamily of Rosaceae containing only one tribe, which he divided into two subtribes, Chrysobalaninae and Hirtellinae. The former includes *Chrysobalanus*, *Grangeria*, *Moquilea*, *Licania*, *Lecostemon* ('*Lecostomion*') and *Stylobasium*, and the latter includes *Hirtella*, *Couepia*, *Parinari*, *Acioa*, *Angelesia* and *Parastemon*. Focke's generic diagnoses are very brief and his keys to the genera do not make use of the best characters. Subsequent work has not supported his subtribal groupings. He included *Lecostemon* and *Stylobasium* with some reservations and suggested a relationship for them with Phytolaccaceae.

(*c*) 1891 *to the present day*

Our own work on Chrysobalanaceae dates from 1960, when one of us began a reassessment of the family at generic level (Prance 1963).

Between 1891 and 1960 there had been no important taxonomic syntheses and no major discoveries. Regional and local floras continued to follow the traditions laid down during the previous century, especially concerning the artificial nature of *Parinari*. Three new genera were described, two of which, *Geobalanus* Small (1913) and *Afrolicania* Mildbraed (1921), we regard as synonymous with *Licania*. The third, *Magnistipula* Engler (1905), is very distinct. The anatomy of the family was studied in some detail and various authors, partly using anatomical criteria, expressed diverse views on the rank, circumscription and relationships of the group (see §5).

At the outset of this study the following genera were widely upheld as members of the Chrysobalanaceae, although divergent opinions were current as to the limits of some and the correct placing of others: *Acioa*, *Afrolicania*, *Angelesia*, *Chrysobalanus*, *Couepia*, *Grangeria*, *Hirtella*, *Licania*, *Magnistipula*, *Moquilea*, *Parastemon*, *Parinari* and *Stylobasium*. This list, except for the inclusion of *Magnistipula* in *Hirtella*, exactly corresponds to Hutchinson's generic concepts as given in his *Genera of flowering plants* (1964).

Prance's original study was based on complete material of about 200 of the 450 or so species of Chrysobalanaceae that we accept today and incomplete material of about 150 others. It was not supported by personal fieldwork. Observations were also made on the pollen grains of all genera, the wood anatomy of all genera except *Hunga* and *Kostermanthus*, and on the seedlings of 26 species.

The following were the principal conclusions.

(i) Chrysobalanaceae is distinct from Rosaceae. There is no evidence for a close relationship between them. For convenience, however, Chrysobalanaceae should be retained in Rosales until unequivocal evidence for a closer relationship elsewhere is forthcoming.

(ii) The true *Lecostemon* is a *Sloanea* (Elaeocarpaceae), and *Rhabdodendron*, to which the 'chrysobalanaceous' Sloaneas had been transferred, is sufficiently distinct to merit recognition at family rank (Prance 1968*a*).

(iii) *Stylobasium* does not belong to Chrysobalanaceae and Agardh's family Stylobasiaceae should be restored (Prance 1965).

(iv) *Angelesia*, *Geobalanus* and *Moquilea* should be merged with *Licania*.

(v) *Magnistipula* is distinct from *Hirtella*, with which it had been persistently confused.

(vi) *Parinari* should be dismembered into the following segregate genera: *Parinari* sensu stricto, *Bafodeya* Prance (in White 1976*a*), '*Cyclandrophora*' Hassk. (now *Atuna* Rafinesque), *Exellodendron* Prance (1972), *Hunga* Pancher ex Prance (1979*c*), *Kostermanthus* Prance (1979*c*), *Maranthes* Blume and *Neocarya* Prance (in White 1976*a*).

The above-mentioned new ideas on generic delimitation have not been previously published *in toto* except very briefly in a paper (Prance *et al.* 1969) which provided evidence for their objectivity based on taximetric analysis (see §10*b*).

After the completion of the original study both authors found opportunities for extensive travel in the tropics: G.T.P. in America, Fiji and Australia, and F.W. in Africa and Mexico. This has led to revisions of the family at the specific level (Prance 1972; White 1976*a*) for Africa and the Neotropics and to deeper insights into the family as a whole.

There are many more species of Chrysobalanaceae in the American tropics than in the Palaeotropics; the former are still botanically underexplored. Continuing exploration has resulted in the discovery and description of 40 new species since the completion of Prance's (1972) monograph of *Flora neotropica*. They are listed in table 1. The Asiatic species are less well

TABLE 1. NEW SPECIES OF NEOTROPICAL CHRYSOBALANACEAE DESCRIBED AFTER THE PUBLICATION OF THE *FLORA NEOTROPICA* MONOGRAPH (PRANCE 1972)

species	locality	date of type collection
Acioa edulis Prance (1973*a*)	Brazil: Amazonas	1971
Couepia bernardii Prance (1981)	Peru: Loreto	1974
C. cidiana Prance (1983*a*)	Brazil: Pará	1980
C. dolichopoda Prance (1974*b*)	Peru: Loreto	1972
C. glabra Prance (1973*a*)	Brazil: Amazonas	1971
C. longipetiolata Prance (1979*e*)	Brazil: Bahia	1975
C. marleneae Prance (1974*a*)	Brazil: Amazonas	1972
C. nutans Prance (1979*d*)	Colombia: El Valle	1973
Hirtella arenosa Prance (1976*a*)	Brazil: Amazonas	1968
H. barnebyi Prance (1981)	Brazil: Rondônia	1975
H. conduplicata Prance (1976*a*)	Brazil: Amazonas	1973
H. confertiflora Prance (1981)	Venezuela: Amazonas	1979
H. magnifolia Prance (1979*a*)	Brazil: Amazonas	1976
H. parviunguis Prance (1979*e*)	Brazil: Bahia	1979
H. radamii Prance (1983*a*)	Brazil: Rondônia	1975
H. revillae Prance (1979*a*)	Peru: Loreto	1975
H. santosii Prance (1979*e*)	Brazil: Bahia	1968
Licania anneae Prance (1979*d*)	Brazil: Pará	1977
L. aracaensis Prance (1976*a*)	Brazil: Amazonas	1975
L. cabrerae Prance (1976*a*)	Colombia: Antioquia	1957
L. cecidiophora Prance (in Berlin & Prance 1978)	Peru: Amazonas	1974
L. chiriquensis Prance (1977*a*)	Panama: Chiriqui	1975
L. cuatrecasasii Prance (1979*a*)	Colombia: Valle	1972
L. fasciculata Prance (1979*a*)	Panama	1972
L. furfuracea Prance (1976)	Venezuela: Bolívar	1975
L. guatemalensis Lundell (1974)	Guatemala	1971
L. harlingii Prance (1979*b*)	Ecuador: Napo	1969
L. jefensis Prance (1976*a*)	Panama	1969
L. jimenezii Prance (1973*a*)	Suriname	1971
L. joseramosii Prance (1979*a*)	Brazil: Amazonas	1976
L. kallunkiae Prance (1979*a*)	Panama	1976
L. marleneae Prance (1976*a*)	Brazil: Amazonas	1972
L. mexicana Lundell (1974)	Mexico: Sinaloa	1943
L. miltonii Prance (1983*a*)	Brazil: Mato Grosso	1979
L. montana Prance (1976*a*)	Venezuela: Lara	1975
L. morii Prance (1976*a*)	Panama	1975
L. pakaraimensis Prance (1976*a*)	Venezuela: Bolívar	1973
L. santosii Prance (1979*e*)	Brazil: Bahia	1968
L. stewardii Prance (1976*a*)	Brazil: Amazonas	1974
L. tocantina Prance (1983*a*)	Brazil: Pará	1969

known than those from elsewhere and studies of the living plant are badly needed. The revisions by Kostermans (1965*a–d*) of *Parinari* and some of its segregates, however, provide a useful base. Kostermans (1985) has also recently published two new Chrysobalanaceae from New Guinea.

Continuing study of the group by ourselves and others during the past 20 years has led to the following conclusions.

(i) *Afrolicania* should be demoted to subgeneric rank in *Licania* (White & Prance in Letouzey & White 1978*a*, *b*).

(ii) *Dactyladenia* should be resurrected to accommodate the African species of *Acioa* (Prance & White 1979).

(iii) *Magnistipula* is sufficiently diverse to justify the recognition of three subgenera, one of which is further divided into three sections (White 1979).

(iv) The correct name for *Cylandrophora* is *Atuna* Raf. (Kostermans 1969).

(v) *Maranthes* occurs in the Neotropics as well as in the Palaeotropics (Prance 1968*b*; Prance & White 1985).

(vi) In addition to traditional taxonomic characters, there are frequently available syndromes of many characters, which though individually small and rarely absolutely diagnostic, are extremely well correlated and collectively provide highly diagnostic criteria for generic delimitation.

(vii) The syndromes are functional and are of vital importance to the plant. They determine, for instance, the precise way in which nectar and stigmatic and polliniferous surfaces are presented, both in space and time, to potential vectors, and the means of seed protection and dispersal, and of seedling release from the endocarp. Although syndromes can often be detected in the herbarium, they can only be fully understood by study of the living plant in its natural environment. Without fieldwork some would remain undetected for ever.

(viii) The Chrysobalanaceae are still actively evolving. *Inter alia* they document the origin of myrmecophilous adaptations, the transformation of growth form in relation to unfavourable growth conditions, and stages in the origin of sea-dispersed obligate halophytes.

(ix) Some taxonomic problems remain unresolved for want of adequate material. Major deficiencies are indicated in the text. We believe, however, that significant progress will depend more on comparative studies of structure and development in relation to function. We are unlikely to have a more complete picture of relationships and the way in which structures have evolved until studies such as those by Goulding (1980) on dispersal of seeds by fishes in Amazonia, or by C. M. Pannell (Pannell & Kozioł 1987) on dispersal by birds and mammals in Malaya and Sumatra, have been extended to other parts of the tropics. There is also room for detailed and comprehensive studies of all the Chrysobalanaceae growing in limited areas, such as that recently completed by de Souza (1979*a*) for Bénin.

3. Morphology

All species of Chrysobalanaceae are woody and most are trees or treelets. All are leptocaul. Several, including species of *Atuna*, *Kostermanthus*, *Licania*, *Magnistipula*, *Maranthes* and *Parinari*, exceed a height of 30 m and are important constituents of the upper canopy of tropical rain forest or emerge from it. Most species are erect, but a few species of *Dactyladenia* and *Hirtella* are scandent, although lacking special adaptations for climbing. *Neocarya macrophylla* often occurs in wind-trimmed littoral thickets as short-boled deformed individuals 3–5 m tall (A. Raynal 1963). In *Maranthes sanagensis*, which grows on the rocky banks of fast-flowing rivers, the short bole and branches are often prostrate and twisted (White 1976*a*).

In the savanna species *Parinari curatellifolia* the tap root fails to develop. The main roots radiate from the bole near the surface of the soil and frequently produce sucker shoots, which develop into mature trees producing colonies with the appearance of an orchard. According to de Souza (1979*a*) regeneration is principally by this means. *Maranthes polyandra* also reproduces by suckers, although less prolifically.

Six species belonging to *Licania*, *Magnistipula* and *Parinari* are geoxylic suffrutices with massive woody underground parts, but rather exiguous aerial shoots which are capable of only limited upward growth (see §§9*c* and 11*b*).

In their architecture and growth dynamics those Chrysobalanaceae that have been studied exhibit the model of Troll (Hallé & Oldeman 1975; Hallé *et al.* 1978; de Souza 1979*a*). This has been demonstrated for *Chrysobalanus icaco*, *Couepia guianensis* (cf. *versicolor*), *Dactyladenia* spp., *Hirtella glandulosa* (*H. velutina*), *H. physophora* (*H. cauliflora*), *Maranthes polyandra*, *M. robusta*, *Parinari congensis*, *P. curatellifolia* and *P. excelsa*. In this model the axes are all plagiotropic and the architecture is built up by their continual superposition. The main-line axes contribute partly to the trunk and partly to the branches. Growth in height is effected by the ability of the basal part of each shoot to assume an erect position, after leaf-loss, by secondary growth. This method of growth can produce trees as tall as *Parinari excelsa* and *P. rodolphii* (40 m).

Within a single species, *Chrysobalanus icaco*, there is a wide range of growth forms based on the same fundamental pattern of morphogenesis (de Souza 1979*a*). Subsp. *atacorensis* is always a tree, whereas subsp. *icaco* may be a small tree with a twisted trunk, or a wind-trimmed, thicket-forming shrub. In the most exposed places it is a low prostrate chamaephyte. The apical meristem inhibits the development of lateral shoots, but in exposed situations on the littoral it is soon destroyed by exposure to intense insolation, sea-spray and wind-blown sand. In extremely exposed open communities ('*pelouse littorale*') many shoots have only a few internodes and the plant assumes the habit of a mat-forming chamaephyte made up of mainly short, zig-zag, plagiotropic axes. In denser thickets, where it is partly protected by other species, the principal shoots grow longer before their apical meristems are destroyed, but on the exposed side of the thicket the shoots are shorter. Hence the shape of the plant is asymmetric, being taller on the sheltered side and gradually sloping towards the sea. *C. icaco* exhibits a similar morphological variation in its neotropical sand-dune habitats.

In *Parinari excelsa* the orthotropic phase of the seedling is marked by small, spirally inserted leaves, which contrast with the distichous larger leaves of the plagiotropic phase.

Herbarium specimens of *Atuna* show a distinct pattern of branching (figure 34, p. 131) but this would be difficult to describe except in terms of development based on the living plant.

Little information is available on the bark of Chrysobalanaceae, but several species of the cerrado of Central Brazil (e.g. *Couepia grandiflora*, *Hirtella ciliata*) have a thick, corky, fire-resistant bark typical of that fire-adapted savanna region.

Buttresses are normally absent but are frequently well developed in *Parinari excelsa*, *P. hypochrysea* and *P. rodolphii*. They are also sometimes present in *P. congensis*, the trunk of which sometimes (G. Gilbert, personal communication in White 1976*a*) supports a girdle of adventitious roots which function as pneumatophores. This feature, however, does not occur throughout the range of the species (White 1976*a*; de Souza 1979*a*). Pneumatophores also occur in the American species *Licania heteromorpha* when it grows in seasonally flooded areas, and stilt roots also occur in the same species.

Magnistipula bimarsupiata has hollow internodes with a perforation at the base, possibly a myrmecophilous feature.

The buds of many species are naked, but large, conspicuous bud-scales are present in some species of *Couepia* and *Parinari*. All five species from Bénin studied by de Souza (1979*a*) have small buds protected by scales. In the savanna species *Maranthes polyandra* and *Parinari curatellifolia* dormant buds become embedded in cork as the periderm develops. They emerge as shoots after fires, which destroy the younger growth.

The leaves, which are always simple, are spirally inserted, but are frequently arranged distichously. Most species have stiff, coriaceous, evergreen leaves which contain abundant silica inclusions.

Stipules are nearly always present but are sometimes small and caducous. According to de Souza (1979*a*) they are absent in *Chrysobalanus icaco*, which has, however, a trilacunar node. In some species of *Parinari* the stipules reach a length of 7 cm. In *Atuna* they are prominently keeled, a unique feature in the family. Intrapetiolar stipules occur in *Maranthes* and some species of *Licania* and *Magnistipula*. In other species of *Magnistipula* and in *Licania latistipula* the stipules are lateral and foliaceous. In *M. zenkeri* they are sometimes up to 4.5 cm long and are inflated.

The lamina is nearly always entire, but in *Maranthes aubrevillei*, the margin, especially on young plants, is denticulate. *Licania michauxii*, alone in the family, has a crenulate margin. Venation pattern and indumentum provide useful secondary characters of classificatory importance but have not yet been studied in detail; hence the precise terminologies of Hickey (1973) and Payne (1978) have not been consistently employed in this work. In *Bafodeya*, *Neocarya*, nearly all species of *Parinari*, and a few species of *Licania*, the veins on the lower surface are extremely prominent and form a dense network occupying more than half of the leaf surface so that the stomata are confined to relatively small sunken crypts, which are densely filled with short curly hairs. There is an erroneous record (Kuster 1897; Metcalfe & Chalk 1950) of stellate hairs (in *Chrysobalanus*) but in fact the foliar hairs are always simple (Prance 1972, p. 43). In *Couepia*, *Exellodendron* and *Maranthes* they are long, thin-walled, flexuose and arachnoid, and form a web-like covering on the leaves. By contrast, in *Hirtella*, *Magnistipula* and most species of *Dactyladenia* they are straight and stiff and strigose or setose. Some distinctive hair types and other surface features of the lower surface are shown in figure 1.

Foliar glands occur in most, possibly all, species. They secrete nectar which is eaten by ants (see §8*g*), and function chiefly on young leaves. Hence on mature leaves of herbarium specimens they are not always clearly visible. Their structure and distribution on the leaf varies greatly from genus to genus and provide characters of considerable taxonomic importance. Small discoid glands occur in various places on the lower surface or margins of the lamina in *Exellodendron*, *Grangeria*, *Hirtella*, *Neocarya* and *Parastemon*. There are larger, sometimes ill-defined, glandular areas towards the base of the lamina in *Acioa*, *Chrysobalanus*, *Dactyladenia* and *Maranthes*. In *Parinari* and some species of *Licania* and *Couepia* conspicuous glands occur on the petiole. Figure 2 illustrates the range of foliar glands found in the family. The anatomy of the glands in *Chrysobalanus* is described by de Souza (1979*a*).

In seven species of *Hirtella* a pair of conspicuous pouches at the base of the lamina provide

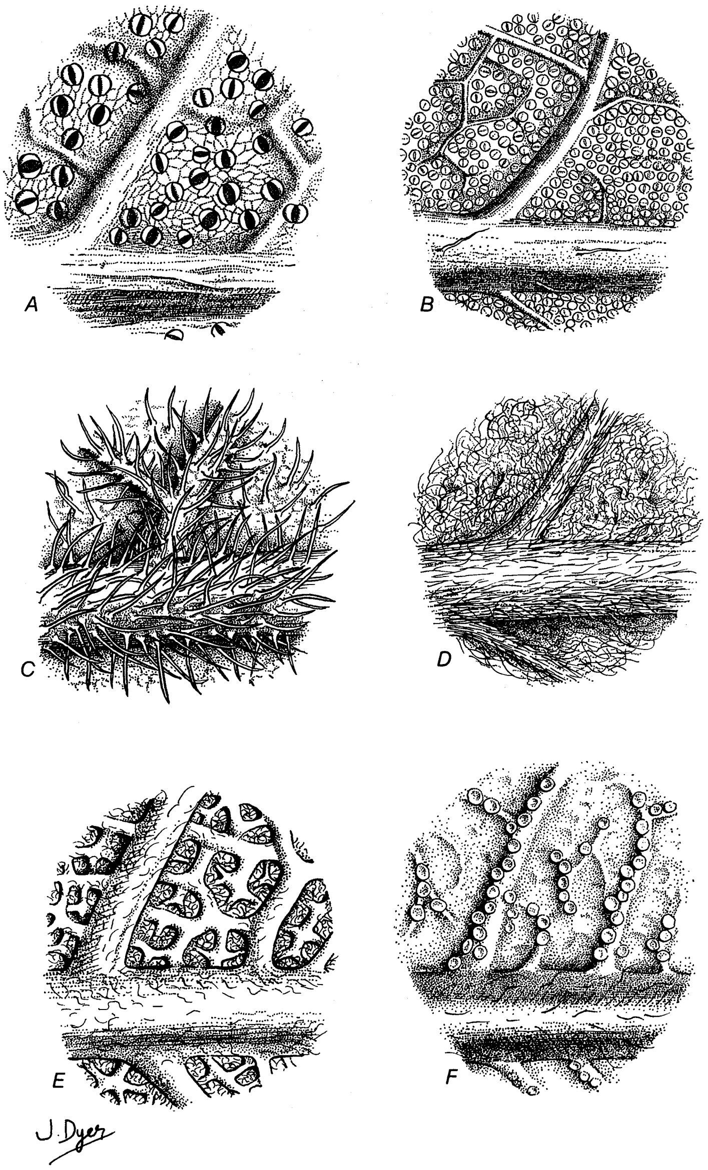

Figure 1. Leaf undersurface (magn. × 50): A, *Hunga minutiflora* (Franc 2029); B, *Licania michauxii* (Nash 734); C, *Hirtella americana* (Shafer 11718); D, *Couepia uiti* (Burchell 7665); E, *Parinari excelsa* (Riedel 1667); F, *Atuna excelsa* (Elmer 2150).

a nesting place for ants. It is believed that similar inflations in *Magnistipula bimarsupiata* have the same function.

The inflorescence is very variable and is of considerable taxonomic importance, but this is obscured when it is described in conventional terms. In *Chrysobalanus* the few-flowered inflorescence is a short raceme of cymules or is cymose throughout, or is a false raceme or a subsessile fascicle. Its structure and development are described in detail by de Souza (1979*a*). In *Dactyladenia*, *Grangeria* and *Parastemon* the inflorescence is a simple or branched raceme which in some cases shows evidence of a cymose origin. *Exellodendron*, *Hunga* and *Neocarya* are characterized by simple or branched racemes of usually congested cymules. More complex

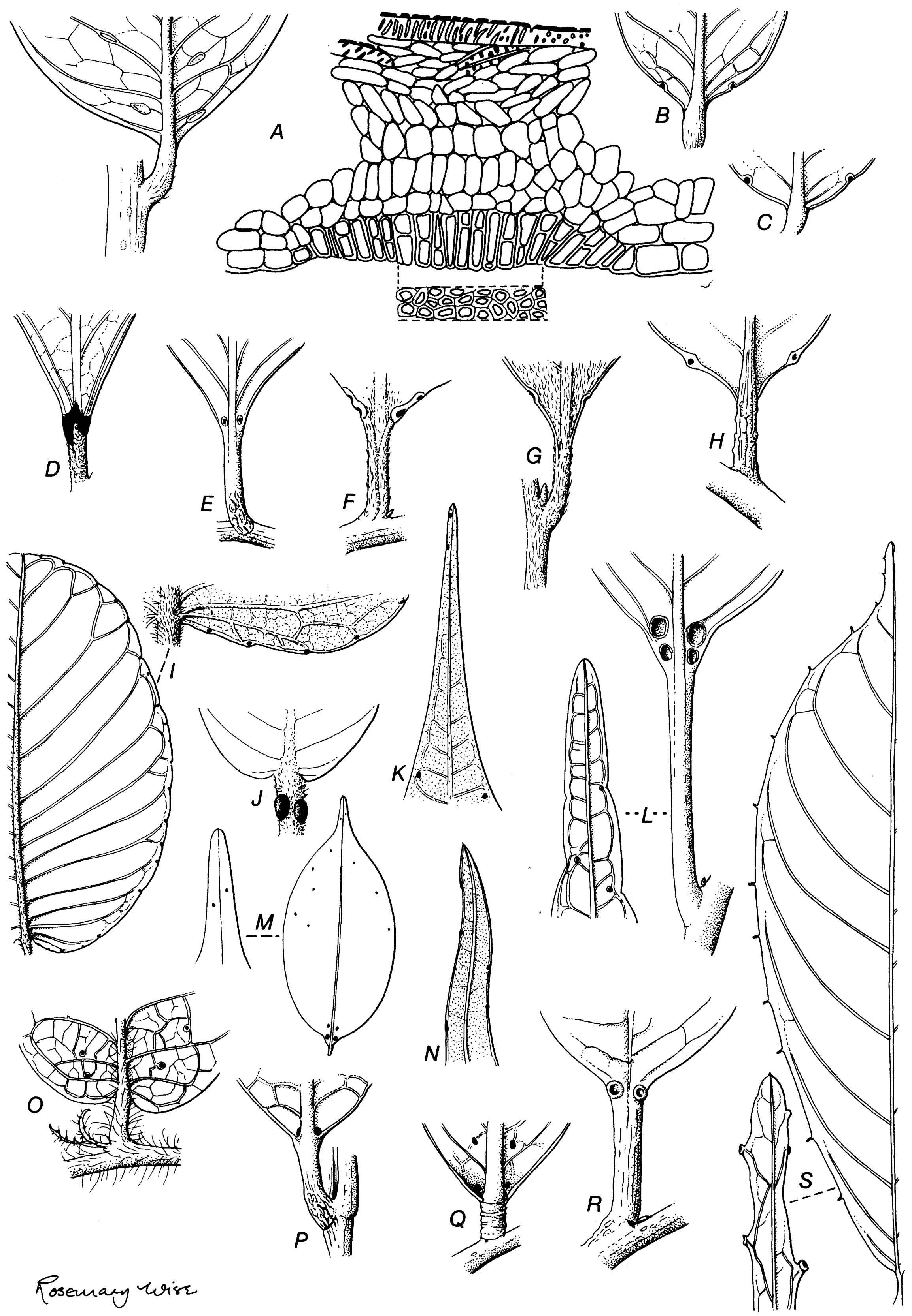

FIGURE 2. Foliar glands. A, *Chrysobalanus icaco* subsp. *icaco*, base of lamina (× 2; F. White 8257) and TS of gland (× 40 (after de Souza 1979)); B, *Grangeria borbonica* (× 2, 'comm. Hooker'); C, *G. porosa* (× 2, Decary 8182); D, *Licania elaeosperma* (× 2, Ainslie 8); E, *Parastemon urophyllus* (× 2, BNBFD 2799); F, *Exellodendron coriaceum* (× 2, Maguire *et al.* 31019); G, *Hunga gerontogea* (× 2, McKee 13564; H, *H. minutiflora* (× 2, McKee 17821); I, *Neocarya macrophylla* (× $\frac{2}{3}$ and × 2, L. P. White 59); J, *Parinari congensis* (× 2, Vermoesen); K, *P. hypochrysea* (× 2, Oakfor FHI 39364); L, *Acioa edulis*, apex of seedling leaf (× 2, Prance 13) and base of mature leaf (× 2, Ramos P 23251); M, *Couepia longipendula* (× $\frac{2}{3}$ and × 2, Prance *et al.* 22622); N, *C. leptostachya* (× 2, Prance *et al.* 9038); O, *Hirtella glandistipula* (× 2, Prance & Silva 58944); P, *Atuna excelsa* (× 2, Symington FD 23343); Q, *Dactyladenia barteri* (× 2, Kennedy 3148); R, *Maranthes chrysophylla* (× 2, Cooper 232); S, *M. aubrevillei* (× $\frac{2}{3}$ and × 2, Hall & Enti GC 38405).

mixed inflorescences with cymose ultimate units are found in *Acioa*, *Bafodeya*, *Couepia*, *Kostermanthus* and *Parinari*. Within each of the genera *Hirtella*, *Licania*, *Magnistipula* and *Maranthes* the range of structure is so great that a succinct designation is not possible. Cauline inflorescences occur in a few species of *Licania* (*L. velata*) and in *Couepia maguirei*.

The inflorescence is fasciculate in two myrmecophilous species of *Hirtella* (*H. myrmecophila* and *H. physophora*) and also in *H. fasciculata* and *Licania fasciculata*.

In the course of our work it became apparent that nearly every genus is unique in the architecture of its inflorescence, but that conventional terminology, even when carefully redefined as by Ricket (1944), is inadequate. Most species could probably be placed in their correct genus by using inflorescence characters alone, especially if it were possible to describe the inflorescence in terms of its development and the precise way in which its individual flowers are distributed in space and time in relation to the size, structure and behaviour of their pollen vectors. For most species information from the living plant is not available. Nevertheless, by means of line drawings based on herbarium specimens, the taxonomic value of the inflorescence can be shown, as figures 3, 4 and 18, illustrating *Couepia*, *Hirtella* and *Licania* respectively, bear witness. Using conventional terms the inflorescences of both *Couepia* and *Hirtella* are often described as panicles. Figures 3 and 4 show, that, notwithstanding the wide range of variation within each, the inflorescences of the two genera can scarcely be confused (see also §6*e*). *Licania* is equally distinct. Species of *Licania* can usually be identified to their genus at a glance. It is the inflorescence which contributes most to the visual impression and so makes this possible.

Because the inflorescence is usually cymose, at least in part, a distinction between bract and bracteole cannot always be drawn. Bracts and bracteoles are usually small but in nearly all species of *Parinari* and a few species of *Couepia* and *Licania* they are relatively large and enclose small groups of developing flowers. Most Chrysobalanaceae have eglandular bracts and bracteoles but in several species of *Dactyladenia* and *Hirtella*, and a few of *Licania* and *Magnistipula*, they are glandular. In *Grangeria* the minute bracts and bracteoles have a single apical gland.

In most species the flowers appear to be bisexual, but future fieldwork may show that this is not always so. Herbarium specimens of *Licania elaeosperma* appear to have unisexual flowers. *Parastemon urophyllus* is said to be polygamodioecious. Lack (1978) has observed that in the bat-pollinated species *Maranthes polyandra* some flowers which have short styles drop off soon after the night of opening and may be functionally male. In most, possibly all, Chrysobalanaceae, some flowers are shed after meristematic activity leading to a well-defined articulation. The precise details in relation to a possible mechanism which resolves the conflicting needs of adequate seed-set and floral display, such as that postulated by Stephenson (1979) for *Catalpa speciosa*, remain to be studied. The 'upper pedicel', above the articulation, is usually well differentiated from the (usually hollow) receptacle tube. In relatively few species is there a gradual transition. In *Magnistipula zenkeri* the persistent pedicels are said to develop an orbicular gland which functions as an extrafloral nectary (Chevalier 1931).

Flower size and shape vary within wide limits, from the minute, patelliform flowers of *Licania elaeosperma*, which are scarcely larger than a pin's head, to the tubular flowers of *Maranthes gabunensis*, more than 10 cm in length. In addition to the gross structural features described below, there are many subtle differences between genera in the proportions and spatial arrangements of the flowers. Although more difficult to describe than orthodox floral characters they are no less useful for classification and identification. Such differences operate

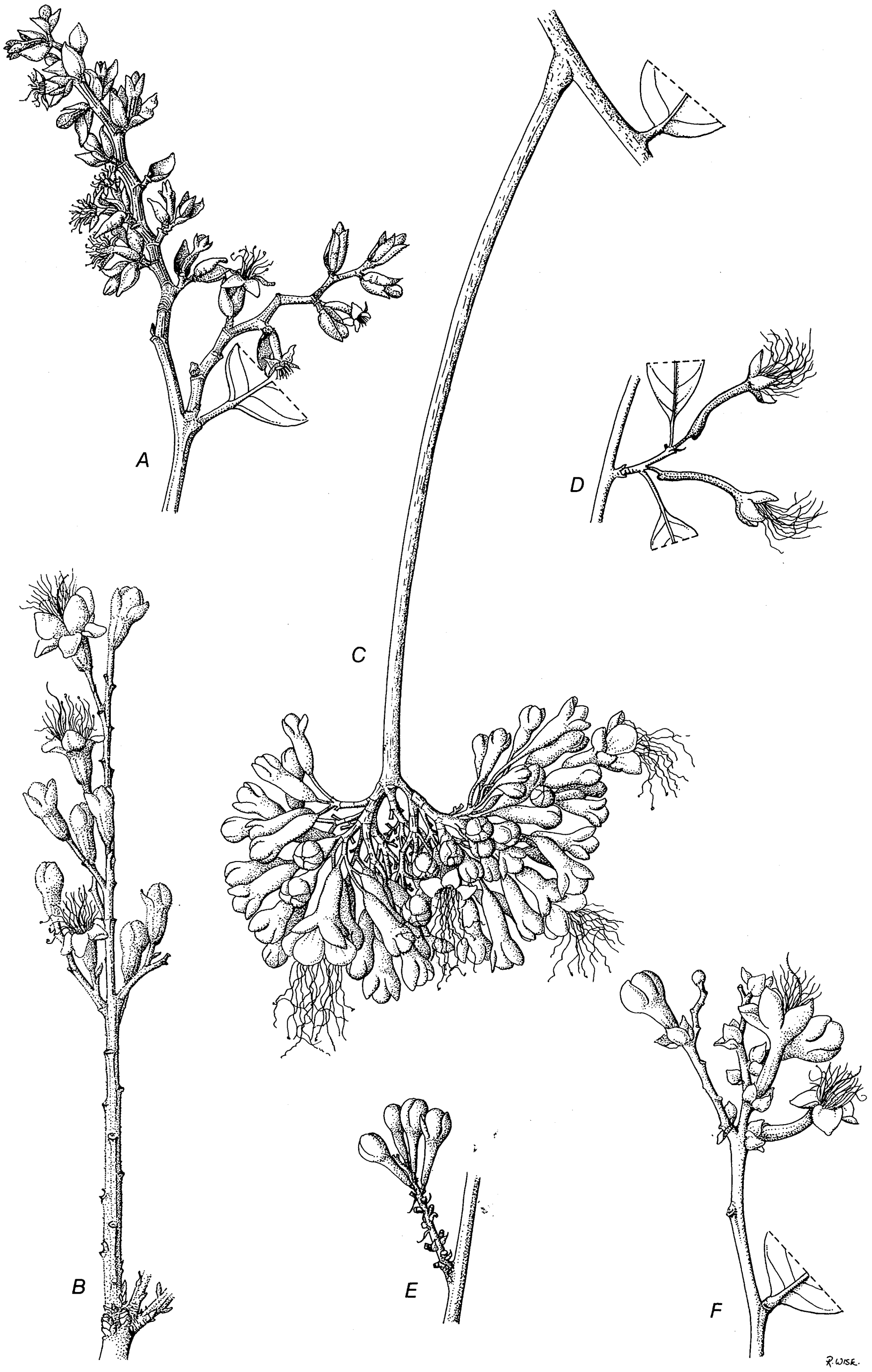

FIGURE 3. *Couepia* inflorescence ($\times\frac{1}{2}$): A, *C. bracteosa* (Silva 59733); B, *C. grandiflora* (Prance & Silva 59043); C, *C. longipendula* (Prance *et al.* 16143); D, *C. parillo* (Silva 1130); E, *C. chrysocalyx* (Prance *et al.* 12079); F, *C. latifolia* (Prance *et al.* 2339).

at both the generic and specific level. Syndromes of such generic characters are described elsewhere in some detail for *Couepia* and *Hirtella* (see §§6*e* and 10*c* and Appendixes 1 and 2). Other genera have not yet been studied in comparable detail. Such work should preferably be done on living material in relation to the behaviour of the pollinating agents. Figures 33 and

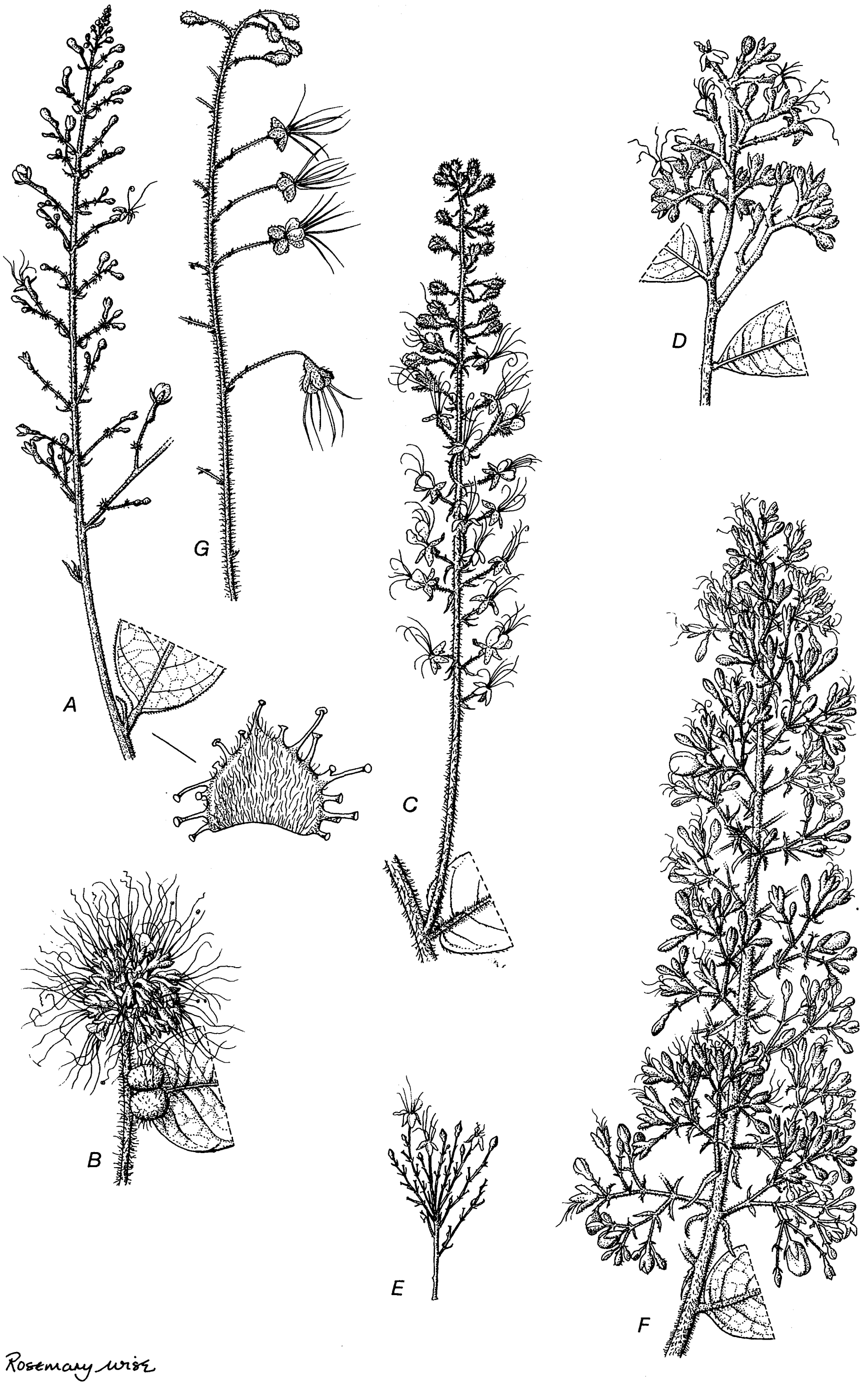

FIGURE 4. *Hirtella* inflorescence ($\times\frac{1}{2}$): A, *H. glandulosa* (Irwin *et al.* 16435; bract × 10); B, *H. myrmecophila* (Prance *et al.* 2201); C, *H. paniculata* (Maguire 35183); D, *H. obidensis* (FD 2166); E, *H. punctillata* (Pires & Cavalcante 52191); F, *H. hoehnii* (Maguire *et al.* 56442); G, *H. angustifolia* (Pohl 4370).

43 show that the species in *Magnistipula* and *Maranthes* are subtly different in size and proportion of the flower, although otherwise the flowers in each genus are remarkably uniform.

Floral symmetry varies from almost completely actinomorphic, apart from the lateral style, in *Chrysobalanus*, *Parastemon* and most species of *Licania*, to strongly zygomorphic in *Kostermanthus*. Actinomorphic flowers are patelliform or shallowly cupuliform, and zygomorphic flowers usually have a long receptacle-tube, but in *Kostermanthus*, *Neocarya*, *Magnistipula cerebriformis* and *M. tamenaka* the strongly zygomorphic flowers have a very short receptacle. *Couepia platycalyx* is anomalous in its genus in having a solid receptacle-tube which is shorter than the calyx. In the Chrysobalanaceae the receptacle-surface is always lined with nectar-secreting tissue, which sometimes, as in many species of *Maranthes*, almost completely fills the tube. In most genera the entrance to the receptacle tube is blocked by long straight retrorse hairs, but these are lacking in *Kostermanthus* and *Magnistipula* subgenus *Tolmiella*. In *Chrysobalanus*, *Licania* (except *L. licaniiflora*) and *Parastemon* the nectariferous lining of the receptacle is freely exposed. In *Grangeria* the dense woolly indumentum of the ovary conceals the nectar. The receptacle-tube is saccate in *Neocarya*, slightly gibbous in some species of *Dactyladenia* and *Hirtella*, and more strongly gibbous in some species of *Magnistipula*.

There are always five, completely free, slightly to strongly imbricate sepals, which vary from subequal in *Chrysobalanus* to markedly unequal in *Acioa*. In most genera they are acute or subacute but in *Acioa*, *Kostermanthus* and *Maranthes* they are suborbicular and deeply concave. In several species of *Dactyladenia* and *Hirtella* the calyx is provided with stalked or sessile marginal glands, and in *Acioa* and a few species of *Couepia* there are one or more discoid glands on the surface of some sepals.

Petals are absent in more than half of the species of *Licania*. Otherwise there are always five. They are mostly caducous. In shape they vary from linear-spathulate (*Chrysobalanus*) to orbicular (*Couepia* spp). They are usually subequal, but in *Kostermanthus* they are very unequal in shape and size and are strongly unguiculate; they are also unguiculate in *Hirtella parviunguis*, *Licania unguiculata* and *L. longipetala*.

Stamens vary in number from two in *Parastemon urophyllus* to more than 300 in some species of *Couepia*. In *Chrysobalanus*, *Grangeria borbonica*, most species of *Licania*, *Parastemon versteeghii*, *Couepia* and *Maranthes* they form a complete or almost complete circle round the entrance to the flower and all or most are fertile. Otherwise the fertile stamens are inserted unilaterally opposite the carpel. Staminodes are frequently present opposite the style. In several genera the filaments appear to be united at the base, but it is sometimes difficult to decide whether this represents true union or whether the filaments are free but inserted on a development of a receptacular rim. In most species of *Couepia* and *Maranthes* the stamens are inserted in two or more rows on the outer surface of what appears to be a receptacular faucal annulus. In length the filaments vary from much shorter than the calyx, as in *Hunga*, *Parastemon* and some species of *Licania*, to very much longer in *Dactyladenia* and *Hirtella*. In *Dactyladenia*, *Kostermanthus* and all but one species of *Acioa* the filaments are united for at least half of their length to form a conspicuous ligule. In those genera with far-exserted stamens the filaments are either spirally coiled in the bud (*Dactyladenia*, *Hirtella*) or undulate (*Couepia*, *Maranthes*).

The gynoecium is fundamentally composed of three carpels, which are free except for the gynobasic style. In most species there is only one functional carpel, though one or two small rudimentary carpels can sometimes be seen (see §4*c*). Two or three functional carpels occur sporadically in about half the genera. Owing to the development of a false dissepiment the ovary is bilocular in *Bafodeya*, *Exellodendron*, *Hunga*, *Neocarya*, *Parinari*, *Maranthes*, *Atuna* and *Magnistipula* subgenus *Pellegriniella*. In *Couepia grandiflora* there is sometimes a trace of a false dissepiment.

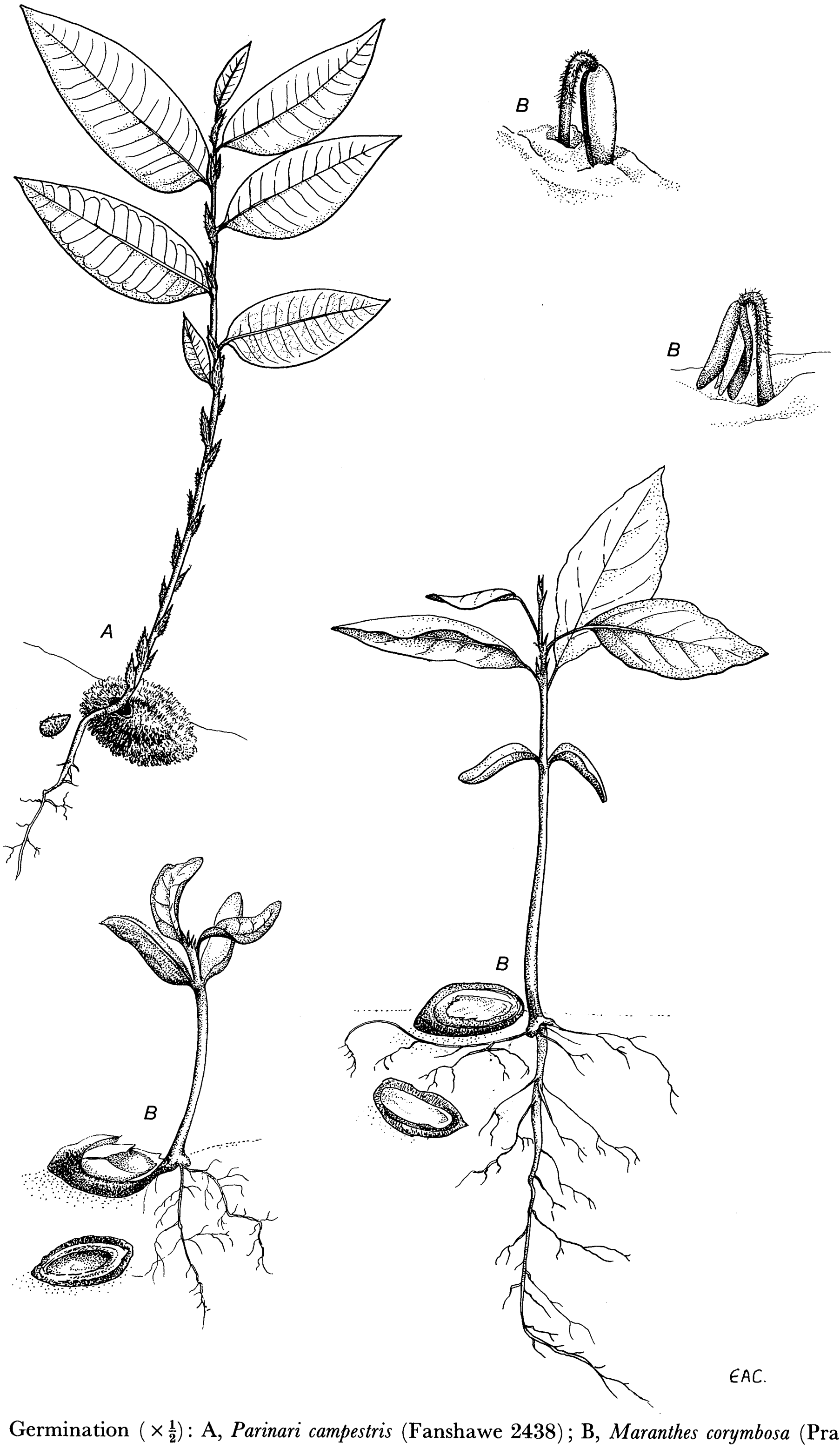

FIGURE 5. Germination ($\times \frac{1}{2}$): A, *Parinari campestris* (Fanshawe 2438); B, *Maranthes corymbosa* (Prance 1203).

To facilitate comparison the drawings of the half-flowers are standardized as if the cut surface went exactly through the median axis of the odd sepal and the ovary. In fact, because the inflorescence is cymose and there is some variation in the gynoecium, this is not always the case. Where the terms posterior and anterior are used, the former refers to the odd sepal, although this is not necessarily correct.

The fruit is basically a drupe but there is considerable variation in detail, apparently associated with dispersal and germination. There are no detailed studies, however, on dispersal, and germination has been studied for only a few species, and then not in the wild. There can be little doubt that a developmental and anatomical study of the fruit and seed carried out in conjunction with field studies would be very rewarding.

In *Chrysobalanus*, *Grangeria*, *Parastemon*, *Hunga* and *Hirtella*, especially the latter, the endocarp has a smooth surface and is sharply differentiated from the mesocarp (but see §6*e*). In the other genera the differentiation is less well defined. In some species of *Couepia* the pericarp is more or less sclerenchymatous throughout, but with some differentiation between outer and inner layers.

In *Chrysobalanus*, *Hunga* and *Hirtella*, seedling escape is effected by means of longitudinal lines of weakness. In *Grangeria*, *Parastemon* and *Maranthes*, two large lateral plates fall away, permitting the seedling to emerge. In *Neocarya* and *Parinari* there are two small basal 'plugs' or obturators. All other genera seem to lack specialized means of seedling escape.

Germination has been studied in 12 genera. The results confirm Léonard's (1957) observation that blastogeny provides useful taxonomic characters, especially for generic delimitation. In *Chrysobalanus*, *Licania*, *Parastemon*, *Neocarya*, *Parinari*, *Couepia*, *Atuna*, *Dactyladenia*, *Hirtella* and *Magnistipula* germination is cryptocotylar, whereas in *Acioa* and *Maranthes*† it is phanerocotylar (according to the terminology of Duke (1965, 1969)). Cataphylls are present in *Chrysobalanus*, *Parinari*, *Couepia* and *Hirtella*. The first eophylls are alternate in *Chrysobalanus*, *Licania*, *Neocarya*, *Parinari*, *Couepia*, *Atuna* and *Hirtella*. They are opposite in *Parastemon*, *Acioa*, *Maranthes* and *Dactyladenia*, whereas in *Magnistipula* they are either opposite or in fours. Figure 5 illustrates the very different seedlings of *Maranthes* and *Parinari*, two genera which until recently have usually been united.

4. ANATOMY, ULTRASTRUCTURE, CHROMOSOME CYTOLOGY, CHEMISTRY

(*a*) *Introduction*

During the past hundred years, several works have been published on the anatomy of the Chrysobalanaceae. Many are of considerable taxonomic importance, but for the most part have been ignored by, or were unknown to, English-speaking botanists. Particularly important are papers by Küster (1897) on the anatomy of the leaf and primary stem, Juel (1915) on the structure of the gynoecium, Morvillez (1918*a*) on leaf-trace anatomy, and Bonne (1926, 1928) on the anatomy of the flower and pedicel. A short paper by Dalziel (1931) draws attention to the taxonomic value of the hairs lining the endocarp of the fruit. In a recent publication, de Souza (1979*a*) has described in considerable detail the anatomy of the five indigenous species of Bénin, West Africa. Tobe & Raven (1984) have given the first modern account of the embryology of a few species of the tribe Chrysobalaneae.

No single author appears to have made a comprehensive study of the anatomy of the

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† In *M. polyandra*, however, the cotyledons do not emerge from the endocarp (de Souza 1979*a*).

secondary xylem. Accounts in general works such as those by Solereder (1899) and Metcalfe & Chalk (1950) are syntheses of the scattered observations of others.

During our study supplementary observations were made for all anatomical features under consideration, except the primary stem, the leaf, and the embryo and seed. The secondary xylem of 72 species representing all genera other than *Hunga* and *Kostermanthus* was examined. The palynological information given by Erdtman (1952) was supplemented by study of 30 species representing all genera of Chysobalanaceae and a selection of species of Rosaceae and other families with which Chrysobalanaceae has sometimes been associated. Details of all source materials are given elsewhere (Prance 1963).

In general, anatomical features proved to be much more useful in the delimitation and diagnosis of the Chrysobalanaceae in relation to other families than in classification below the family level. This is discussed below.

We have not made original observations on the chromosome cytology nor on the chemistry of the group. The literature is summarized at the end of this section.

The ultrastructure of a few species has been described by ter Welle (1975, axial parenchyma; 1976, silica content) and Patel *et al.* (1983, pollen). These studies are insufficiently complete to permit an assessment of the potential usefulness of ultrastructure in the taxonomy of the group.

(*b*) *Primary stem and leaf*

Küster (1897) studied 76 species belonging to 11 genera of Chrysobalanaceae, and three species of *Rhabdodendron* and one each of *Stylobasium* and *Prinsepia*, three genera which are no longer included in the family. He obtained his material from herbarium sheets in the Munich herbarium which one of us (G.T.P.) examined to confirm their generic identity. Küster's detailed study is summarized in tabular form by Prance (1963). Küster himself drew no taxonomic conclusions from his work, but Hallier (1903) cited it as evidence for giving Chrysobalanaceae family rank.

(*c*) *Gynoecium*

The reason why the Chrysobalanaceae has usually been treated as a subfamily of Rosaceae, placed next to Prunoideae, is no doubt largely because of the superficial resemblance in the receptacle and ovary. This similarity is most marked in *Prinsepia* Royle, which has a lateral style, and indeed was placed in Chrysobalanaceae by Lindley (1936) from which it was removed by J. D. Hooker (1865).

In a remarkably thorough study of *Parinari curatellifolia* var. *fruticulosa* (now *P. capensis*) and *P. bangweolensis* (now *Magnistipula butayei* subsp. *bangweolensis*), Juel (1915) showed that the gynoecium of Chrysobalanaceae differs fundamentally from that of true Rosaceae and suggested family rank.

In *Parinari* the style is distinctly three-lobed at the apex, and arises from the receptacle at the base of the carpel. Only one carpel is normally well developed, but careful sectioning revealed two minute rudimentary carpels at the base of the style. The structure of *Magnistipula* is similar, except that in some flowers a second carpel is also fully formed. Juel suggested that the primitive gynoecium of the Chrysobalanaceae consisted of three free carpels united by a gynobasic style, similar to that of a trimerous Limnanthaceae. She did not, however, suggest any relationship to that family, contrary to the statements of Bonne (1926) and Hauman (1951). All the plants examined during the present work have at least a shallowly three-lobed style, and in some the style is deeply lobed. Two or three carpels occur sporadically in flowers of certain species belonging to about half the genera, and in some species of *Maranthes* they represent the normal number.

Juel misinterpreted some details of the ovary of *Prinsepia* but these have been corrected by Sterling (1963), who found *Prinsepia* to be so different from Rosaceae *sensu stricto* that she described a new subfamily to accommodate it.

(*d*) *Leaf-trace anatomy*

Morvillez (1918*a*) showed that the leaf-trace of the Chrysobalanaceae differs from that of Rosaceae in having, at the distal end of the petiole, an abaxial closed ring of xylem and phloem which shows various modifications in different genera and species. He described seven types of modification (see Metcalfe & Chalk 1950). Because he studied relatively few species and there are transitions between his types, his results cannot be used at generic level. He suggested that leaf-trace anatomy in Chrysobalanaceae more closely resembles Caesalpinioideae than Rosaceae and that the group deserves family rank.

(*e*) *Vascular anatomy of the flower and pedicel*

Bonne (1928) described a wide range of genera in Rosaceae including Chrysobalanaceae (summarized by Prance 1963). She showed, and the present work has confirmed, that Chrysobalanaceae differ from Rosaceae *sensu stricto* in the structure of the pedicel and the nature of the vascular supply to the flower. This, according to Bonne, justified their separation.

In most Chrysobalanaceae a constriction is noticeable on the pedicel. Most flowers are caducous but some pedicels are 'subarticular' and the flowers do not fall. These subarticular pedicels bear the fruit.

The articulation is a meristematic region characterized by large amounts of inclusions in the cells. The region below the articulation has the same structure as the axis of the inflorescence; the region above is anatomically distinct and, according to Bonne's terminology, constitutes the true pedicel. A well-defined articulation is not found in Rosaceae but traces are found in the Prunoideae and Sanguisorbeae. It seems that in Chrysobalanaceae those flowers that fail to be fertilized are actively shed not long after anthesis (see §3), and that pedicel anatomy is of more functional than phylogenetic significance.

(*f*) *Hairy lining of the endocarp*

In a brief note Dalziel (1931) showed that three species of '*Parinari*', which we, on other grounds, have assigned to three different genera, have hairs lining the endocarp of fundamentally different types. Thus, in *P. mobola* (now *P. curatellifolia*) the hairs are long, slender and twisted, forming a loose wool almost filling the cavity. In *P. robusta* (now *Maranthes robusta*) they are shorter and twisted and form a velvety lining to the cavity. In *P. benna* (now *Bafodeya benna*) they are perfectly straight, hollow, needle-shaped 'spines' which project stiffly into the cavity. We have found that some other genera are distinctive in this feature. Details are given under these genera in Part II.

(*g*) *Secondary xylem*

The family Chrysobalanaceae is uniform in wood structure. The differences between some genera are no greater than the differences between species in other genera in the family.

Growth rings are often present, marked by periodic wider spacings of parenchyma bands; they may be present or absent in different samples of the same species. *Vessels* are typically exclusively solitary, but occasionally in radial multiples of 2–5 cells, especially in *Dactyladenia*; typically they have an oblique arrangement and are moderately large in most genera; the mean tangential diameter is 200–300 µm; they are always fewer than 20 per square millimetre and fewer than 5 per square millimetre in some species; they are without spiral thickenings; perforations are exclusively simple; intervascular pitting is alternate, never minute; the ray-vessel pits are large and of various shapes, and alternate; tyloses are frequent, especially in *Magnistipula*, *Maranthes* and *Licania*, and are occasionally sclerosed in *Licania*; the mean vessel length is 0.6–0.8 mm. Parenchyma is exclusively apotracheal and abundant, and usually occurs in numerous fine continuous bands one cell (locally two cells) wide; there are 6–11 bands per millimetre; less often the bands are 2–3 cells wide and are less than 6 per millimetre in *Parinari* sensu stricto; the bands are obscure in *Neocarya*; the parenchyma strands are up to 16 cells high; gum deposits are frequent. Spiral thickenings occur in the axial parenchyma of many species. *Rays* are predominantly uniseriate, exclusively so in *Chrysobalanus*, *Exellodendron*, *Grangeria*, *Hirtella* and *Licania* and with biseriate rays in all other genera; rays are never more than 2-seriate, and are commonly more than 1 mm high in *Couepia*, *Parastemon*, *Parinari*, *Maranthes* and *Atuna*; they are usually heterogeneous (Kribs type III) but almost homogeneous in *Parastemon*; gum deposits are abundant; the pits to axial parenchyma are large. *Silica inclusions* are present in the ray cells of all species. *Fibres* are usually thick-walled, but somewhat thinner in *Parinari* and *Neocarya* and in some species of *Licania*; they have numerous distinctly bordered pits on the tangential walls; these pits are more numerous and often biseriate in wider cells bordering vessels; pits on the radial walls are almost entirely limited to areas in contact with the rays; the mean length is 1.3–1.4 mm.

The wood varies from moderately to very hard and is heavy. Specific gravity is 0.75–1.10. It is difficult to saw owing to abundant silica inclusions in the ray cells in all species, and in the parenchyma of a few species. Silica content is summarized by Amos (1952) and described in greater detail by ter Welle (1976), who has also shown (1975) that the axial parenchyma of many Chrysobalanaceae shows spiral thickenings. Spirals have been found in all species examined in *Chrysobalanus*, *Exellodendron* and *Hirtella* and in some species of *Dactyladenia*, *Couepia*, *Atuna*, *Licania* and *Maranthes*. They have not been found in *Parinari* sensu stricto.

The family Chrysobalanaceae differs from Rosaceae in several important features (figure 6, plate 1). These features include the rather infrequent, oblique vessels, the banded parenchyma composed of long strands, the predominantly uniseriate rays, the larger intervascular pitting, and the abundance of silica. Notwithstanding these differences, the secondary xylem of the two families is in many ways similar. In both, the perforations are simple, the parenchyma is usually apotracheal, and the fibre-pits are bordered. The vessels in Rosaceae are typically small (i.e. less than 100 µm diameter), but they may be moderately large in some genera, e.g. *Hagenia* and *Prunus* (*Pygeum*); they may also be partly solitary as in *Eriobotrya*, *Cydonia* and *Malus*, but in these genera they are usually more crowded than in Chrysobalanaceae.

Some authors (e.g. Record & Mell 1924) have united the Chrysobalanoideae and Prunoideae to form the family Amygdalaceae. There is no support for this from wood anatomy, as Record himself (in Record & Hess 1943) pointed out at a later date.

The Prunoideae are distinct in their wood structure from the rest of the Rosaceae as their fibres have less distinctly bordered pits and these are less numerous on the tangential than on the radial walls; in addition their vessels are commonly arranged in an oblique radial pattern in cross section. The Prunoideae is, in fact, the only tribe of the Rosaceae *sensu stricto* that can be distinguished from the others by wood structure. The differences given above are clearly less than those between the Chrysobalanaceae and the Rosaceae. Record & Hess (1943) and Metcalfe & Chalk (1950) point out that the Chrysobalanoideae is distinct enough in wood anatomy to be regarded as a family, and that the affinities of the Prunoideae as judged by wood structure are with other Rosaceae. Metcalfe & Chalk (1950), however, continue to refer to the Chrysobalanaceae as 'Rosaceae–Chrysobalanoideae'.

Because of its uniformity the secondary xylem of Chrysobalanaceae is of little classificatory use below family level. The woods, for instance, of *Chrysobalanus* and *Maranthes*, and of *Licania* and *Parinari* are scarcely different. A few genera, however, appear to have distinctive features; thus *Parastemon* has almost homogeneous rays. The secondary xylem of *Parinari* sensu stricto is extremely uniform. It differs from that of other genera in having wider parenchyma bands, a feature which is constant in the samples examined from all parts of its geographical range. *Exellodendron* is distinguishable from other segregates of *Parinari* by its exclusively uniseriate rays. Similarly, *Neocarya* is distinct in having relatively few vessels, and in its more diffuse and scarcely banded parenchyma.

A few species of *Licania*, including both the Asiatic subgenus *Angelesia* and some American species, are the only Chrysobalanaceae known to have sclerosed tyloses; this observation indicates that these two groups, which are united in this work, are closely related.

(*h*) *Pollen*

The pollen of Chrysobalanaceae is very uniform, but is different from that of Rosaceae. It is of little value for distinguishing between the genera of Chrysobalanaceae or for arranging them in groups, but the pollen of *Rhabdodendron* and *Stylobasium* is so different that it supports their exclusion from the family (Prance 1965, 1968*a*).

Most species have grains with three furrows, but some species have three or four; there are no special features except occasional equatorial constrictions. With light microscopy the pores are indistinct, and in some species are difficult to observe. The grains are usually distinctly triangular in shape in polar view, except when four-furrowed; they are elliptical to circular in equatorial view and are oblate-spheroidal, prolate-spheroidal or subprolate in shape, as indicated by the following ratio: polar length × 100, divided by the equatorial length = 85–150. The size is very variable from one genus to another; the polar area is usually small, sometimes medium, but never large. The exine is medium to rather thick with very little patterning on the walls; it is usually scabrous to verrucose, but never striate.

The pollen of Chrysobalanaceae and Rosaceae is similar but readily distinguishable. The former is markedly triangular in polar view in the expanded grain, whereas in Rosaceae it is never more than weakly triangular. Most Rosaceae have more distinctive pores, and many have more patterning on the walls. A feature that occurs frequently in the Rosaceae is a distinct wedge-shaped protrusion from the middle of the furrow, obvious in polar view, which does not occur in Chrysobalanaceae. Erdtman (1952) states 'pollen morphological objections cannot be raised against regarding the Chrysobalanaceae as a separate family.' Our own study of Rosaceae pollen (*sensu lato*) confirmed that three main types of pollen occur: the Rosaceae *sensu stricto*, the Chrysobalanaceae, and the Neuradoideae types (Prance 1963).

The differences between pollen of Chrysobalanaceae and Rosaceae are, however,

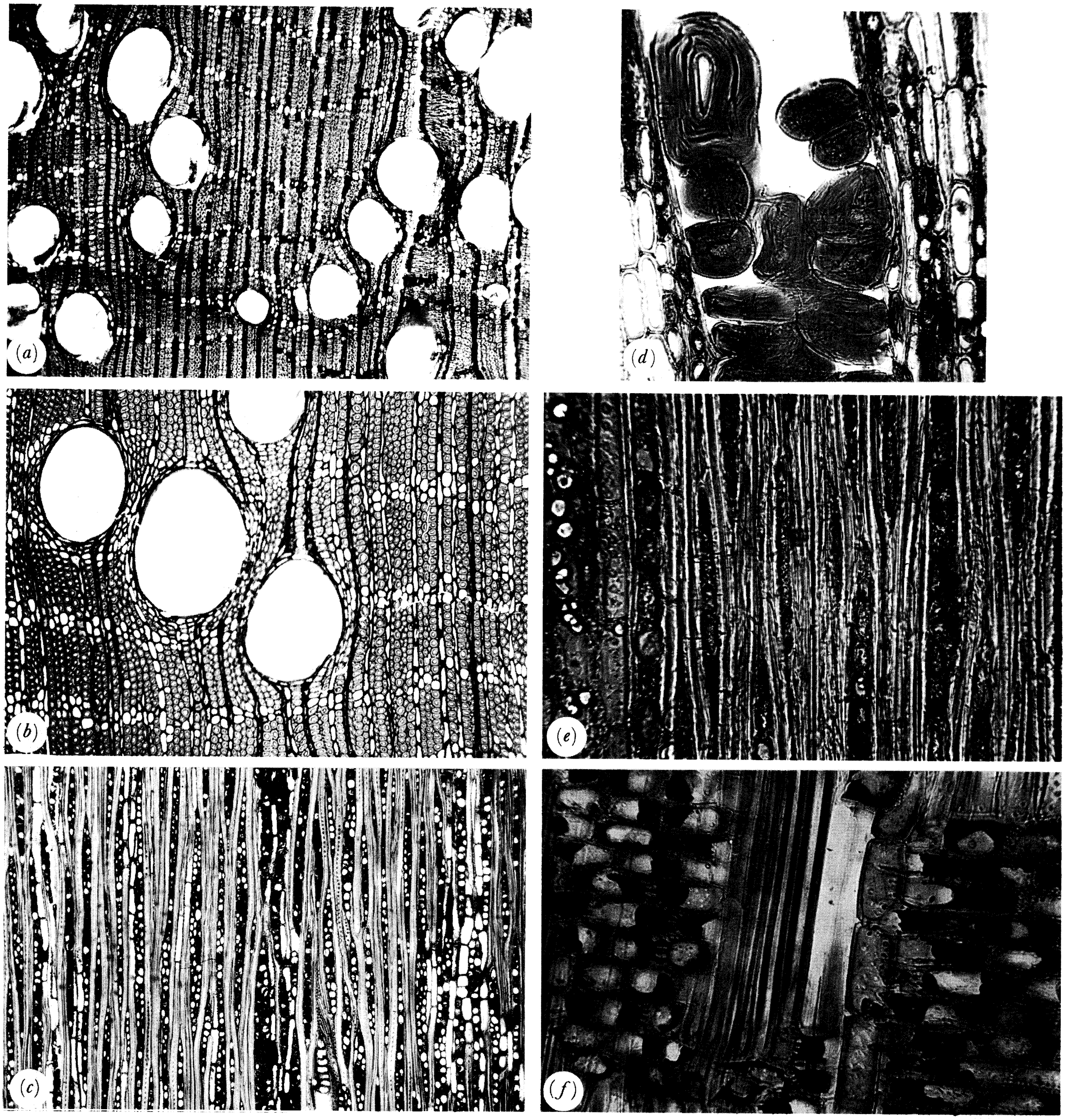

FIGURE 6. Secondary xylem: (*a*) *Licania heteromorpha*, ts (× 70, FPRL 7178); (*b*) *Parinari excelsa*, ts (× 70, CFI 874); (*c*) *Maranthes corymbosa*, ls (× 70, CFI 7722); (*d*) *Licania splendens*, ls showing sclerosed tyloses (× 350, CFI 12002); (*e*) *Couepia guianensis* subsp. *glandulosa*, ls showing silica grains (× 350, CFI 5353); (*f*) *Chrysobalanus icaco*, ls showing gum deposits in ray cells (× 350, CFI 5906).

comparatively small. By contrast, the pollen of the Tropaeolaceae, Geraniaceae, Limnanthaceae, Linaceae, Polygalaceae and Sapindaceae, families which various phylogenists (Hallier 1923; Bonne 1926; Hauman 1951; Gutzwiller 1961) have suggested are closely related to Chrysobalanaceae, is very different. Pollen morphology thus provides reasons for keeping the Chrysobalanaceae near to the Rosaceae in the Rosales, and not for removing it to the Geraniales or Sapindales.

The pollen of Chrysobalanaceae is so uniform that it does not provide good generic characters. *Neocarya macrophylla* has larger (50–100 µm) grains than other *Parinari* sensu lato *Licania* subgenus *Afrolicania* has the smallest grains (15–25 µm). Grain-size, however, is hardly an important generic character. The grains of the three species of *Magnistipula* examined have a conspicuous ridging in polar view. This has not been recorded in *Hirtella*, with which *Magnistipula* has sometimes been united. *Kostermanthus heteropetala* is distinct from all other Chrysobalanaceae examined, including *Dactyladenia* and *Acioa*, with which it shares a staminal ligule, in having three swellings on each of the triangular sides of the exine walls visible in polar view. Apart from *Kostermanthus*, no other genus is clearly definable on pollen characters.

The above account is based on Prance's original study (1963) with a light microscope. Subsequently a few additional species have been described, also with the use of light microscopy, namely by Barth & Silva (1963) (*Hirtella hebeclada*), Melhem & de Paula (1966) (*Couepia grandiflora*, *Hirtella americana* and *Licania humilis*), and by Demchenko (1973). The last author deals with *Angelesia* (now *Licania*) *splendens*, *Couepia bracteosa*, *Grangeria borbonica*, *Licania arborea*, *Parastemon urophyllus*, *Parinari brasiliensis* and *Lecostemon macrophyllum* (now *Rhabdodendron macrophyllum*). Demchenko confirmed that, in their pollen, Rosaceae and Chrysobalanaceae are distinguishable and that *Rhabdodendron* differs from Chrysobalanaceae. More recently Patel *et al.* (1983) have investigated three species (*Licania michauxii*, *Couepia* (now *Acioa*) *edulis* and *Parinari klugii*), with scanning and transmission electron microscopy.

(*i*) *Embryology*

Before a recent publication by Tobe & Raven (1984), little was known about the embryology of Chrysobalanaceae. These authors studied the embryology of *Chrysobalanus icaco* and two species of *Licania* and thus provided basic data for the tribe Chrysobalaneae.

The tetrasporangiate anthers have five-layered walls including a glandular tapetum with cells two-nucleate. Cytokinesis in the microspore mother cell is simultaneous. The ovule is anatropous and tenuinucellate; the nucellus is very small and the nucellar tissue soon disintegrates except for the megapore or embryo sac; antipodal cells are absent. The ovule is bitegmic; the inner integument (II) and outer integument (OI) are initiated dermally; the II is up to five or eight cells thick and the OI more than five cells thick; the inner epidermis of II develops into the endothelium, which directly borders the embryo sac and accumulates starch grains; the micropyle is formed by both integuments. Endosperm formation is of the nuclear type and the seed is exalbuminous. The young seed coat is composed of both testa and tegmen.

Tobe & Raven (1984) have shown that in its embryology the Chrysobalanaceae does not closely resemble the Myrtales (see §5*c*). They proposed a Thealean relationship, for which we find no basis when other parts of the plant are considered.

(*j*) *Chromosome cytology*

There is little to report. Mangenot & Mangenot (1957, 1958, 1962) and de Souza (1979*a*) have published chromosome counts as follows.

$2n = 20$: *Maranthes* ('*Parinari*') *glabra*, *M. polyandra*, *M. robusta*, *Parinari congensis*, *P. curatellifolia*, *P. excelsa* ('*holstii*').

$2n = 22$: *Chrysobalanus icaco* ('*orbicularis*'), *Dactyladenia* ('*Acioa*') *barteri*, *Licania* ('*Afrolicania*') *elaeosperma*.

(*k*) *Chemistry*

The chemistry of the Chrysobalanaceae remains poorly studied, but a few interesting compounds have been discovered.

(i) *Cyanogenic glycosides*

Gibbs (1974) pointed out that the lack of HCN from Chrysobalanaceae has been used since early in its history to separate the family from the Rosaceae. This was originally based on a single analysis of *Chrysobalanus icaco*. However, his own studies extend to *Couepia paraensis*, *Hirtella racemosa*, *Licania heteromorpha* and *Parinari excelsa*. Hegnauer (1966) also reports cyanogenic compounds in many Rosaceae but not in Chrysobalanaceae.

(ii) *Fatty acids*

The compounds that have been most studied in Chrysobalanaceae are the seed-fats, which include some quite unusual fatty acids. The following have been found: α-elaeostearic acid (*n*-octadeca-9c, 11t, 13t-trienoic), α-licanic acid (4-keto-α-elaeostearic), α-parinaric acid (*n*-octadeca-9c, 11t, 13t, 15c-tetraenoic) and 4-keto-α-parinaric acid.

The extremely scattered literature in which these compounds are described is summarized in table 2. None of these publications was concerned with their taxonomic significance, a subject which might repay further study. Most records are from species with seed kernels of known economic importance, such as *Licania rigida*, the oiticica nut used in paints as a substitute for tung oil, and *Parinari macrophylla* (= *Neocarya macrophylla*), the neou, another oil seed. In addition to the more unusual compounds, the seeds contain the common fatty acids such as palmitic, stearic, oleic and linoleic.

(iii) *Phenolics*

Bate-Smith (1961, 1962, 1965), in a study of Rosaceae, included a few Chrysobalanaceae (*Chrysobalanus pellocarpus* (= *C. icaco*), *Licania rigida* and *Parinari campestris*). This is the first report for the family. He found myricetin and delphinidin in the first two species, quercetin in all three and kaempferol in the last two, as well as caffeic acid in *Chrysobalanus*. He pointed out that quercetin, kaempferol, leucocyanidin and caffeic acid are common in the Rosaceae *sensu lato* but that the pyrogallol B-ring flavonoids myricetin and leucodelphinidin occur in Chrysobalanaceae but not Rosaceae (with the exception of *Potentilla anserina*). Gibbs (1974) confirmed the presence of the following compounds in at least some of the few species of Chrysobalanaceae examined: myricetin, delphinidin, quercetin (always present), cyanidin, and kaempferol. A flavonoid study of *Parinari* (Coradin *et al.* 1985) has confirmed the presence of quercetin 3-0-glycoside, naringenin 7-0-glycoside, quercetin aglycone and various other compounds. All species analysed contain kaempferol and quercetin and only some contain myricetin. It is too early to comment on the taxonomic significance of this study.

TABLE 2. PUBLISHED REPORTS OF FATTY ACIDS IN THE SEEDS OF CHRYSOBALANACEAE

species	name used in reference if different	substances	references[a]
Atuna excelsa	*Parinari glaberrima*	α-elaeostearic α-licanic	Frahm (1941)
		α-parinaric	Sklar *et al.* (1977)
	Parinari laurina	α-elaeostearic	Riley (1950), Winter (1948)
	Cylandrophora laurina	α-parinaric	Hopkins *et al.* (1969)[b], (1974: 512)
Chrysobalanus icaco		α-elaeostearic α-licanic α-parinaric 4-keto-α-parinaric	Gustone & Subbarao (1967)
Licania arborea		α-licanic	Rose & Jamieson (1943)
Licania elaeosperma	*Afrolicania elaeosperma*	α-licanic	
		α-elaeostearic	Hegnauer (1966)
?*Licania elaeosperma*	*Parinari sherbroensis*[c]	α-licanic	Steger & Van Loon (1934); Mendelowitz (1952)
Licania incana	*Licania crassifolia*	α-licanic	Sessler & Rowaan (1939)
Licania rigida		α-licanic	Kaufmann & Baltes (1936); Van Loon & Steger (1930); Machado (1938)
		α-elaeostearic	Mendelowitz (1952); Kaufmann & Sud (1960)
Licania alba	*Licania venosa*	α-licanic	Bennett *et al.* (1950); Gibbs (1974)
Maranthes corymbosa	*Parinari corymbosa*	α-elaeostearic α-licanic	Frahm (1941)
Neocarya macrophylla	*Parinari macrophylla*	α-elaeostearic	Ivanov (1944); Hilditch & Riley (1950); Sosa (1944); Steger & Van Loon (1934); Brown & Farmer (1935)
Parinari anamensis		α-licanic α-elaeostearic	Kaufman *et al* (1960)
Parinari campestris		α-elaeostearic	Steger & Van Loon (1934)
		α-elaeostearic	Chisholm & Hopkins (1966)
Parinari capensis		α-elaeostearic	Du Plessis & Vladár (1974)
Parinari curatellifolia		α-elaeostearic	Grindley (1950); Du Plessis & Vladár (1974)
Parinari excelsa		α-elaeostearic	Cornelius *et al.* (1970)
Parinari insularum		α-elaeostearic	Chisholm & Hopkins (1966)

[a] Most of these references are not cited in the general bibliography at the end of this monograph. Further details can be found in Gibbs (1974) and Hegnauer (1966).

[b] Hopkins *et al.* also examined seed oil of *Licania platypus* and found that it contained no conjugated acids, unlike other species examined.

[c] The name *Parinari sherbroensis* was not validly published. The authors use the local name Po-Yoak, which is usually applied to *Licania elaeosperma*.

5. RANK, CIRCUMSCRIPTION AND RELATIONSHIPS

(*a*) *Rank*

The group was first described as a family by Robert Brown (1818). Since then, several botanists, for the most part authors of general works, have accepted the Chrysobalanaceae as a family, notably Bartling (1830), Zuccarini (1832), Lindley (1836), Endlicher (1840), Bentham (1840), Walpers (1843), Miquel (1855), Agardh (1858), Warming & Mobius (1902), Wettstein (1935), Exell (1944), Gundersen (1950), Dandy (1960), Schulze-Menz in Melchior (1964), Takhtajan (1966, 1969, 1980), Cronquist (1968, 1981), Dahlgren *et al.* (1981) and Thorne (1981).

The authors of some of the older and widely used systems of classification, however, have treated it as a tribe or subfamily of Rosaceae; see, for example, de Candolle (1825), J. D. Hooker in Bentham & Hooker f. (1865), Focke in Engler & Prantl (1891), and Hutchinson (1926, 1959, 1964). This is in marked contrast to the opinions of nearly all workers with a detailed knowledge of the group, especially of its anatomy. Thus Fritsch (1889*a*), after careful study, concluded that it should be given family rank and placed between Rosaceae and Leguminosae. Küster (1897) drew no taxonomic conclusions from his work on the anatomy of the leaf and primary stem, but Hallier (1903), using Küster's data, recommended separation from Rosaceae as a family. Juel (1915), who correctly interpreted the ovary of the Chrysobalanaceae for the first time, considered the differences from Rosaceae to justify elevation to family rank, but somewhere near Rosaceae. On the basis of leaf-trace anatomy, Morvillez (1918*a*) reached a similar conclusion. Bonne (1928) found that the pedicel anatomy and floral vascular supply of Chrysobalanaceae and Rosaceae are quite different and suggested family status for the former. Both Metcalfe & Chalk (1950) and Erdtman (1952) imply that no objections could be raised against the rank of family on the basis of wood anatomy and pollen-grain structure respectively. There are also differences in basic chromosome numbers and chemistry. All these differences between Chrysobalanaceae and Rosaceae, which are discussed in the previous section, are summarized in table 3.

In the floral morphology, as a glance at the illustrations in part II will show, the differences between Chrysobalanaceae and Rosaceae are no less striking than those in anatomy. The resemblance between the flowers of *Chrysobalanus* and those few other species of Chrysobalanaceae with actinomorphic or subactinomorphic flowers, and those in Prunoideae are entirely superficial. The flowers of all other species of Chrysobalanaceae are very different from Rosaceae.

(*b*) *Circumscription*

When Robert Brown (1818) proposed the Chrysobalanaceae as a family he included in it only genera which are still regarded as true members, namely *Chrysobalanus*, *Moquilea* (now *Licania*), *Grangeria*, *Couepia*, *Acioa*, *Licania*, *Hirtella*, *Thelira* (now *Hirtella*) and *Parinari*. All authors of general systems subsequent to Brown, up to recent times, have included extraneous elements, just as certain earlier authors had associated non-chrysobalanaceous genera with true representatives. The taxonomic history of the genera which are now excluded is summarized in table 4.

Although Jussieu (1789) failed to separate Chrysobalanaceae from Rosaceae, all the genera of the former that were known to him were included in two tribes of Rosaceae, albeit with some others. Thus, Prockieae contains *Tigarea*, *Delima*, *Prockia* and *Hirtella* (of which only the last is still retained in Chrysobalanaceae), and Amygdaleae includes eleven genera, namely *Licania*, *Grangeria*, *Chrysobalanus*, *Cerasus*, *Prunus*, *Amygdalus*, *Armeniaca*, *Moquilea* (now *Licania*), *Couepia*, *Acioa* and *Parinari* (of which only the first three and the last four are true Chrysobalanaceae). The remainder are now usually united as *Prunus*.

Of the extraneous genera included in table 4, *Stylobasium* and *Lecostemon* have been most persistently included in Chrysobalanaceae, though sometimes with reservation. They were still widely regarded as Chrysobalanaceae when the present study began. Prance (1965, 1968*a*) has given reasons for their exclusion.

Stylobasium (Prance 1965) was found to differ from true Chrysobalanaceae in all important

TABLE 3. NON-MORPHOLOGICAL DIFFERENCES BETWEEN CHRYSOBALANACEAE AND ROSACEAE

Chrysobalanaceae	Rosaceae
Primary stem and leaf	
silica deposits abundant and occurring in five different forms	silica absent
stone cells in the pericycle thickened only on one side and thus appearing U-shaped in transverse section	stone cells in the pericycle not so thickened
stomata paracytic ('Rubiaceous')	stomata anomocytic ('Ranunculaceous')
petiole with an abaxial closed ring of xylem and phloem which is variously modified on the abaxial side	petiole various but not as in Chrysobalanaceae
Secondary xylem	
vessels oblique, infrequent, usually 200–300 µm diameter	vessels not oblique, abundant, usually less than 100 µm diameter
parenchyma banded, composed of long strands	parenchyma sparse, not banded, composed of short strands
rays predominantly uniseriate	rays multiseriate
intervascular pitting large	intervascular pitting never large, usually minute
silica abundant in the rays	silica absent
Pollen	
pollen markedly triangular in expanded grain	pollen usually not triangular or only weakly triangular
always without a protrusion in the mouth of the furrow	often with a wedge-shaped protrusion in the mouth of the furrow
grain scarcely patterned	grain often distinctly patterned
Floral anatomy	
ovary basically of 3 carpels with a gynobasic style	ovary never gynobasic
ovule basal, erect	ovule apical, pendulous
flowers at least slightly zygomorphic in all genera, strongly zygomorphic in many.	flowers actinomorphic
Embryology	
ovule tenuinucellate	ovule crassinucellate
nucellus small and early disintegrating	nucellus large, apical epidermal cells dividing to form a nucellar cap
endothelium present	endothelium absent
Basic chromosome numbers	
$x = 10, 11$	$x = 7, 8, 9, 17$
Chemistry	
cyanogenetic glycosides absent	cyanogenetic glycosides present
myricetin and leucodelphinidin present	myricetin and leucodelphinidin absent

respects, including floral morphology and anatomy, leaf and wood anatomy, pollen grain structure and blastogeny. In view of its isolated position it was proposed to restore the family Stylobasiaceae of Agardh (1858).

In another publication, Prance (1968*a*) has shown that Focke and others, following Bentham, misinterpreted the true *Lecostemon* of Sesse & Moc. ex DC., which is a *Sloanea* L. (Elaeocarpaceae), and that *Lecostemon* sensu Bentham, Focke and most recent authors is the same as *Rhabdodendron* Gilg & Pilg., which was previously placed in the Rutaceae. The differences between *Rhabdodendron* and all other angiosperm families appear to be sufficiently

Table 4. Excluded genera of Chrysobalanaceae

genus	authors who associated these genera with Chrysobalanaceae	subsequently proposed taxonomic position
Ferolia Aubl.	Aublet (1775)	*Brosimum* Sw. (Moraceae) – Standley (1929); Berg (1968)
Delima L.	Jussieu (1779)	*Tetracera* L. (Dilleniaceae)
Prockia P. Br. ex. L.	Jussieu (1779)	Flacourtiaceae
Trilepisium Thou.	De Candolle (1825); Meisner (1837–8); Endlicher (1840; 1842)	Moraceae: *Trilepisium* Thou. (syn. *Bosqueia* Baill.) – Capuron (1968); Berg (1977).
Stylobasium Desf.	Bartling (1830; Lindley (1836); Meisner (1838); Endlicher (1840); Bentham (1864); J. D. Hooker (1965) Baillon (1869); Fritsch (1889*a*); Focke (1891); Hutchinson (1964)	Stylobasiaceae – Agardh (1858); Prance (1965)
Prinsepia Royle	Lindley (1836); Endlicher (1840; 1842).	Rosaceae: Prunoideae – Hooker f. in Bentham & Hooker f. (1865) Rosaceae: Prinsepioideae – Sterling (1963)
Roydsia Roxb.	Meisner (1837–8)	*Stixis* Lour. (Capparidaceae)
Bartlingia Brogn.	Meisner (1837–8)	*Pultenaea* Sm. (Leguminosae: Papilionoideae)
Lecostemon sensu auct. non *DC*	Bentham (1853); C. Mueller (1858); J. D. Hooker (1865; 1867); Baillon (1869); Fritsch (1889*a*); Focke (1891); Hallier (1903)	*Rhabdodendron* Gilg & Pilg.(Rhabdodendraceae) – Prance (1968*a*)

great to justify recognition at family rank. A place in the Centrospermae was tentatively suggested. Subsequent work, however, has failed to demonstrate the occurrence of betalains (T. J. Mabry, personal communication) or of the specific P-type plastids that occur in the sieve tubes of Centrospermae (Behnke 1976). Puff & Weber (1976) believe that the morphology, anatomy and karyology of *Rhabdodendron* confirm a close affinity with Rutaceae. On the other hand, P. G. Waterman (1983, p. 384) found no typical rutaceous secondary metabolites, i.e. no alkaloids, no coumarins, no limonoids etc. in *Rhabdodendron*, and also that the phenolics in Rutaceae and *Rhabdodendron* are different. Hence, the taxonomic position of *Rhabdodendron* remains uncertain.

(*c*) *Relationships*

The majority of authors of general systems of classification who treat Chrysobalanaceae as a family distinct from Rosaceae leave it in Rosales. Only Dahlgren & Thorne (1984; Dahlgren 1984) question this practice and, without stating a positive opinion, suggest that it might be useful to investigate the possibility of relationships between Chrysobalanaceae and Myrtales. In contrast to the conservative opinion of most authors of general systems, some other workers, usually on limited evidence, have suggested connections with a wide diversity of taxonomic groups. Thus Bonne (1926), Gornall *et al.* (1979), Gutzwiller (1961), Hallier (1923), Hauman (1951), Horaninow (1847) and Tobe & Raven (1984) collectively have postulated affinity with Linaceae, Polygalaceae, Limnanthaceae, Dichapetalaceae, Trigoniaceae, Geraniaceae, Tropaeolaceae, Sapindaceae, Rhizophoraceae, Vochysiaceae, Proteaceae and Theaceae (see previous chapter). None of these views can be taken seriously. In gross morphology of flower and fruit Chrysobalanaceae do not even remotely resemble any of these families. In several features of anatomy and palynology they are also very different.

Our own work has shown that the resemblances of Rosaceae and Chrysobalanaceae are superficial, but it has not indicated any close connection between the latter and any other family. Therefore, on present evidence, we see no grounds for removing Chrysobalanaceae from Rosales even though they may not be closely related. We do not agree with Takhtajan (1980, p. 282) that within Rosaceae the Chrysobalanaceae is most closely related to the subfamily Spiraeoideae.

6. Delimitation of the genera

(a) *Introduction*

This section does not attempt to deal comprehensively with all genera. Rather, by means of selected case histories, it concentrates chiefly on two contrasting themes which are well exemplified by the taxonomic history of the family.

(i) With reference to *Parinari*, it shows how the uncritical adoption of an artificial character to define the genus, in this case the false dissepiment of the ovary, can lead to persistent confusion and error.

(ii) Illustrated by *Couepia* and *Hirtella*, it is shown that taxonomic and nomenclatural stability can result from the use of intuitively perceived overall resemblance or 'habitus', even when the taxonomic differences are expressed by reference to very few diagnostic characters.

Much of the early taxonomic confusion concerning generic delimitation, however, arose from the dispersal of Aublet's herbarium. Hence, it is necessary first of all to say a few words about this.

In our opinion the great majority of species of Chrysobalanaceae fit unequivocally into the 17 genera we recognize. Inevitably, a few species are problematical. They are briefly discussed at the end of this section.

In addition to *Couepia* and *Hirtella*, and *Parinari* and its segregates, certain other genera have been confused in the past. They are of less general interest and are dealt with in part II, the conspectus.

(b) *The history of Aublet's genera*

In 1775 Aublet added to the two genera of Chrysobalanaceae already described by Linnaeus, namely *Chrysobalanus* and *Hirtella*, six South American genera, *Acioa*, *Couepia*, *Licania*, *Moquilea*, *Parinari* and *Tachibota*, which subsequently have universally been assigned to the group.

After his death in 1778, Aublet's herbarium was dispersed and his type specimens were not available to most workers (Stafleu 1971). This was the cause of considerable confusion, partly taxonomic, partly nomenclatural, which persisted well into the second half of the nineteenth century, and with echoes up to modern times.

In the eighth edition of Linnaeus's *Genera plantarum*, Schreber (1789) corrected a few mistakes in Aublet's description of *Licania*, but by deliberately altering the 'barbaric' names of other genera and, in some cases, their circumscription, he was responsible for much subsequent uncertainty. He changed the name of *Licania* to *Hedycrea*, and re-named *Parinari* as *Petrocarya*, and *Acioa* as *Acia*. Of Aublet's remaining genera, *Couepia* was regarded as being doubtfully distinct from *Acia*, and *Moquilea* and *Ferolia* were not mentioned.

At this time the taxonomic confusion extended beyond Aublet's genera to *Hirtella*. Thus, among many similar instances, *Licania octandra* (Hoffmgg. ex Roem. & Schultes) Kuntze and

L. apetala (E. Mey.) Fritsch were originally (in 1825) described in *Hirtella*. *Couepia polyandra* (Kunth) Rose was likewise first placed in *Hirtella* in 1823, and its synonym, *H. dodecandra* Moc. & Sesse ex DC., was described two years later.

In 1827 Martius, who had not seen Aublet's types, used the name *Moquilea* for species which, in fact, belong to *Couepia* and *Acioa*, but shortly afterwards in collaboration with Zuccarini (Martius & Zuccarini 1832; Zuccarini 1832) excluded *Acioa*. Taxonomically Martius & Zuccarini (1832) made an important contribution by clarifying the distinction between *Couepia* and *Hirtella*, and thereby laid sound foundations for all subsequent work on these genera. It is unfortunate, however, that they used the name of the very different *Moquilea* for the former. *Moquilea* is now regarded as a synonym of *Licania*.

The name *Moquilea* continued to be used for *Couepia*, e.g. by Meisner (1837–8) and Endlicher (1840), until Bentham (1840) restored *Couepia* to generic rank and showed that all post-Aublet species of *Moquilea* belong to it. He, however, was still uncertain about the status of *Acioa*.

Acioa was still widely regarded as a synonym of *Couepia*, e.g. by J. D. Hooker (1865, 1867), until it was resurrected as a genus by Baillon (1869). In our opinion *Acioa* is confined to South America, but Baillon and all subsequent authors, by emphasizing the staminal ligule as a generic character, have also included African, and sometimes also Asiatic, species. In our opinion the African species of *Acioa* belong to *Dactyladenia* (Prance & White 1979) and the Asiatic to *Kostermanthus* (Prance 1979*c*).

Baillon (1869), following Grisebach (1857), also suggested that *Licania* and *Moquilea* are synonymous, an opinion which was endorsed by Fritsch (1889*b*), and one we share. Some workers, however, e.g. Focke (1891) and Hutchinson (1964), continued to keep them apart. Nevertheless, at the onset of the present study, only three species of *Moquilea* had not been transferred to *Licania*, and two of them we consider synonymous with already established *Licania* species.

Aublet's remaining genus, *Parinari*, at first fared better than the others, but Bentham (1849) so enlarged its concept that its subsequent history became even more tangled than those of the genera mentioned below.

(*c*) *The history of Parinari*

The taxonomic history of *Parinari* is very complex. Of the 16 genera, other than *Parinari* itself, upheld in the present study all but five (*Chrysobalanus*, *Parastemon*, *Grangeria*, *Acioa*, *Dactyladenia*) include at least one species which at one time or another has been placed in *Parinari*. For some genera (*Magnistipula*, *Licania*, *Couepia* and *Hirtella*) only a very small minority of species have been so misplaced and then mostly by taxonomists without a comprehensive knowledge of the group, who were working on the floras of restricted geographical areas.

For most other genera (*Atuna*, *Bafodeya*, *Exellodendron*, *Hunga*, *Maranthes*, *Neocarya*) it is a very different story. Despite their considerable differences from *Parinari* sensu stricto in virtually all other respects, these genera have one feature in common: a bilocular ovary. Above all else, it was the adoption of this character, especially by Bentham (1849), as a generic criterion that has led to the increasingly artificial nature of *Parinari*. As *Parinari* became more and more heterogeneous even some species with unilocular ovaries were included, for example the species now segregated into *Kostermanthus*.

In the original description of *Parinari*, which was based on *P. campestris* and *P. montana*, Aublet (1775) mentions the bilocular ovary, but does not appear to have attached much importance to it.

Jussieu (1789), who brought all previously described genera of Chysobalanaceae together for the first time, knew some of them only from the original descriptions and illustrations. His implication that *Parinari* differs from the other genera principally in its bilocular ovary seems to have laid the foundations for the subsequent confused history of the group.

Parinari was latinized as *Parinarium* by Jussieu. The former, however, is legitimate and takes priority. Because the latter name is merely an orthographic variant, it is not necessary to make new combinations for those species first described in *Parinarium*, as is done, for instance, by Dandy (in Andrews, *Fl. Pl. Anglo-Egypt. Sudan*: 105 (1952)). In the present work all species are treated as if they had been first published as *Parinari*.

Jussieu was the first to extend the concept of *Parinari* to another continent by citing in synonymy two manuscript names of Adanson from Senegal, *Mampata* and *Neou*. The former was subsequently described as *P. excelsa* and the latter as *P. macrophylla* by Sabine in 1824.

The following year, in his *Prodromus*, de Candolle (1825), who only knew the four species mentioned above, divided *Parinari* into two sections. Section *Petrocarya* (correctly section *Parinari*) was based on a superfluous generic name which Schreber (1789) substituted for the earlier *Parinari*. It included Aublet's original species. Section *Neocarya* was based on *P. senegalensis* DC. (now *Neocarya macrophylla* (Sabine) Prance) but *P. excelsa* was associated with it, probably because its type-description is inadequate to characterize it properly. *P. macrophylla* is not mentioned by de Candolle. He was also apparently unaware of the first true *Parinari* to be described from Asia, *P. sumatrana* Benth., which had been described by Jack in the illegitimate genus *Petrocarya* in 1822. de Candolle indirectly emphasized the importance of the bilocular ovary of *Parinari* by describing the ovary of all other genera as unilocular.

During the first half of the nineteenth century, in addition to *Neocarya macrophylla*, a few other species, which we regard as belonging to other genera, were described in *Parinari* or its illegitimate synonym *Petrocarya*, doubtless because of their bilocular ovary. Thus Jack (1822) described *Petrocarya excelsa* (now *Atuna excelsa*), and Bentham (1840) published *Parinari coriacea* (now *Exellodendron coriaceum*), but it was Bentham's treatment of *Parinari* in Hooker's *Niger Flora* (1849) that firmly established *Parinari* as an artificial genus.

Whereas earlier workers had implied that the bilocular ovary is a diagnostic character of *Parinari*, Bentham was explicit, and referred to the spurious dissepiment which separates the ovules as 'the essential character'.

Bentham divided *Parinari* into three sections as follows:

Section 1. *Petrocarya* (correctly *Parinari*) included the African species, *P. excelsa* and *P. curatellifolia*, all the known American species including *P. coriacea* (now *Exellodendron coriaceum*), and, with some doubt, three species Bentham had not seen, namely *P. sumatrana* Benth. (a true *Parinari*), *P. glaberrima* (Hasskl.) Hasskl. (now *Atuna excelsa*) and *P. scabra* Hasskl. (now *Atuna scabra*).

Section 2. *Sarcostegia* Benth. included two new species, *P. polyandra* (now *Maranthes polyandra*) and *P. griffithiana* (now *Maranthes corymbosa*), and, with some doubt, also *P. jackiana* Benth. (based on *Petrocarya excelsa*, now *Atuna excelsa*) which Bentham had not personally examined.

Section 3. *Neocarya* DC. contained *P. macrophylla* (now *Neocarya macrophylla*) and its synonym *P. senegalensis*.

Bentham's circumscription of *Parinari* was probably much wider than he imagined, largely because of the inclusion of the Asiatic species he only knew from the literature. He appears to have adopted it with some reservation. *P. polyandra* has *ca.* 40 fertile stamens and Bentham mentions that this, in conjunction with the glandular leaves and fleshy 'calyx', might 'suggest the establishment of a distinct genus'. He clearly believed that stamen number of *Parinari* varies more or less continuously, but the evidence he cites is partly based on the species he did not know at first hand.

Bentham's circumscription of *Parinari* embraced no fewer than five genera which we regard as distinct, namely, in addition to *Parinari* itself, *Atuna* Rafin., *Exellodendron* Prance, *Maranthes* Blume and *Neocarya* Prance. Two of these, although Bentham was apparently unaware of this, had enjoyed a brief period of generic recognition. Thus *Maranthes* was described by Blume in 1825, but three years later he transferred the type species to his illegitimate *Exitelia*. *Atuna* was described by Rafinesque in 1838, but remained disregarded for more than 100 years, though one of its species was independently described by Hasskarl in 1842 as the type of his new genus *Cyclandrophora*. It appears that Hasskarl had little faith in his new genus, for he united it with *Parinari* within a year of its publication, although it has little in common with the latter, other than the bilocular ovary. Of the remaining genera, *Neocarya* has always occupied an isolated place in *Parinari*. Various authors, e.g. Ducke (1922) and Hill (1937), have commented on the distinctness of the species now placed in *Exellodendron*.

Such was the authority of Bentham, however, that after 1849 nearly all species of Chrysobalanaceae with a false dissepiment (and even some without) were automatically placed in *Parinari* regardless of any other consideration. Few authors challenged the wisdom of this and those who did, e.g. J. D. Hooker (1878), did nothing about it.

As new species now placed in *Exellodendron*, *Maranthes* and *Atuna* were discovered they inevitably found their way to *Parinari*. Likewise, equally disparate elements, which are now placed in *Bafodeya* Prance, *Hunga* Pancher ex Prance and *Kostermanthus* Prance, joined the assemblage. Accretion did not stop even there, and a few new species of *Couepia*, *Licania* (but not of the American species of the latter) and *Magnistipula* were also attributed to *Parinari*. The misplaced species of *Parinari*, together with their currently accepted names, are given in table 5. The differences between *Parinari* and its segregates are summarized in the next section.

(*d*) *The segregates of Parinari*

The differences between *Parinari* and its seven segregate genera are fully described and illustrated in part II, the conspectus. The conventional taxonomic characters which separate them are very briefly summarized below.

In *Parinari* the principal character states which contrast with those of the segregate genera are as follows.

Branchlets not divaricate. Stipules not keeled. Petiole with two large glands on the upper surface. Lamina with stomatal crypts on lower surface. Bracts and bracteoles enclosing groups of flower buds. Flowers slightly zygomorphic. Receptacle-tube subcampanulate, more or less equalling the deltate sepals in length. Petals subequal, not unguiculate. Stamens 6–10, posterior; filaments more or less as long as sepals. Ovary inserted in upper half of receptacle-tube, unilocular. Epicarp verrucose. Endocarp rough. Obturators present. Cotyledons not ruminate. Germination cryptocotylar.

The segregate genera differ as follows.

Atuna has divaricate branching, keeled stipules, eglandular petioles, exserted stamens and ruminate cotyledons; it lacks stomatal crypts, bracts and bracteoles enclosing groups of flower buds, and obturators.

Bafodeya has eglandular petioles, strongly zygomorphic flowers, a ventricose receptacle-tube, an oblique throat, conspicuous, claviform staminodes and a smooth endocarp; it lacks bracts and bracteoles enclosing groups of flower buds, and obturators.

Exellodendron has eglandular petioles, a smooth epicarp, a smooth ridged endocarp; it lacks stomatal crypts, bracts and bracteoles enclosing groups of flower buds, and obturators.

Hunga has eglandular petioles, filaments much shorter than the sepals, an ovary inserted half-way up the receptacle-tube, a smooth epicarp and endocarp; it lacks stomatal crypts, bracts and bracteoles enclosing groups of flower buds, and obturators.

Kostermanthus has eglandular petioles, strongly zygomorphic flowers, very unequal, unguiculate petals, 30–70 stamens, ligulately connate filaments, unilocular carpels, slightly ruminate cotyledons; it lacks stomatal crypts, bracts and bracteoles enclosing groups of flower buds, and obturators.

Maranthes has eglandular petioles, suborbicular deeply concave sepals, 20–60 stamens which form a complete circle, filaments undulate in bud, far-exserted at anthesis, and phanerocotylar germination; it lacks stomatal crypts, bracts and bracteoles enclosing groups of flower buds, and obturators.

Neocarya has eglandular petioles, strongly zygomorphic flowers, a saccate, gibbous receptacle-tube much shorter than the sepals, and 12–17 stamens; it lacks bracts and bracteoles enclosing groups of flower buds.

The summary above reveals that each segregate genus differs from *Parinari* in from 7 to 11 conventional characters. They are thus more distinct from *Parinari* and from each other than are some other genera of Chrysobalanaceae, e.g. *Chrysobalanus* and *Licania*, which have been kept apart since the earliest times. They are also more distinct than many genera in most other families.

If the conventional characters used to separate the segregates of *Parinari* had been broken down into the 'unit characters' of numerical taxonomy their number would have been greatly increased.

(*e*) *The relationships of Couepia and Hirtella*

It has previously been mentioned that *Couepia* and *Hirtella* were often confused at the beginning of the nineteenth century until Martius and Zuccarini (Martius 1827; Martius & Zuccarini 1832; Zuccarini 1832) redefined them. Their work remained the most significant treatment of these genera until the family monograph in *Flora neotropica* (Prance 1972) 140 years later.

Martius and Zuccarini separated *Hirtella* and *Couepia* on two diagnostic characters, namely the definite number of stamens (3–9) and the thin and fragile endocarp of *Hirtella*, in contrast to the indefinite number of stamens (20–100) and the 'woody' endocarp of *Couepia*. They also state that the genera differ in overall resemblance, in 'habitus', and cautiously point out that, because for some species of *Hirtella* the fruit was unknown, and because the disposition of its fertile stamens indicated reduction from a larger number, the two genera might ultimately be found to be connected by intermediates, in which case they would have to be united.

Martius & Zuccarini (1832) say nothing about the taxonomic method they used but it would appear that they were following the tradition of the great Parisian school of the late eighteenth and early nineteenth centuries, as exemplified by Adanson, Cuvier, Lamarck, Jussieu and de Candolle. In this method (for discussion see Cain (1959*a*, *b*)), as explained by Cuvier, the subdivisions are not established arbitrarily but are based on the 'fundamental

TABLE 5. SPECIES OF CHRYSOBALANACEAE WHICH HAVE BEEN MISPLACED IN *PARINARI*

name in *Parinari*	present position
P. asperula Miq. (1861)	Atuna excelsa (*Jack*) *Kosterm.*
P. aubrevillei Pellegr. (1931)	Maranthes aubrevillei (*Pellegr.*) *Prance*
P. bangweolensis R.E. Fr. (1913)	Magnistipula butayei *De Wild* subsp. bangweolensis (*R.E.Fr.*) *F. White*
P. barbata Ducke (1922)	Exellodendron barbatum (*Ducke*) *Prance*
P. benna Scott Elliot (1894)	Bafodeya benna (*Scott Elliot*) *Prance*
P. bequaertii De Wild. (1944)	Maranthes floribunda (*Bak.*) *F. White*
P. canescens Gleason (1931)	Couepia canescens (*Gleason*) *Prance*
P. chrysophylla Oliv. (1871)	Maranthes chrysophylla (*Oliv.*) *Prance*
P. cordata Hook.f. (1867)	Exellodendron cordatum (*Hook.f.*) *Prance*
P. coriacea Benth. (1840)	E. coriaceum (Benth.) *Prance*
P. corymbosa (Blume) Miq. (1855)	Maranthes corymbosa *Blume*
P. curranii Merr. (1909)	Atuna excelsa (*Jack*) *Kosterm.*
P. elata King (1897)	A. elata (*King*) *Kosterm.*
P. elliptica Kosterm. (1965)	A. elliptica (*Kosterm.*) *Kosterm.*
P. fleuryana (A. Chev.) Aubrév. (1936)	Magnistipula zenkeri *Engl.*
P. floribunda Bak. (1897)	Maranthes floribunda (*Bak.*) *F. White*
P. gabunensis Engl. (1893)	M. gabunensis (*Engl.*) *Prance*
P. gardneri Hook. f. (1867)	Exellodendron gardneri (*Hook.f.*) *Prance*
P. gilletii De Wild. (1906)	Maranthes glabra (*Oliv.*) *Prance*
P. glaberrima (Hassk.) Hassk. (1843)	Atuna excelsa (*Jack*) *Kosterm.*
P. glabra Oliv. (1871)	Maranthes glabra (*Oliv.*) *Prance*
P. goetzeniana Engl. (1904)	Maranthes goetzeniana (*Engl.*) *Prance*
P. gracilis Kuhlmann (1940)	Exellodendron gracile (*Kuhlmann*) *Prance*
P. griffithiana Benth. (1849)	Maranthes corymbosa *Blume*
P. guyanensis Fritsch (1890)	Hirtella guyanensis (*Fritsch*) *Sandwith*
P. hahlii Warb. (1902)	Atuna excelsa (*Jack*) *Kosterm.*
P. heteropetala Scortech. ex King (1897)	Kostermanthus heteropetalus (*Scortech. ex King*) *Prance*
P. hostmannii Fritsch (1890)	Couepia cognata (*Steudel*) *Fritsch*
P. indica (Bedd.) Bedd. (1874)	Atuna indica (*Bedd.*) *Kosterm.*
P. ingangensis Pellgr. (1923)	Magnistipula tessmannii (*Engl.*) *Prance*
P. iodocalyx Mildbr. (1921)	?Maranthes chrysophylla (*Oliv.*) *Prance* subsp. coriacea *F. White*
P. jackiana Benth. (1849)	Atuna excelsa (*Jack*) *Kosterm.*
P. kerstingii Engl. (1911)	Maranthes kerstingii (*Engl.*) *Prance*
P. krukovii Gleason (1933)	Couepia glandulosa *Miq.*
P. kunstleri King (1897)	Kostermanthus heteropetalus (*Scortech. ex King*) *Prance*
P. latifolia M. R. Henderson (1933) non (Oliv.) Exell (1928)	Atuna latifrons (*Kosterm.*) *Prance & F. White*
P. latifrons Kosterm. (1965)	A. latifrons (*Kosterm.*) *Prance & F. White*
P. laurina A. Gray (1854)	A. excelsa (*Jack*) *Kosterm.*
P. macrophylla Sabine (1824)	Neocarya macrophylla (*Sabine*) *Prance*
P. macrophylla Teijsm. & Binn. (1867) non Sabine	Atuna excelsa (*Jack*) *Kosterm.*
P. maingayi (King (1897)	A. excelsa (*Jack*) *Kosterm.*
P. margarata A. Gray (1854)	A. excelsa (*Jack*) *Kosterm.*
P. mindanaensis Perkins (1904)	A. excelsa (*Jack*) *Kosterm.*
P. minutiflora Bak.f. (1921)	Hunga minutiflora (*Bak.f.*) *Prance*
P. montana Engl. (1911) non Aubl.(1775)	Maranthes glabra (*Oliv.*) *Prance*
P. multiflora (Korth.) Miq. (1855)	M. corymbosa *Blume*
P. myriandra Merr. (1929)	Kostermanthus heteropetalus (*Scortech. ex King*) *Prance*
P. myrsinoides Schlechter (1906)	Hunga myrsinoides (Schlechter) Prance
P. nannodes Kosterm. (1965)	Atuna nannodes (*Kosterm.*) *Kosterm.*
P. neocaledonica Bak.f. (1921)	Hunga gerontogea (*Schlechter*) *Prance*
P. nitida Hook.f. (1878)	Licania splendens (Korth.) Prance

TABLE 5 (*cont.*)

name in *Parinari*	present position
P. palauensis Kanehira (1934)	Maranthes corymbosa *Blume*
P. pilosa Standley (1937)	Couepia canomensis (*Mart.*) *Benth. ex Hook.f.*
P. poggei Engl. (1899)	Maranthes sp.
P. polyandra Benth. (1849)	M. polyandra (*Benth.*) *Prance*
P. racemosa Merr. (1904)	Atuna excelsa (*Jack*) *Kosterm.*
P. robusta Oliv. (1871)	Maranthes robusta (*Oliv.*) *Prance*
P. salicifolia (Presl.) Miq. (1855) non Engl. (1895)	Maranthes corymbosa *Blume*
P. sargosii Pellegr. (1920)	Magnistipula butayei *De Wild.* subsp. sargosii (*Pellegr.*) *F. White*
P. scabra Hassk. (1844)	Atuna scabra (*Hassk.*) *Kosterm.*
P. spicata King (1897)	A. excelsa (*Jack*) *Kosterm.*
P. tessmannii Engl. (1911)	Magnistipula tessmannii (*Engl.*) *Prance*
P. tibatensis Engl. (1911)	Maranthes glabra (*Oliv.*) *Prance*
P. tisserantii Aubrév. & Pellegr. (1950)	Magnistipula butayei *De Wild.* subsp. tisserantii (*Aubrév. & Pellegr.*) *F. White*
P. tontoutensis Guillaumin (1959)	Hunga minutiflora (*Bak.f.*) *Prance*
P. travancorica Bedd. (1874)	Atuna travancorica (*Bedd.*) *Kosterm.*
P. versicolor Engl. (1907)	Magnistipula zenkeri *Engl.*
P. villamillii Merr. (1915)	Atuna villamillii (*Merr.*) *Kosterm.*

relationships', on the 'essential resemblances' of things; but, so as not to overburden the memory, the properties of the entities are expressed in the 'least terms'. All the major practitioners of the Parisian school were concerned with overall resemblance but they differed greatly in the details of their method and the philosophical rationalizations that they offered (de Candolle 1819; Cain 1959*a*, *b*; Stafleu 1964; Burtt 1965). Although rigorous analysis played an important part in the natural method, overall resemblance detected in the first instance by 'eye' was no less important. Some discussions on the natural method have been concerned with theory rather than practice. In an important exception, a commentary on Adanson, Burtt (1965) has suggested that a successful classification depends more on the perception of the trained mind and eye of the taxonomist than on a deliberately reasoned analysis of the data.

The example of *Couepia* and *Hirtella* discussed below shows that stable genera can be detected by intuitive perception, early in their taxonomic history, and that their objectivity can subsequently be confirmed by analysis, depending, in the first instance, on the remarkable properties of the human eye and brain.

The soundness of Martius & Zuccarini's judgement is shown by the fact that, although they were acquainted with only about 15 % of the species known today, their concepts of *Couepia* and *Hirtella* have persisted with little change up to the present time.

In a modified form, the two diagnostic characters of Martius & Zuccarini, together with a third (method of seedling escape), were used to separate the genera in *Flora neotropica* (Prance 1972), as follows:

Stamens (10) 14–300; endocarp thick, with no lines of dehiscence	*Couepia*
Stamens 3–10; endocarp thin, opening by longitudinal lines of weakness	*Hirtella*

Presented in this form it would appear that species intermediate in stamen number, a possibility envisaged by Martius & Zuccarini, actually exist. Subsequent work, however, in which stamen number was carefully scrutinized for all available species, has failed to confirm this. It was found that in *Couepia* fewer than 15 stamens only occur in a few flowers in one or two species that normally have more than 15, whereas in *Hirtella* no species was found to have as many as 10 stamens. The figure of 10 which comes from the literature must be regarded as unconfirmed. If *maximum* stamen number is the criterion, and depauperate flowers are ignored, the diagnostic character of Martius & Zuccarini is restored, but with a smaller discontinuity between its character states.

It is, however, evident from reading the protologues of most of the species correctly placed in *Couepia* and *Hirtella*, subsequent to the time of Martius & Zuccarini, that their authors did not classify them primarily on the diagnostic characters, but rather on general resemblance to other species with which they were familiar. We therefore decided to conduct two experiments with the intention of discovering whether habitus has an objective basis, and if so, whether it can be resolved into additional diagnostic characters. It was also decided to compare the fruits more critically.

So far as we are aware this was the first time that such experiments have been undertaken as part of a monographic study. Their results greatly influenced our subsequent thinking, and, we believe, have some bearing on such subjects as the relationships between taxonomy and ecology and priorities in taxonomic research (see § 12*b*). For these reasons the experiments are described below, and the information on materials used and some ancillary matters are given in Appendixes 1 and 2.

(i) *The objectivity of habitus*

For each genus a few species were selected to illustrate as economically as possible the range of variation in that genus. Three species were chosen from *Couepia* and four from *Hirtella*. These were the standards against which three 'subjects' were asked to match a selection of species from both genera. 28 'unknowns' were available from *Couepia* and 40 from *Hirtella*. They were all flowering specimens.

The results of the experiment were remarkable. All three subjects worked quickly. The time taken to make 68 critical comparisons varied from one to two hours, an average of less than two minutes for each. Each subject was almost 100 % successful (94–96 %). The few failures in matching could be attributed in part to a fault in the experiment (the flowers of one of the standard species of *Couepia* were not fully developed). Only four species, *Hirtella bahiensis*, *H. guyanensis*, *H. martiana* and *H. obidensis*, were mismatched; of these all but *H. martiana* are anomalous in some respects and have a relatively low index of generic conformity (see Appendixes 1*c* and 2).

This experiment clearly confirms what is suggested by the taxonomic history of *Couepia* and *Hirtella*, namely that they are objective entities. Furthermore, it shows that successful taxonomy 'by eye' is not the exclusive preserve of the trained and specialist taxonomist. All three subjects were interested in plants, but had no previous knowlege of the group; although one was a trained taxonomist, she had only limited herbarium experience. All three subjects, despite their widely different backgrounds, achieved very similar results.

(ii) *Analysis of habitus*

When flowering material of *Couepia* and *Hirtella* was compared, it soon became apparent that they differ in the architecture of the inflorescence, particularly in the pattern of branching of the main axes and the relative position of individual flowers in space, both in relation to the main axes and to other flowers. It also seemed that, although there is some overlap in flower size, the relative proportions of the parts were different in almost every detail. The following key to *Couepia* and *Hirtella* was then made:

1. Inflorescence usually a congested thyrse with ascending lateral branches and flowers, less often a raceme or a spike, but then the flowers or inflorescence or both are often pendulous. Flowers large, usually more than 0.8 cm long (measured from base of receptacle-tube to tip of odd sepal), usually congested. Pedicel often shorter and sometimes very much shorter than the receptacle-tube. Receptacle-tube usually longer, and sometimes much longer than the calyx-lobes. Filaments usually scarcely longer than the combined length of calyx and receptacle-tube . . . . *Couepia*
1. Inflorescence usually a lax raceme or an elongate narrow thyrse with flowers or lateral branches wide-spreading, sometimes a corymb but then usually with zig-zag lateral branches bearing several sterile bracts and ending in a single functional flower, rarely a very short subcapitate raceme. Flowers small, less than 0.8 cm long, usually in lax inflorescences. Pedicel usually longer and often much longer than the receptacle-tube. Receptacle-tube usually shorter than the calyx-lobes. Filaments usually much longer than the combined length of calyx and receptacle-tube . . . . *Hirtella*

Three undergraduates without previous herbarium experience or knowledge of the group were asked to 'run down' specimens belonging to 69 species belonging to the two genera.

The results of this exercise conclusively demonstrate that the 'habitus' of Martius & Zuccarini can be verbally expressed. Of the 207 identifications made, only one (*H. bahiensis*) was incorrect. The time taken to identify 69 specimens varied from one hour to one and one half hours. The comments of the investigators were revealing: 'at first the genera looked somewhat diverse, but it soon became apparent that the proportions of the flower are different'; 'a few specimens were critical and required careful scoring'.

The five characters used in the key are highly correlated among themselves and form a character-complex which is probably a functional syndrome (see §10*c*). These characters, plus three others, namely colour of filaments, presence of glands on bracts and bracteoles, and disposition of filaments in unopened flower buds, were then scored for every species used in the exercise.

When all these data were compared and the character states expressed more precisely, the diagnostic value of each character was calculated. Only one character was found to be absolutely diagnostic. In all species of *Hirtella* the filaments are spirally coiled in the bud; in *Couepia* they are undulate with three or more bends. Although the other characters have high diagnostic value, they cannot be used singly if all species are to be correctly placed.

The extent to which they can be used successfully, one at a time, depends on the precise way in which they are formulated (see Appendix 1). For every species used in the study, the values for each of the characters investigated are recorded in an appendix (see Appendix 2), which also expresses the diagnostic value of each character in numerical terms and gives a quantitative indication of the distinctness of the two genera.

(iii) *Fruit characters*

All fruiting specimens in the Forest Herbarium, Oxford, were examined, in some cases anatomically, with the following results:

1. Drupe 2.5–10 cm long; mesocarp and endocarp not very sharply differentiated; mesocarp nearly always more than 0.2 cm and usually more than 0.3 cm thick; endocarp surface rough and irregular owing to fusiform anticlinal aggregations of stone cells and fibres which penetrate the mesocarp more or less deeply; vascular supply to endocarp deeply embedded, not occupying superficial channels, usually visible on inner surface . . . . *Couepia*

1. Drupe up to 2.2 cm long, very rarely longer; mesocarp and endocarp sharply differentiated; mesocarp (*in sicco*) always less than 0.1 cm thick; endocarp surface smooth except for 4–6 shallow longitudinal channels; vascular supply to endocarp superficial, occupying the channels . . . . *Hirtella*

For those species that have been studied, germination is different in the two genera, and *Couepia* is dispersed by bats and rodents (see §16.11) and *Hirtella* by birds (see §16.15). It would appear that the fruits are similar to the inflorescence and flowers, in that they also show complex syndromes of several highly correlated but individually small component characters, which are related to ecology. Further field work is needed, though the evidence at present available suggests that the syndromes are remarkably constant.

One, possibly highly significant, exception, however, has recently come to light (Pannell & White 1988). *Hirtella zanzibarica* occurs in East Africa and Madagascar. Its leaves, inflorescences and flowers are so uniform that the populations on the two sides of the Mozambique Channel have been regarded as conspecific. The fruits, however, are different. Those from the mainland are similar to those of *H. racemosa* (see §16.15) and are thought to be dispersed in a similar way. The Malagasy plant has a larger drupe. Its pericarp is much more fibrous with a less clear distinction between the layers. Lines of weakness are not evident. Mode of dispersal is possibly different, especially in view of the faunal differences between Madagascar and the African mainland. In some ways the Madagascar fruits more closely resemble *Couepia* than *Hirtella* but this does not undermine the distinctness of these genera. In nearly all other respects Malagasy *H. zanzibarica*, unequivocally, is *Hirtella.*

(*f*) *Taxonomically isolated species*

Earlier in this section and in part II it is shown that the genera of Chrysobalanaceae are as distinct as most genera in most families. Normally no difficulty is experienced in placing their members correctly. A few species, mentioned below, however, as is to be expected, are problematical. Either they lack one or more important diagnostic characters or they occupy isolated positions within their respective genera; other authors might have treated them differently.

Acioa The four species form three groups which are so different that subgeneric rank might be justified.

Couepia The Andean species *C. platycalyx* is unique in the genus in its flattened almost solid receptacle and in this respect, but no other, resembles *Maranthes.*

Licania The 150 or so American species form a closely knit group, except for *L. licaniiflora*, which has a laterally inserted ovary and is placed in the monotypic subgenus *Parinariopsis.*

The only African species, *L. elaeosperma*, is sufficiently distinct to need its own subgenus, *Afrolicania*, which was formerly accorded generic status.

The two Asiatic species, *L. splendens* and *L. palawanensis*, similarly are placed in a subgenus, *Angelesia*, which has been demoted from generic rank.

The 'taxonomic distance' between the sections of *Licania* is appreciably less than that between *Licania* and other genera of Licanieae.

The only North American *Licania*, *L. michauxii*, bears a superficial resemblance to *Chrysobalanus*, with which it has sometimes been united, but it belongs to *Licania* in all important respects (see §16.1).

Magnistipula Despite its small size, this genus is more variable in its flowers and fruits than any other genus of Chrysobalanaceae. Three subgenera, one of which is subdivided into three sections, are necessary to do justice to its internal pattern of relationships. *M. tessmannii* (subgenus *Pellegriniella*) has a spurious dissepiment, a feature which is otherwise constant within genera. The two Malagasy species (subgenus *Tolmiella*) have very small flowers of simple construction which are possibly reduced.

Parinari Two Asiatic species, *P. canarioides* and *P. argenteosericea*, lack stomatal crypts but are otherwise typical; Kostermans (1965*c*) places them in sectio *Anareolata*.

7. GROUPING OF THE GENERA

Most previous groupings of the genera, beginning with Baillon's (1869), were based on the symmetry of the flower, and especially the position of insertion of the ovary, although Baillon clearly had little faith in his classification: 'il est difficile de sectionner les Chrysobalanées d'une manière nette et précise, au moyen du mode d'insertion de l'ovaire sur le receptacle'. This is because there is a complete gradation in this character, which may be summarized as follows.

Exactly central: *Chrysobalanus*.
Nearly central: *Licania* and *Parastemon*.
Lateral: *Grangeria*, *Hunga*, *Licania licaniiflora*, a few *Hirtella*, a few *Parinari*.
Terminal: *Acioa*, *Atuna*, *Bafodeya*, *Couepia*, *Dactyladenia*, *Exellodendron*, *Kostermanthus*, *Magnistipula*, *Maranthes*, *Neocarya*, most *Hirtella*, most *Parinari*.

Baillon proposed the following two groups, which he did not formally recognize.

'Group a': *Chrysobalanus*, *Licania*.
'Group b': *Acioa*, *Couepia*, *Grangeria*, *Hirtella*, *Parastemon*, *Parinari*.

Subsequent classifications, such as those of Focke (1891), Hallier (1903) and Hauman (1951), are basically similar to Baillon's although with some difference in detail, e.g. with *Grangeria* and *Parastemon* sometimes included in the first group. Focke treated the groups as subtribes, Chrysobalaninae and Hirtellinae respectively. For convenience these two groups were originally maintained by Prance (1963), who reaffirmed their arbitrary nature and suggested tribal rank, as follows:

Chrysobalaneae. Ovary inserted at or near the base of the receptacle. *Chrysobalanus*, *Licania*, *Parastemon*.

Hirtelleae. Ovary inserted at least mid-way up the receptacle or at its mouth. *Acioa*, *Atuna*, *Bafodeya*, *Couepia*, *Dactyladenia*, *Exellodendron*, *Grangeria*, *Hirtella*, *Hunga*, *Kostermanthus*, *Magnistipula*, *Maranthes*, *Neocarya*, *Parinari*.

This in fact is the way Hallier (1903) divided the genera, as far as he had seen them. Defined in this way the tribes do not cut across any generic limits, with the exception of *Licania*, one species of which , *L. licaniiflora*, has a laterally inserted ovary. In the taximetric analyses (Prance 1963; Prance *et al* 1969) the two tribes were studied separately. Increased acquaintance with the family, however, has suggested a more natural grouping into four tribes based on a much wider range of characters.

We have found these groups useful in organizing and presenting the data included in the conspectus, and believe that they *may* correspond to four main lines of divergence within the family, but this is no more than a hypothesis to be tested when more information becomes available. Because so many of the genera are sharply defined, contemporary missing links are few in number, and for that reason it may ultimately be found that some genera, e.g. *Hunga* and *Grangeria*, would be better placed elsewhere.

8. Distribution and ecology

This chapter is a brief synthesis of many scattered observations, both published and unpublished, made by ourselves and others. Further details on ecology can be found in part II, under the individual genera, where bibliographic and other references are given. Detailed distribution maps of the African species (excluding *Dactyladenia*) have been published by White (1976*a*, *b*), and have been prepared for the American species (Prance 1988). Our knowledge of the family in the Indo-Australian region is less complete; few maps are available, but detailed information on distribution for some genera is given by Kostermans (1965*a*, *c*, *d*) and for *Hunga* by Prance (1979*c*). Terminology of vegetation types follows Prance (1979*f*, 1987) for the Neotropics, and White (1983*a*, *b*) for Africa.

(*a*) *Distribution*

(i) *General distribution*

The Chrysobalanaceae is a pantropical family (figure 7). It extends eastwards as far as Samoa, and elsewhere occurs on some remote islands such as Mauritius and Réunion. In all but the driest parts it is prominent in the vegetation. It ranges beyond the tropics only in the southeastern United States, southern Brazil and South Africa, but only four of its 494 species are involved. Most species are concentrated near the Equator, and numbers diminish rapidly to the north and south. Thus, in America, only 24 species (16 endemic) are found on the mainland north of the Panama Canal, and only six species (three endemic) occur on the Caribbean islands, if Trinidad is excluded. Similarly, on the African mainland only seven species extend beyond 15° N and 15° S.

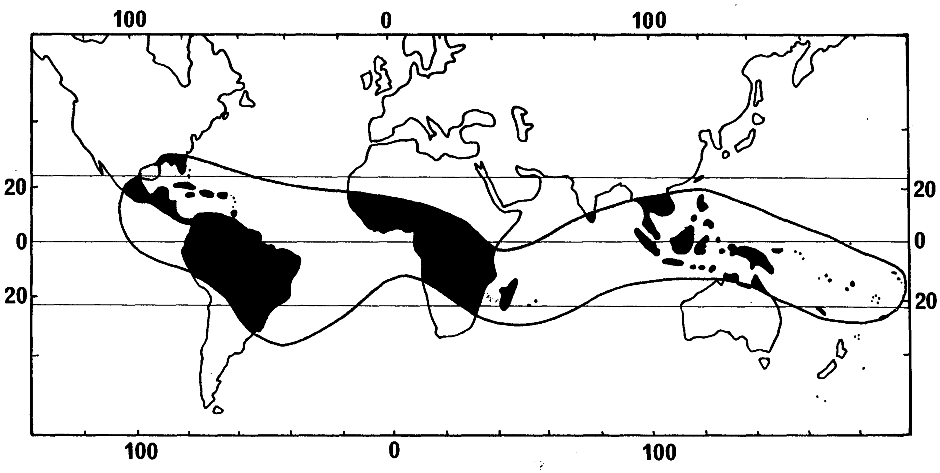

Figure 7. Distribution of Chrysobalanaceae.

Most Chrysobalanaceae occur in frost-free areas, but *Hirtella hebeclada* in South America and *Parinari capensis* in South Africa extend southwards into regions that experience regular frosts. A little further north, *Couepia grandiflora* and *Licania humilis* in the cerrados of Brazil (Silberbauer-Gottsberger *et al.* 1977), and *Parinari excelsa* in montane forest in south-central Africa (Chapman & White 1970) are damaged by, but recover from, occasional severe frosts. *Licania michauxii* also survives occasional frosts in the southern U.S.A.

The family is predominantly lowland and is poorly represented at high elevations. Thus, in

America only about 17 species of *Couepia*, *Hirtella* and *Licania* are confined to high mountains, but mostly below 1900 m. In Africa six species (*Hirtella zanzibarica*, *Magnistipula butayei*, *Maranthes glabra*, *Parinari capensis*, *P. curatellifolia* and *P. excelsa*) ascend at least as high as this, but none is restricted to upland areas and all of them are widespread in the lowlands.

The distribution of the tribes, genera and species in the American, African and eastern tropics is summarized in table 6, and the distributions of individual genera are shown in figures 8–14. All four tribes are pantropical, but the distribution of genera and species is very uneven. More than three quarters of the species occur in the Neotropics, but less than half of the genera. By contrast, all but three genera occur in the Old World.

TABLE 6. DISTRIBUTION OF THE TRIBES, GENERA AND SPECIES OF CHRYSOBALANACEAE IN THE AMERICAN (1), AFRICAN (2) (INCLUDING MALAGASY) AND EASTERN (3) TROPICS†

		area		
	1	2	3	notes
Chrysobalaneae				
Chrysobalanus	2	1	—	*C. icaco* in America and Africa
Grangeria	—	2	—	—
Licania	188	1	3	—
Parastemon	—	—	2	—
Parinarieae				
Bafodeya	—	1	—	—
Exellodendron	5	—	—	—
Hunga	—	—	11	—
Neocarya	—	1	—	—
Parinari	18	6	21	*P. excelsa* in America and Africa
Couepieae				
Acioa	4	—	—	—
Couepia	67	—	—	—
Maranthes	1	10	1	—
Hirtelleae				
Atuna	—	—	11	—
Dactyladenia	—	27	—	—
Hirtella	102	1	—	—
Kostermanthus	—	—	2	—
Magnistipula	—	11	—	—
endemic genera	3	5	4	—
total genera	8	10	7	—
total species	387	61	51	total 497 species

Three genera, *Licania*, *Maranthes* and *Parinari*, are pantropical, and two others, *Chrysobalanus* and *Hirtella*, are amphiatlantic. *Hirtella*, *Magnistipula* and *Parinari* occur in both Africa and Madagascar. In general, the group seems to be well adapted to crossing the oceans. Two species, *Chrysobalanus icaco* and *Parinari excelsa*, occur on both sides of the Atlantic, and two others, *Hirtella zanzibarica* and *Parinari curatellifolia*, are common to Africa and Madagascar. A few species, including *Atuna excelsa*, have reached many islands in the South Pacific.

(ii) *Intracontinental disjunctions and vicariance*

Several species show wide intracontinental disjunctions. Thus, in Africa, seven species, namely *Licania elaeosperma*, *Magnistipula butayei*, *M. cupheiflora*, *M. zenkeri*, *Maranthes aubrevillei*,

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† See note (4) added in proof, p. 184.

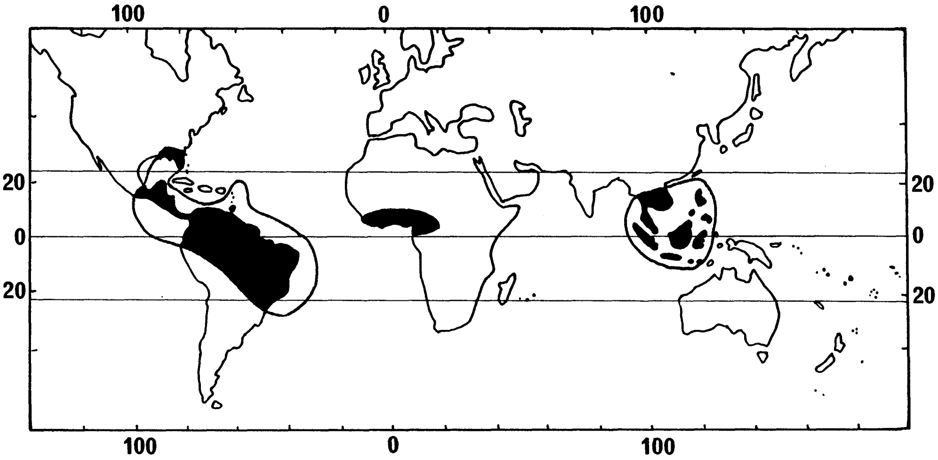


FIGURE 8. Distribution of *Licania*.

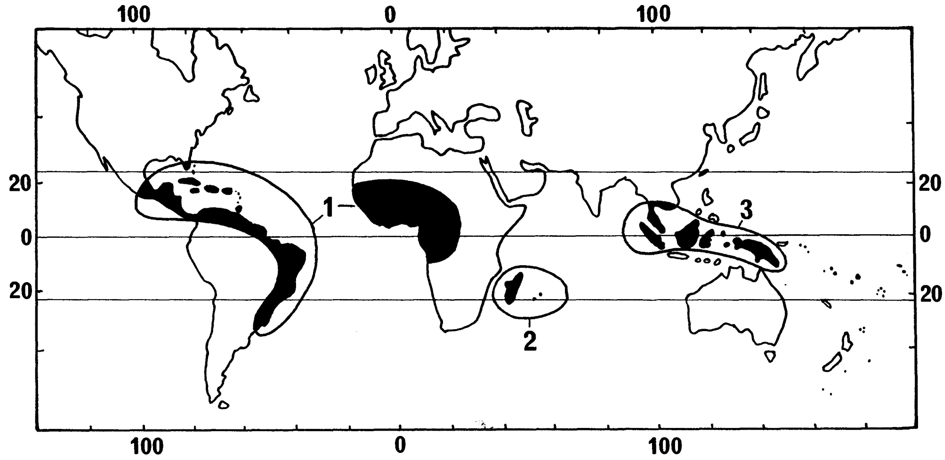


FIGURE 9. Distribution of *Chrysobalanus* (1), *Grangeria* (2) and *Parastemon* (3).

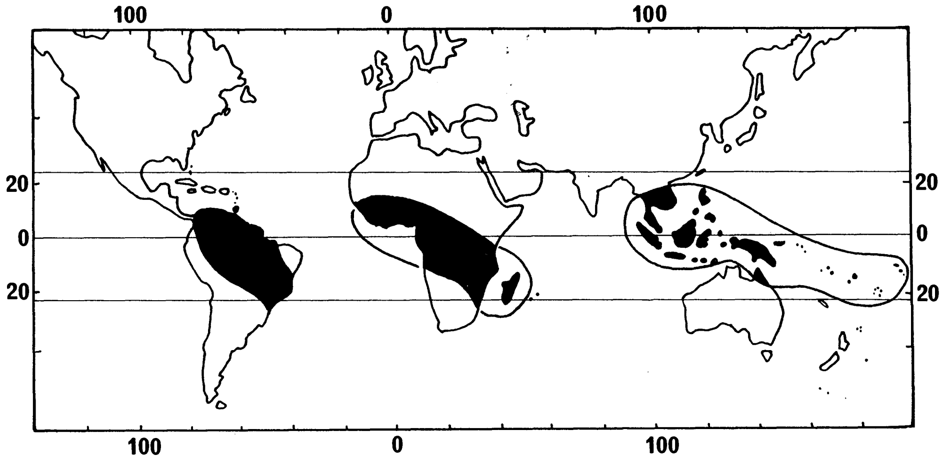


FIGURE 10. Distribution of *Parinari*.

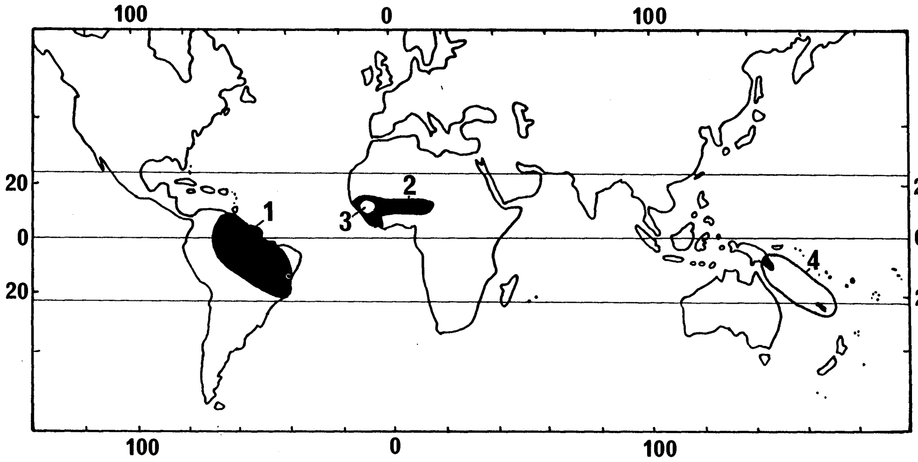


FIGURE 11. Distribution of *Exellodendron* (1), *Neocarya* (2), *Bafodeya* (3) and *Hunga* (4).

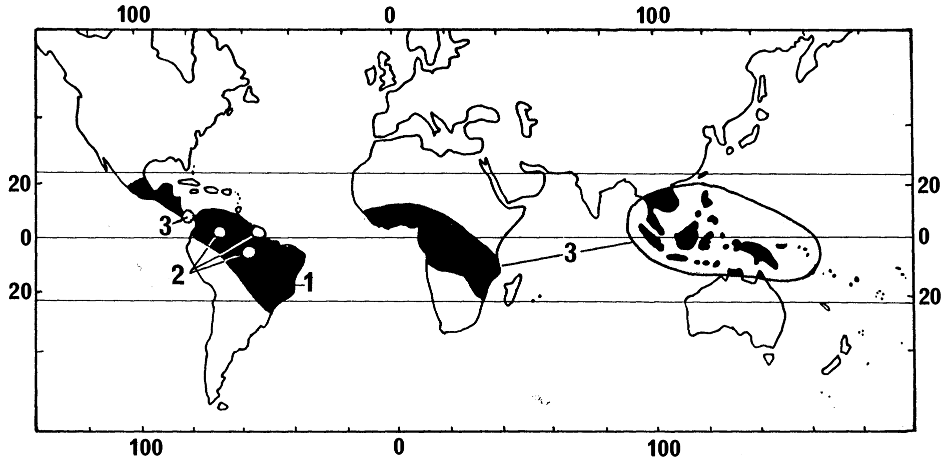


FIGURE 12. Distribution of *Couepia* (1), *Acioa* (2), and *Maranthes* (3).

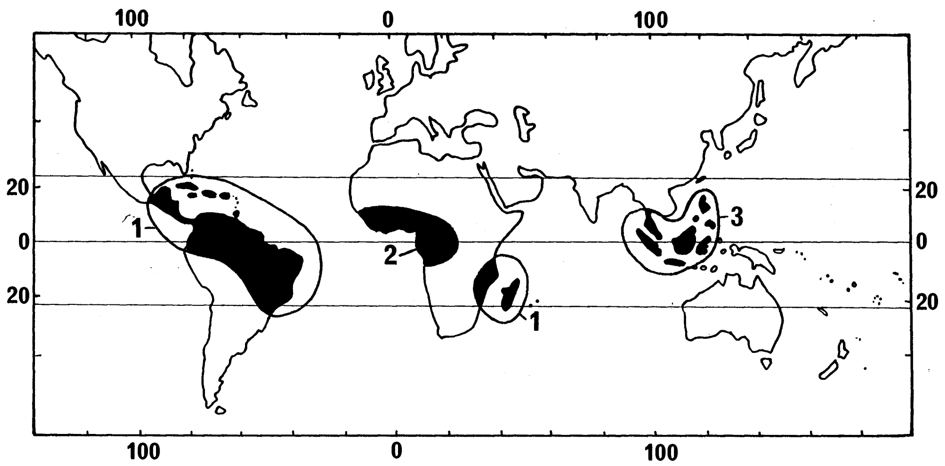


FIGURE 13. Distribution of *Hirtella* (1), *Dactyladenia* (2) and *Kostermanthus* (3).

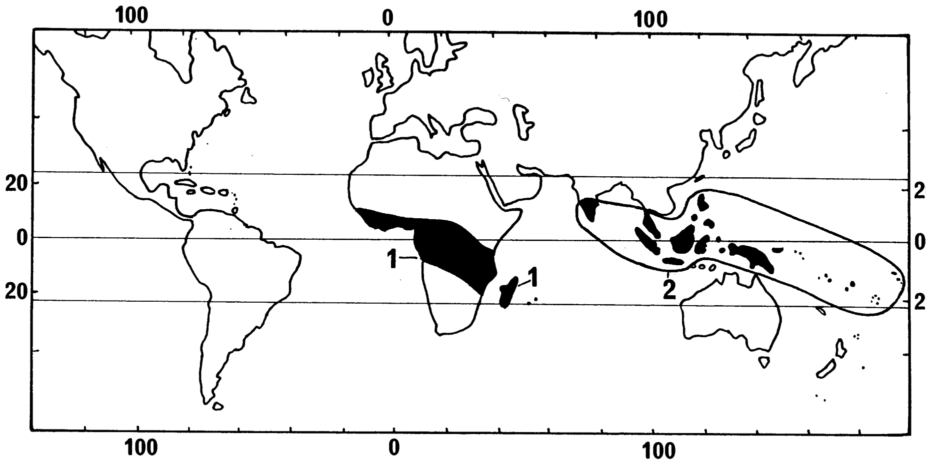


FIGURE 14. Distribution of *Magnistipula* (1) and *Atuna* (2).

M. chrysophylla and *M. glabra*, occur in each of the two main blocks of Guineo-Congolian rain forest and are absent from the Dahomey Gap which separates them (White 1979*b*). Except for *Magnistipula cupheiflora*, the disjunct populations are regarded as taxonomically identical. Only one species, *Magnistipula butayei*, is common to the Guineo-Congolian and East African rain forests; the East African population is subspecifically distinct, but collectively the species is an ecological and chorological transgressor.

Disjunctions also occur in the Neotropics (Prance 1981), e.g. between Central America and the Guianas (*Licania affinis*, *L. glabriflora*), between Amazonia and the coastal forests of Bahia (*L. cymosa*, *L. leptostachya* and *L. micrantha*), and between the Guianas and western Amazonian Peru (*L. guianensis*).

In general, vicariance involving closely related species is not very clearly shown among African Chrysobalanaceae. Three species, *Chrysobalanus icaco*, *Magnistipula butayei* and *Maranthes chrysophylla*, have geographically replacing, largely parapatric, subspecies. Two closely related species, *Parinari excelsa* and *P. hypochrysea*, are also parapatric. Quite frequently, however, closely related species, e.g. *Parinari excelsa*, *P. curatellifolia* and *P. capensis*, have overlapping distributions. For some geographically isolated species, e.g. in *Maranthes*, is is not possible to detect their closest relatives with a high degree of confidence (see § 10*d*).

Vicariance is somewhat better shown among neotropical species. *Licania macrophylla*, which occurs in periodically inundated várzea forest in the Guianas and Eastern Amazonia, is replaced by *L. oblongifolia* on terra firme in Central and Western Amazonia. *L. aracaensis*, which is only known from savanna on the top of a sandstone mountain north of the Amazon, is most closely related to *L. nitida* of the savannas of the cerrado of central Brazil. Many of the species isolated in the rain forests of the Chocó, west of the Andes, and in the forests of Atlantic coastal Brazil, have vicariant relationships with Amazonian species. Two vicarious species, *Licania arborea* of Mexico and Central America, and *L. rigida* of northeastern Brazil, occur in much drier habitats than most species in this family.

(iii) *Local endemics*

In South America 154 species (44 %) have extremely restricted distributions (Prance 1982). For Africa the proportion (18 species, 32 %) is somewhat lower.

(iv) *Chorological and ecological transgressors*

Most Chrysobalanaceae have neither very localized nor very extensive distributions, and occur under a relatively restricted range of ecological conditions. A significant minority, however, including *Chrysobalanus icaco*, *Licania apetala*, *L. heteromorpha*, *L. hypoleuca*, *L. kunthiana*, *L. octandra*, *Magnistipula butayei*, *Neocarya macrophylla* and *Parinari excelsa*, are ecological and chorological transgressors, in that they occur in more than one major phytochorion and more than one major physiognomic vegetation type, and often show a wide range of growth forms (White 1978*b*; de Souza 1979*a*; Prance 1982).

(*b*) *Habitat and vegetation types*

The majority of species occur in lowland rainforest, both on well-drained soils and in swampy places, and species of *Couepia*, *Licania*, *Maranthes* and *Parinari* are often prominent members of the canopy. Chrysobalanaceae are often also abundant in other vegetation types, although the number of species is relatively small. Thus in South America the family is represented in:

(a) *savanna* (wooded grassland) by *Exellodendron coriaceum*, two species of *Couepia*, 11 species of *Hirtella*, six species of *Licania* and *Parinari maguirei*;

(b) *restinga* (coastal scrub behind sand bars in eastern Brazil) by *Chrysobalanus icaco*, two species of *Couepia* and four species of *Licania*;

(c) *caatinga* (open scrub forest of arid northeastern Brazil, characterized by abundance of cacti and spinous Leguminosae) by *Licania rigida*;

(d) *cerrado* (open woodland of the planalto of central Brazil) by two species of *Couepia*, two species of *Exellodendron*, two species of *Hirtella*, seven species of *Licania* and *Parinari obtusifolia*;

(e) *campina* (islands of scrub on sterile white sands of the Amazon basin) by *Couepia racemosa*, *Hirtella arenosa*, *Hirtella glabrata* and two species of *Licania*; and

(f) the inner margin of mangrove swamp by *Hirtella carbonaria*.

Three South American species, *Couepia cataractae*, *C. maguirei* and *Hirtella angustissima*, are rheophytes (G.T.P., personal observations; van Steenis 1981).

Chrysobalanus icaco subsp. *icaco* is one of the most characteristic species of coastal thicket on both sides of the Atlantic, but it also occurs further inland in open vegetation on waterlogged soils. The subspecies *atacorensis* is widely distributed on river banks in tropical Africa. Most other African species of Chrysobalanaceae are confined to forest, especially lowland rainforest, but *Bafodeya benna*, *Magnistipula butayei*, *Maranthes floribunda*, *M. polyandra*, *Neocarya macrophylla* and *Parinari curatellifolia* occur in various types of woodland and wooded grassland.

The savanna species show various adaptations to fire. In *Maranthes polyandra* and *Parinari curatellifolia* in Africa, and in *Couepia grandiflora*, *Hirtella ciliata* and the tree form of *Licania humilis* in America, the older branchlets are covered with cork in which buds, protected by hairy scale-leaves, are embedded. Fire destroys the younger shoots and stimulates the development of epicormics from the dormant buds (de Souza 1979*a*; G.T.P., personal observations). In the absence of fire, the geoxylic suffrutex *Parinari capensis* is capable of a limited amount of upward growth, but eventually the shoots become moribund and die. It seems as if in this species, as in other obligate suffrutices, fire is necessary for the maintenance of healthy growth and full reproductive vigour (White 1976*c*).

Within the family there are six species of these geoxylic suffrutices ('trees which have gone underground' (White 1976*c*)). They show an extreme form of ecological specialization in that, compared with their arboreal relatives, they have lost their main vertical axes both above and below ground. The principal axes lie just beneath the surface of the soil and radiate outwards for considerable distances. In *P. capensis* they closely resemble the root systems of *P. curatellifolia* described and illustrated by de Souza (1979*a*), although they are usually referred to as 'rhizomes'. Their true nature remains to be established. The African species *Magnistipula sapinii* and *Parinari capensis*, both obligate suffrutices, are widespread in sparse, wiry, edaphic grassland on certain nutrient-deficient, seasonally waterlogged soils in the Zambezian region. In two American species, *Licania humilis* and *Parinari obtusifolia*, which occur in the cerrados of central Brazil, the suffruticose habit is not fixed and populations of shrubby individuals or small gnarled trees also occur. *Licania dealbata*, also a species of cerrados, appears to be an obligate suffrutex, as is *L. michauxii*, which is abundant in pinelands, oak scrubland and on sand dunes in the south-eastern United States. Two tree species of savanna, *P. curatellifolia* in Africa (F.W., personal observations) and *P. nonda* in Australia (G.T.P., personal observations), when subjected to recurrent fires, can survive as non-flowering coppice from the roots, less than 1 m high, and so simulate the suffruticose condition.

(*c*) *Edaphic specialization*

Little precise information is available on the ecology of Chrysobalanaceae, but it seems that in general the group is characteristic of nutrient-deficient soils, especially those derived from sandstone or acid igneous and metamorphic rocks. Thus in South America several species of *Couepia*, *Hirtella* and *Licania* are abundant on sterile white fluviatile sands in the Amazon and Essequibo basins. In Africa, two species of *Parinari*, *P. congensis* and *P. congolana*, are locally abundant on sandbanks in the Zaire basin, and *Neocarya macrophylla*, throughout its wide range in West Africa, seems to be confined to sandy soils. Some species of restricted distribution, such as *Hirtella cowanii*, *H. orbicularis*, *Licania aracaensis*, and *Parinari maguirei* in the Guyana Highlands, and *Bafodeya benna* in West Africa, occur on sandstone outcrops. The oligotrophic Kalahari Sands of the Upper Zambezi basin are the centre of an extremely diversified geoxylic suffrutex flora, of which *Parinari capensis* and *Magnistipula sapinii* are conspicuous members (White 1976*c*). Elsewhere in the Zambezian region, Chrysobalanaceae are absent from the most fertile, rejuvenated and alluvial soils (F.W., personal observations). In West Africa de Souza (1979*a*) found that *Chrysobalanus icaco*, *Maranthes robusta* and *Parinari congensis* occur principally on Quaternary sand in Bénin. In Ghana *Maranthes glabra* is characteristic of base-poor soils (Hall & Swaine 1981).

The high mountains of East Africa are either of recent volcanic origin or are formed from ancient crystalline rocks of the Basement Complex. Four species of Chrysobalanaceae, *Hirtella zanzibarica*, *Magnistipula butayei*, *Maranthes goetzeniana* and *Parinari excelsa*, occur on the crystalline mountains, but the family seems to be absent from the volcanic mountains.

Some Chrysobalanaceae which are not confined to the poorest soils become much more abundant when competition is diminished because of low soil fertility. *Grangeria borbonica* behaves in this way on Réunion, where the soils, although derived from volcanic rocks (basalt), are heavily leached owing to the high rainfall and the steepness of the slopes. Similarly, *Parastemon urophyllus* in Sarawak is abundant in scrub forest towards the centre of peat swamps, whereas on better soils it grows much taller but is also much rarer. *Couepia racemosa* shows similar characteristics. It is an occasional species in lowland rainforest, but becomes much more abundant in the white sand campinas of Central Amazonia, where it is greatly reduced in size.

Three endemic species of *Hunga* in New Caledonia are confined to serpentine soils.

(*d*) *Sclerophylly*

The majority of Chrysobalanaceae, possibly all, have, to varying degrees, scleromorphic leaves, characterized by some or all of the following features: thick cuticle, dense pubescence, sunken stomata, and a high incidence of sclerenchyma. The foliar anatomy of an ecophyletic series in *Parinari* has been described by Homès *et al.* (1951). The species studied, namely *P. tenuifolia* (= *P. excelsa*), *P. holstii* (= *P. excelsa*), *P. mobola* (= *P. curatellifolia*) and *P. latifolia* (= *P. capensis*) occur in a wide range of vegetation types, including lowland rainforest, montane forest, savanna woodland and suffruticose grassland. Homès *et al.* found no qualitative differences in the anatomy within this series and suggest that its xeromorphy was acquired during a former epoch when a xerophytic flora was more widespread in central Africa.

More recently it has been suggested that some sclerophyllous leaves might be an adaptive response, not primarily to climatic conditions, but to nutrient-deficient soils, especially those low in phosphorus (Loveless 1961, 1962; Beadle 1966). At least some sclerophyllous vegetation seems to have a metabolism that functions at phosphorus and nitrogen levels which are too low for mesophytic plants. This hypothesis is supported by the study of Sobrado & Medina (1980) in Venezuelan Amazonas of sclerophyllous bana vegetation, which includes *Hirtella punctillata* among its members.

The open, stunted bana occurs on the more elevated parts of a catena on sandy oligotrophic soils where there is a widely fluctuating water table. The lower slopes are occupied by a more luxuriant campina vegetation. Annual rainfall is more than 3000 mm and the soils are very acidic (lowest recorded pH value 3.6) and have high levels of exchangeable Al and Mn. Sobrado & Medina (1980) concluded that the sclerophylly had evolved in response to the oligotrophic soils and fluctuating water table, that the leaf structure reduces water loss, and that the leaf metabolism functions at low levels of N and P.

(*e*) *Pollination*

For most genera little is known, and for others there are only scattered observations, which are summarized in the Conspectus. Only two species, *Couepia longipendula* and *Maranthes polyandra*, have been studied in detail. Both are pollinated by bats. The majority of *Couepia* species, however, appear to be sphingophilous, as are possibly some species of *Maranthes*. The small flowers of *Licania*, *Exellodendron*, *Parinari* and *Magnistipula butayei* are visited by bees. The majority of species of *Hirtella* appear to be butterfly-pollinated, but at least one species may be secondarily pollinated by bees; the few white-flowered species may be pollinated by moths. The experiments of de Souza (1979*a*) have shown that *Chrysobalanus icaco* is self-compatible.

(*f*) *Dispersal*

The fruits of Chrysobalanaceae are very uniform in basic structure but remarkably diverse in functional detail. Despite their uniformity they have become adapted to a wide range of dispersal agents, sometimes within a single genus or species. The adaptive features are usually lost in museum specimens and few species have been studied in the field.

Chrysobalanus icaco subsp. *icaco* is dispersed by ocean currents, and also by bats, rodents and monkeys, and possibly by birds; *C. cuspidatus* is said to be dispersed by birds.

Some species of *Licania* are bat-dispersed, whereas the fruits of several South American riverine species float and are also eaten by fish; those of the African species *L. elaeosperma* are also transported by water. In the Far East, *L. splendens* is dispersed by the fruit pigeon, *Ducula aenea*.

Various species of *Parinari* are known to be dispersed by bats, elephants, baboons and other primates, a scatter-hoarding squirrel, fruit pigeons, rheas, emus, agoutis and fish. *P. congensis* is dispersed by fresh water. Species of *Couepia*, *Licania* and *Parinari* are frequently eaten by bats in the Neotropics.

The fruits of *Acioa guianensis* are transported by fresh water and those of *A. edulis* are eaten and possibly dispersed by agoutis. Some species of *Couepia* are dispersed by agoutis, and others, apparently, by bats.

Maranthes corymbosa is dispersed by birds, most notably hornbills and fruit pigeons, and, at least for short distances, by a scatter-hoarding squirrel. The fruits of some African species of *Maranthes* are eaten by monkeys, which are possibly mainly destructive.

Atuna is dispersed by ocean currents and a scatter-hoarding squirrel and possibly by wild pigs.

Bird dispersal has been observed for *Hirtella racemosa* and apparently is prevalent in the genus.

(*g*) *Myrmecophily*

(i) *Introduction*

The presence of extrafloral nectaries in nearly all Chrysobalanaceae suggests that they are myrmecophytes in the sense of Warburg (1892) in that they have regular associations with ants. No species of Chrysobalanaceae, however, has been studied in detail, and the nature of the association is clearly variable within the family.

Since the early days of tropical ecology there has been controversy over the nature of myrmecophily, especially its mutualistic aspects. The great naturalist explorers, such as Belt and Schimper, have favoured a symbiotic explanation, whereas some physiologists, e.g. Liebig, have suggested that the function of extrafloral nectaries is purely to secrete superfluous carbohydrates in growing organs (for discussion see van der Pijl 1955; Bentley 1976, 1977). Recent work has shown beyond any doubt that in many cases the association is to the benefit of both plant and ant.

The first record of myrmecophily in Chrysobalanaceae is that of Spruce in a paper read to the Linnean Society in 1869, although not published until nearly 40 years later (Spruce 1908). Spruce described a variety of plant modifications, principally sacs on leaves, hollow petioles, and hollow, sometimes swollen, stems which provide residences for ants. Some of the ant species were said to bite but not to sting, whereas others are ferocious and virulent. Spruce thought that the ants were of no more use to their hosts, than fleas and lice to theirs, and that the modifications of the plant originated as a direct response to the activities of the ants and subsequently became inherited. In his paper, Spruce devotes much space to plants with leaf sacs, especially in Melastomataceae, but also in Rubiaceae, and in *Hirtella physophora* in Chrysobalanaceae. He noticed that in some species with myrmecophilous inflations the ants make covered ways of intercommunication along the outside of the stem and branches, and commented that in all the leaf-sac plants he knew, regardless of systematic position, the pubescence consists of long hairs having a tubercular base, although he could not suggest an explanation.

Recent studies, notably by Janzen (1966, 1968, 1972, 1974), Bentley (1976, 1977) and Huxley (1978, 1980, 1986), some of them experimental, have unequivocally confirmed the mutualistic relations between ants and plants, and have shown their remarkable complexity. Leaving aside pollination and seed dispersal, it seems that there are five main types of relation:

(i) ants protect plant;
(ii) ants provide plant with nutrients;
(iii) plants provide food;
(iv) plants provide brood chambers;
(v) plants provide protection for ants from *their* predators.

Even in the most fully investigated cases much remains to be done (C. R. Huxley & M. Jebb, unpublished observations, concerning Rubiaceous epiphytic ant plants). Nevertheless, it is apparent that five types of relation may interact in different ways and to different degrees, and in many cases the full range of potential relation has not been explored. For these reasons the complex terminology of van der Pijl (1955) is difficult to apply. It is possible that all five interactions occur in Chrysobalanaceae, although evidence for relation (ii) is, at present, weak.

(ii) *Extrafloral nectaries*

Extrafloral nectaries probably occur on the leaves of all species of Chrysobalanaceae, but are more conspicuous on juvenile than on mature leaves, and are not always readily discernible in the herbarium. They may occur on the petiole, at the base of the lamina, or elsewhere on the lower leaf-surface. Their structure and distribution appear to be of considerable taxonomic significance (see §3).

Conspicuous nectaries are found on the bracts and bracteoles and often also on the calyx in *Grangeria* and in many species of *Dactyladenia*, *Hirtella* and *Magnistipula*. Small discoid glands occur on the sepals of *Acioa* and less conspicuous glands on the calyx of two species of *Couepia*.

The defensive role of nectar-feeding ants in general is now well established. For Chrysobalanaceae no detailed studies have been made but G.T.P. (personal observations) has seen a species of *Iridomyrmex* (Dolichoderinae) visiting the foliar glands of *Couepia racemosa*, and Chevalier (1931) has recorded swarms of small black ants obtaining nectar from the extrafloral nectaries of *Magnistipula zenkeri*.

In Bénin, *Chrysobalanus icaco* is sometimes inhabited by the ant *Oecophylla longinoda*, which constructs its nest from *Chrysobalanus* leaves held together by a silky secretion. This extremely aggressive species feeds on the ripe fruits and foliar secretions of *Chrysobalanus* and defends the plant against unwelcome intruders. Other, as yet unidentified, species of ant obtain nectar from aphids, which they tend on the *Chrysobalanus* plant (de Souza 1979*a*).

(iii) *Brood chambers*

In addition to *Hirtella physophora* (mentioned by Spruce) conspicuous inflations, within which ants rear their young, occur in several other related species of *Hirtella*, namely *H. dorvalii*, *H. duckei*, *H. guainiae*, *H. myrmecophila*, *H. revillae* and *H. vesiculosa*. They all have the coarse bristle-like indumentum, first noticed by Spruce, which the ants frequently use as a scaffolding when building their protective runways from organic and inorganic debris. The ants inhabiting *Hirtella* have not been studied in the field but W. W. Benson (personal communication) has looked at herbarium specimens and found considerable ant–plant specificity. Ants inhabiting *H. duckei* have been identified as a species of *Solenopsis* (Guarim Neto & Asakawa 1978). Ants belonging to the genera *Allomerus* (Myrmicinae) and *Azteca* (Dolichoderinae) have been recorded as colonizers of *Hirtella* by Benson (1985).

The advantage conferred on *Hirtella* by the ants remains unstudied. It is not known whether the inner surface of the brood chambers is able to absorb nutrients derived from the ant's faeces or from any other source. Nor is it known how effective the ants are in defending the plant. Janzen (1974, p. 257) reports that the ants inhabiting the foliar pouches of some neotropical melastomes are notable for their timid nature but that some species fill the foliar pouches with organic debris.

It is possible that the poorly known *Magnistipula bimarsupiata* from Gabon, which also has a coarse tomentum, provides brood chambers. It has two small inflations at the base of the lamina and some internodes are swollen and perforated.

(iv) *Protective armature provided by the plant*

A neglected aspect of myrmecophily is the way in which the structures of the plant have become modified so as to provide protection for the ants against their predators. It seems that within the *H. physophora* group of species we can see such transformations happening today. The ants build most of their runways in close proximity to the brood chambers and it is there that the protective bristles are best developed. The bristles are typical hairs, mostly borne on the leaf-bearing stems, but in some species the axillary inflorescences sometimes lose their reproductive function and are changed into bristle-bearing axes. Thus in *H. physophora* the hairs on inflorescences borne near the brood chambers are generally longer, denser and stiffer than those on cauliflorous inflorescences on the main trunk far from the nesting sites of the ants. In this species, in some axillary inflorescences the flowers fail to develop but the bracts are elongate and bear long hairs. In *H. duckei* all the flowers in some inflorescences remain at an arrested state of development and are densely setose. An even more extreme condition is shown by *H. guainiae* where, in some inflorescences, the vestigial flowers are few and very small or even completely absent, and the inflorescence consists of little more than an elongated axis which is densely covered with setose hairs.

(v) *Origin of myrmecophilous features*

In addition to the armature just described, the family Chrysobalanaceae possibly provides clues to the origin of the inflations, though not in *Hirtella* itself. The most frequent position of extrafloral nectaries is towards the base of the lamina on the lower surface. In some species they are paired and quite large. In *Dactyladenia barteri* they are paired and occur at the bottom of shallow inflations. An intermediate stage between *Dactyladenia barteri* and the myrmecophilous Hirtellas possibly occurs in *Magnistipula bimarsupiata*. Its inflations sometimes have a circular gland inside them.

These and other evolutionary problems can only be resolved by comparative studies, principally on the living plant and using experimental techniques. A start has been made by

Benson (1985) who, since the above was written, has published some interesting hypotheses on the evolution of ant domatia in general.

(*h*) *Ecological phytochemistry*

Ecological aspects of phytochemistry might be more directly relevant to evolutionary studies than chemotaxonomy *sensu stricto* (see §12). The Chrysobalanaceae provides a virtually virgin field in this respect. In a study of the ecological implications of phenolic content of vegetation in two African rain forests, McKey *et al.* (1978) found that at one of their sites (Kibale forest in Uganda) the highest value for total phenolics in mature leaves occurred in *Parinari excelsa*, but the significance of this is difficult to assess in the absence of comprehensive community studies.

9. ECONOMIC USES

Members of the Chrysobalanaceae are used by the local people everywhere, for building, fuel, charcoal and in folk medicine. The fruits and seeds of some species are highly esteemed, and others are eaten in times of scarcity; some are used in the preparation of alcoholic beverages. At present, Chrysobalanaceae are mostly only of local importance commercially, but, with improved communications and technology, their potential as a source of construction timber, fruits, and edible and industrial oils appears to be promising.

(*a*) *Edible fruits and seeds*

Chrysobalanus icaco is tinned and bottled in syrup and sold in Colombia and Venezuela under the name *Icacos*, but in some other places the fruit is said to be inedible or insipid. *Couepia bracteosa* is sold in the markets of Manaus (as *Pajurá*) and also in Guiana. *C. rufa* is marketed as *Oiti coro* in Pernambuco. *C. chrysocalyx* also has an edible fruit. *C. longipendula* is cultivated around Manaus for its edible cotyledons, from which oil is also extracted. The cultivar is a low bushy tree, in constrast to the tall tree of primary forest. *C. edulis* is also cultivated in villages in the Rio Purus and Solimões region of Amazonia for its oil, which is used in cooking and for making soup. In the Peruvian Amazon *C. subcordata* is frequent in the gardens of Indians, who prize its edible seeds. *Licania pyrifolia*, *L. platypus* and *L. tomentosa* all have edible seeds and are locally cultivated. Several species of *Parinari* have edible fruits or seeds; the latter are sometimes roasted. Charred kernels of a species of *Parinari* have been found at archaeological sites on the Nyika Plateau in Malawi. In parts of Africa *P. curatellifolia* provides one of the best wild fruits, and both a non-intoxicating and a very potent liquor are made from them. In Amboina a dish called *Koku koku* is prepared from the mashed seeds of *Atuna excelsa* mixed with raw or fried small fish, ginger, onions, chillies and lime juice. The African species *Neocarya macrophylla* and *Parinari curatellifolia* are regarded as potential fruit trees in Northern Australia (T. Willing, personal communication, 9 June 1982).

(*b*) *Industrial oils*

The oil of *Licania elaeosperma* was formerly used in paints and varnishes as a substitute for tung oil. In 1941 Brazil exported 16606 t of *L. rigida* seeds for the same purpose, and the species is still grown for oil in northeast Brazil. The closely related *L. arborea* produces a flammable oil, and the seeds are strung on sticks to provide illumination by the indigenous people in Central America. It is also used in the manufacture of candles, soap and axle grease.

(*c*) *Wood*

Small trees, which often provide durable, termite-resistant wood, are used locally for building and for fuel and charcoal. *Chrysobalanus icaco* is an important source of merchantable fuel in Bénin (de Souza 1979*a*). The specific name of *Hirtella carbonaria* reflects its use as a source of charcoal. In Nupe, Nigeria, *Maranthes polyandra* formerly provided the blacksmiths with the best charcoal.

Despite the large supplies potentially available, commercial sawn timber is produced only in relatively small amounts. This is because its high silica content blunts even tungsten-tipped saws, although this limitation is likely to be overcome in the future (F. A. Hughes, personal communication). Even at present, because the wood of many species is resistant to marine borers, it is used throughout the tropics for piers and other marine constructions.

(*d*) *Folk medicine*

The family is an important source of remedies. In Bénin alone, the local species are used in dental care, the treatment of wounds, and in the cure of coryza, fevers, bronchial disorders, asthma and diarrhoea (de Souza 1979*a*). In Brazil *Chrysobalanus icaco* is used as a remedy for diarrhoea and in the treatment of diabetes (Almeida Costa 1977).

(*e*) *Shade plants*

Licania tomentosa is widely planted for this purpose outside its natural range in Brazil. It is one of the most used shade plants in the streets of Belém and Manaus as it can be pruned into any shape and produces abundant thick growth. *Couepia subcordata* is also used as a street plant in Manaus, Lábrea and elsewhere.

(*f*) *Ceramics*

Throughout Amazonia the bark of various species of *Licania*, e.g. *L. apetala*, *L. longipetala* and *L. octandra*, is burnt and the ash, which is full of silica grains, is mixed with clay to strengthen pottery. This usage by the Deni Indians has been described by Prance (1973*b*).

(*g*) *Human ornamentation*

Leaf galls of *Licania cecidophora* are made into necklaces and used in the manufacture of gigantic mail-like capes by the Aguaruna Jivaro Indians in north-central Peru (Berlin & Prance 1978). The use of insect galls in human ornamentation has not apparently been reported for any other human society.

Oil from the seed of *Licania elaeosperma* is used by women in West Africa as a hair pomade. That from *Atuna excelsa* is an ingredient of a hair dressing in the Caroline Islands.

(*h*) *As a caulking and waterproofing agent*

In the Solomon Islands the principal use of *Atuna excelsa* sensu lato is for caulking the seams of plank-built canoes. The seeds, which are known as 'putty nut' are pounded to a putty-like consistency. After application the putty hardens and darkens, but if exposed too long to the sun it cracks, so canoes drawn up on the beach are often kept in the shade of sheds. In the central and southeastern Solomons it is used for setting shell inlay in wood bowls, figures and other articles. The northwestern Solomon Islanders also use it for waterproofing bottles made from gourds. In the Admiralty (Manus) Islands, coiled baskets are coated with it to make them waterproof (B. A. L. Cranstone, personal communication, 14 June 1983).

10. THEORETICAL CONSIDERATIONS

(*a*) *Introduction*

During the period devoted to the present study there have been many publications on the theory and methods of taxonomy, phylogeny and biogeography. Much of this work is controversial and several antagonistic schools have emerged. In this debate, so far as we are aware, monographs of large, widespread and diverse groups have played little part, but they can provide one of the most effective means of testing the general application of new ideas. It is with this in mind that, *inter alia*, we consider in the following pages, in the light of our knowledge of Chrysobalanaceae, such controversial topics as numerical taxonomy, cladistics and vicariance biogeography, and the detection of monophyletic groups. This does not mean that we think that a monograph can be used as a simple yardstick to evaluate new methods and ideas; the group in question may be so atypical that the test is of limited value. But we have no reason to think that this is true for Chrysobalanaceae. Our knowledge of other families, notably Ebenaceae, Lecythidaceae and Meliaceae, and our general acquaintance with tropical floras and vegetation, leads us to believe that the Chrysobalanaceae is sufficiently representative for our conclusions to be of general interest.

We do not intend to review the literature on the topics mentioned above, but merely to refer to a few publications relevant to our argument. Further references can be found in works by Sneath & Sokal (1973) on the early development of numerical taxonomy, Wiley (1981) and Nelson & Platnick (1981) on cladistics and vicariance biogeography, and Funk & Wagner (1982) on botanical cladistics. For a recent review of computer-assisted taxonomic analysis in biology see Abbott *et al.* (1985).

A disappointing feature of some of the recent theoretical developments is that their protagonists effectively divorce taxonomy and phylogeny from ecology and pay little regard to the living organism. During this same period, however, there has been a great increase in fieldwork in the tropics, and some recent advances in tropical ecology, especially in plant–animal interactions, are having a beneficial impact on taxonomy and evolutionary studies. To some extent we have been directly or indirectly involved in these developments and have taken them into account in the present work. We would go further, however, and assert that taxonomy can rarely be fully effective without such knowledge, and in its absence attempts at evolutionary interpretation, if fossil evidence is not available, are often futile. The theoretical and practical implications in taxonomy of an ecological approach are discussed below (§§10*c* and 12*b*).

Some of our conclusions, especially those concerned with methods of evolutionary interpretation, are largely negative. We do believe, however, that, even when fossils are sparse or absent, valuable evolutionary hypotheses can sometimes be derived from the study of living organisms and the communities they form, not necessarily about the precise branching patterns within taxonomic groups, but rather about broad trends within taxonomic groups and the history of the biotas to which they belong. This is discussed in §11.

(*b*) *Numerical taxonomy*

When we started our work, numerical taxonomy was in its early stages and curiosity prompted us to investigate its possible role in establishing an objective taxonomy of the Chrysobalanaceae at generic level. This seemed particularly appropriate because the classification which was emerging from our study was radically different from those previously proposed and it seemed that these new procedures might offer a means of testing its consistency. Six investigations were undertaken, and the results of four of them have been published in some detail (Prance *et al.*, 1969). Continuing study has provided us with much more information on the group, and new insights. A brief reappraisal of our earlier work, together with some comments on the possible role of taximetrics in practical taxonomy, is appropriate, because the relative importance of taximetric and other methods is still a matter of contention, and uncertainty persists as to which mathematical models best serve the needs of taxonomy. Our taximetric analyses were confined to Hirtelleae as we then defined it (see §7). It included all but three of the 17 chrysobalanaceous genera. The analyses were based on only 140 of the 254 species included in the wider study, because complete material was not available for the others.

The character states for 21 characters were recorded: 11 double-state qualitative characters, 8 multistate qualitative characters, and 2 quantitative characters. In the light of the (in our opinion mistaken) recommendation of extreme pheneticists such as Sokal & Sneath (1963; Sneath & Sokal 1973) that at least 60 characters should be used, this might appear to be a small number. But of necessity it was confined to characters which are constant (or almost so) within species and vary between them. It also included all characters used by previous workers to delimit genera, plus some others.

The published taximetric analyses included two ordinations and two clustering procedures, as follows:

1. Principal-component analysis based on only the eight multi-state qualitative and the two quantitative characters.
2. Principal-component analysis based on all 21 characters.
3. Rubin's iterative model of clustering analysis based on all 21 characters.
4. The Wirth, Estabrook & Rogers model of single-link clustering with subgraph representation based on all 21 characters. This, alone of the four procedures, was designed to simulate as closely as possible what taxonomists actually do when they make a classification. It also presents the results in such a way that the investigator and his critics can follow the building of the hierarchical levels of resemblance.

It seemed from a preliminary analysis of the results that all four procedures, but to different degrees, confirmed the tentative conclusions we had reached, based largely on morphology but backed up by various anatomical studies. At that stage, however, we had not reached a final decision on three species, *Parinari benna*, *P. macrophylla* and *P. tessmannii*, and our decision to place them in *Bafodeya*, *Neocarya* and *Magnistipula* respectively was influenced by the results of the analyses.

Not surprisingly, in view of its design, the Wirth, Estabrook & Rogers model reproduced our classification virtually unchanged. The Rubin model also identified several of our proposed genera but produced an extremely heterogeneous 'dump cluster' which included several very distinct taxa.

At this stage in our work we probably read more into the results of the principal-component analyses than was justified. All of our genera could be identified on at least one projection, but some were confluent and could only be circumscribed by using pre-existent knowledge. In all the projections there was at least one mixed group. Some applications of ordination methods to other groups (see below) have produced results which appear to be less taxonomically meaningful than those we obtained for Chrysobalanaceae. The reason for this may be that several of the 'unit' characters we used were subsequently found to belong to functional character-complexes (see §10*c*) which seem to indicate monophyletic groups of species (see §10*f*).

In a much more detailed comparison of the range of procedures then available for taximetric analysis, Bisby (1973; Bisby & Polhill 1973) found that only single-link clustering (also using the Wirth, Estabrook & Rogers model) produced taxonomically meaningful results. He also found that the results of principal coordinate analysis, even though it represents an advance in ordination technique, were difficult to interpret.

In our own study, the single linkage procedure formed clusters which correspond to our generic concepts and account for all but three of the 144 species. These three anomalous species were classified as follows.

Parinari canarioides: with *Magnistipula.*

P. argenteosericea: provided a link between '*Cyclandrophora*' (now *Atuna*) and *Exellodendron.*

Kostermanthus heteropetalus: with '*Cyclandrophora*'.

After the taximetric analyses were published, the morphology of all genera was reinvestigated. This study showed that *Parinari canarioides* and *P. argenteosericea* can readily be accommodated in *Parinari. Kostermanthus* was found to differ from all other Chrysobalanaceae in floral and fruit morphology to such an extent that generic rank seemed appropriate. The reinvestigation also revealed a multitude of additional taxonomically useful characters not used in the earlier work. In particular, it showed that some of the characters used in the analyses, e.g. stamen length and receptacle shape, are part of character complexes, which can be resolved into many individual diagnostic characters, as we have shown for *Couepia* and *Hirtella* (see §6*e*).

In publishing the results of our taximetric analyses, we did not subscribe to a widely held belief, publicized by Sokal & Sneath in their *Principles of numerical taxonomy* (1963), that numerical taxonomy would involve the replacement of orthodox taxonomy by a revolutionary automated process designed on a phenetic model of classification. That is why we preferred the term 'taximetrics' to numerical taxonomy. We said that we 'considered the computer as just another instrument available to make the work of the taxonomist more objective or more reliable or more understandable'. We published the paper in the belief that 'examples of the application of computer methods to actual taxonomic problems are worth much more than volumes of theorizing'.

Although the Wirth, Estabrook & Rogers model had been previously used in taxonomy, our own study was the first to apply it to a moderately large pantropical family in a monographic context. Bisby (1973; Bisby & Polhill 1973) subsequently used it to test Polhill's classification of the large and complex pantropical genus *Crotalaria* (Leguminosae: Papilionoideae). This study not merely confirmed the usefulness of the model as a taxonomic tool but showed that it is superior to others. Despite this, it has not yet been much used in monographic studies.

In retrospect, we believe that the analysis that used single-link clustering was worthwhile. It gave us confidence in the validity of our tentative taxonomic conclusions and led us to investigate floral and fruit morphology more deeply in order to account for the three anomalously placed species. The subgraphs showing the stages in cluster formation illustrated in precise quantitative terms the relationships of each species to all the others and, within the limitations of the characters selected, visually demonstrated the objectivity of the taxa proposed. But our subsequent experience has also confirmed our previously expressed belief that the computer is no more than a useful tool among many. In particular, for tropical groups of Angiosperms, and it is in the tropics that the future of taxonomy lies, we believe that there are other priorities. At the present time progress in taxonomy is more dependent on adequate material than on numerical methods, and the integration of taxonomy with general biology is only possible when the function of taxonomically important structures is known.

We believe that the use of numerical methods during the early stages of monographic study can provide a useful basis for further work, particularly since they involve a thorough investigation of all potentially useful taxonomic characters, during which the values for all characters must be scored and carefully analysed. When, however, function is unknown, or only dimly perceived, the results could be misleading. This is because of problems associated with the detection, selection and weighting of characters. This conclusion, based on our experiences of Chrysobalanaceae, has been strikingly confirmed by Prance & Mori (Prance 1976*b*; Mori *et al.* 1978; Prance & Mori 1978, 1979) for Lecythidaceae. In the latter, it was found that each genus has a suite of floral characters associated with its distinctive pollinators and precise mode of pollination. Each genus also has a distinctive fruit type corresponding to its mode of dispersal. Improvements on previous classifications depended on the collection of much new material backed up by extensive biological observations. A taximetric study without such resources could have been worthless.

Bisby (1970, 1973), using a program, CHARANAL, devised by G. F. Estabrook & D. J. Rogers, has shown that clustering procedures based on a smaller number of characters selected for high intercorrelations give taxonomically significant results, whereas those based on a larger number of unselected characters do not. Bisby's characters are correlated in a statistical sense; he does not mention functional correlation.

(*c*) *Unit characters and functional syndromes*

In the previous section we have described how we found some methods of numerical taxonomy to be of real, though limited, value. We believe that the small impact numerical taxonomy has had on practical taxonomy stems, in large part, from the failure of some of its advocates to understand the strengths of non-numerical precedures, and the limitations of particular numerical methodologies which are claimed to be universally valid. This can result in putting the cart before the horse.

In some methodologies the basic unit is the 'unit character' (Sneath & Sokal, 1973, p. 72), which 'within the study in hand cannot be subdivided logically, except for subdivision brought about by the method of coding'. Unit characters form the data matrices on which taxa are constructed. The shortcomings of this and related approaches have been discussed by Johnson (1970).

The character-complexes we have described for *Couepia* and *Hirtella* (see §6*e*, §18 and §19), we believe, can provide clues to truly objective and biologically significant taxonomy. We believe they are of wide application, though not necessarily at every taxonomic level, nor in all groups of organisms.

More than 150 years ago Martius & Zuccarini (1832) recognized *Couepia* and *Hirtella* on general appearance and diagnosed them correctly, using, for convenience, only a few characters. We have shown that, even in the herbarium, with little or no information on function, habit can be resolved into at least two character complexes. We have also shown experimentally that the rapid identification of specimens 'by eye' on general appearance alone is not the exclusive preserve of the trained taxonomist. It is the taxonomist's job to check whether the eye is being deceived by superficial resemblance, and, if it isn't, to attempt to translate habit into taxonomically useful characters. This we have also done, for *Couepia* and *Hirtella*, again experimentally. Some of the characters we discovered in this way cannot be expressed concisely, although they can easily be shown pictorially. These newly discovered characters are individually small; although they have high diagnostic values, few are absolutely diagnostic (see Appendixes 1 and 2). In isolation they would appear unconvincing to most herbarium taxonomists. Their significance lies in being highly correlated among themselves. It is the character complex that is absolutely diagnostic, or almost so. The individual characters of the complex we prefer to call 'component characters' rather than 'unit characters': the two methodologies we are discussing are so very different that a different terminology is called for.

There is nothing new about the visual methods we have described. They were used by the great masters of the past, on whose labours present-day and future taxonomy still depends. All that is new is that we have taken more trouble than is usual in trying to convert habit into usable characters and we attach a great deal of importance to function.

Evidence we have subsequently obtained suggests that the character complexes we have described for *Couepia* and *Hirtella* are in fact functional syndromes related to pollination, and to dispersal and establishment. The architecture and development of the inflorescence and the exact proportions of the flowers determine primarily the disposition in space and time of the polliniferous and stigmatic surfaces in relation to the structure and behaviour of potential pollinators, although they may also be effective in preventing the theft of nectar, or be associated with the development and dispersal of the fruit. Similarly, the precise details of the structure of the fruits appear to be closely related to dispersal, seedling emergence from the endocarp, and protection of seeds during development and at maturity.

When two such complex syndromes consistently occur together, as they do in *Couepia* and *Hirtella*, it seems likely that the taxa they characterize are monophyletic.

Detailed fieldwork is necessary to confirm that the character complexes we have described are in fact functional syndromes in the ways we suspect. That this is in fact so is suggested by the recent work of others on other groups of tropical trees. In a detailed study of the taxonomy and reproductive biology of the bat-pollinated genus *Parkia*, Hopkins (1981, 1983, 1984, personal communication) has shown that in the architecture and structure of the inflorescence there is a wealth of morphological detail closely related to the precise mechanism of pollen transfer, and that it is readily translatable into taxonomically useful characters. Indeed, it is only when function is understood in *Parkia* that a convincing taxonomy becomes possible. Pannell & Kozioł (1987) have found that within the Far Eastern genus *Aglaia* two main fruit types, dispersed by birds and primates respectively, differ in a host of morphological and chemical features related to the structure, behaviour and nutritional requirements of the dispersers.

(*c*) *Parallelism, sister groups and cladistics*

Our attempts to apply cladistic analysis to the Chrysobalanaceae were largely unsuccessful. We have found that the widespread occurrence of parallelism and the difficulty in identifying sister species preclude the construction of convincing cladograms except to a limited degree.

According to Wiley (1981), cladistics ('phylogenetic systematics') is a total approach to systematics, and by implication can be applied at all taxonomic levels and throughout the animal and plant kingdoms. By contrast, however, discussion has largely centred on abstract philosophical principles, theoretical examples, superficial comparisons ('the salmon, the lungfish and the cow'), taxa of the highest rank, and small groups of closely related species, among plants chiefly in Compositae, e.g. *Leysera* (Bremer 1978) and *Anacyclus* (Humphries 1981) and a few other families. We do not know of any critical, let alone successful, attempt to apply cladistic methods *in toto* to a large, widespread, taxonomically complex and recently revised group of plants such as Chrysobalanaceae. For this reason we believe our comments to be of general interest.

Some cladists, e.g. Bremer & Wanntorp (1978), mention possible limitations of cladistics, but they seem to consider them unimportant. Bremer & Wanntorp specifically mention two possible limitations, namely the widespread occurrence of parallelism and a lack of sufficient advanced characters ('apomorphies'). To these we would add a third: the frequent impossibility of detecting sister groups.

(i) *Parallelism and the lack of synapomorphies*

Bremer & Wanntorp (1978) realize that parallelisms may be so common as to make phylogenetic reconstruction impossible, but they evade the issue by stating that 'if one is interested in phylogeny this is a useless approach'. The approach, however, should be commensurate with the facts, and not influenced by preconceived ideas as to what the facts should be.

In Chrysobalanaceae we can show that parallelism is so rife as to exclude anything other than a very limited amount of phylogenetic interpretation. This can be done by applying a general theorem, as follows.

> If in a taxon two characters show two contrasting states, e.g. A and a, and B and b, and if they are distributed as ab, aB, Ab, AB (see below), then it logically follows that at least one character state must have originated at least twice in the group either through parallel gain or loss. It may not be possible to decide which character state is diphyletic, nor which is the primitive condition, but that is not necessary for the argument. If in a group several characters show this kind of relationship then it follows that parallelism has played an important part in the diversification of that group.

In the Chrysobalanaceae so many characters show the ab, aB, Ab, AB pattern that too few remain to satisfy the requirements of cladistic analysis.

Although the ideas underlying this 'principle of discordant characters' appear to be widely known (F. A. Bisby, personal communication; Cain 1982; Estabrook 1980; Le Quesne 1969; Patterson 1982; Wilson 1965) the principle itself does not seem to have been used as an analytical tool in taxonomic work. Cain, in a detailed discussion of homology and convergence, states that 'the possibilities of parallel or convergent development of characters have never been fully explored'. His independent formulation of the theorem is essentially the same as ours. He shows that its application to closely related forms in the animal kingdom brings to light many examples of independent variation. He also points out that apparent concordance might conceal convergence.

To return to the Chrysobalanaceae. The principle of discordant characters can be applied at any level, but we will only consider the relationships of genera. There are relatively few characters which are constant within genera and vary between them and hence are available for cladistic purposes above the generic level. Most of them show the ab, aB, Ab, AB pattern.

This is true, among others, for the following pairs.

(1) Staminal ligule present (a) or absent (A); ovary uni- (b) or bi- locular (B); e.g. *Dactyladenia* (ab), *Magnistipula* subgenus *Pellegriniella* (aB), *Couepia* (Ab), *Maranthes* (AB).

(2) Stomatal crypts present (a) or absent (A); ovary uni- (b) or bilocular (B); e.g. *Licania* p.p. (ab), *Parinari* (aB), *Hirtella* (Ab), *Maranthes* (AB).

(3) Receptacle-tube gibbous (a) or not (A); stomatal crypts present (b) or absent (B); e.g. *Neocarya* (ab), *Dactyladenia* (aB), *Parinari* (Ab), *Exellodendron* (AB).

(4) Seedling escape by lateral plates (a) or not (A); ovary inserted centrally (b) or laterally (B); e.g. *Parastemon* (ab); *Maranthes* (aB), *Chrysobalanus* (Ab), *Dactyladenia* (AB).

(5) Calyx strongly zygomorphic (a) or not (A); lateral plates present (b) or absent (B); e.g. *Maranthes* (ab), *Acioa* (aB), *Parastemon* (Ab), *Chrysobalanus* (AB).

We are therefore unable to offer any very definite views on the phylogenetic relationships of the genera. For convenience, we have grouped them into four tribes and we believe that this treatment may partly reflect a major pattern of divergence within the family, but we are not sure that we have correctly placed all genera, and are unable to suggest convincing branching patterns within the tribes.

(ii) *Parallelism, extinction and the detection of sister groups*

According to Bremer & Wanntorp (1978) (see §10*a*ii),

> phylogeny is reconstructed step by step. This involves the search for the sister group or 'Hennig's principle'. Every species or monophyletic group has a sister species or species group, which is derived from the closest ancestor common to both groups.... The concept of sister groups is independent of extinction. If the sister group becomes extinct another group takes its place.... Sister groups are monophyletic and established on the joint possession of apomorphous [i.e. advanced] character states.... When the sister group has been identified, the two groups are united into a single monophyletic group and the procedure is repeated. The reconstruction is presented in a phylogenetic diagram.... The reconstruction can often be tested against the distribution of the group, where vicariance patterns indicate sister group relationships.... This has been called the chorological phylogenetic reconstruction.

In Chrysobalanaceae, as in other families, some sister species are readily detected. In woody plant groups in the tropics, allopatric speciation seems to be the predominant mode (White 1962) but is not always dichotomous. Again and again one encounters vicarious subspecies and species that appear to be derived from the same common ancestor. To this extent cladistic analysis may be possible. For most chrysobalanaceous species, however, despite a thorough search, we have failed to detect sister species, and the same is true at higher taxonomic levels. The extent to which sister groups can be detected will depend on the way in which species have arisen, and on patterns of extinction within the group. Sister species will be difficult to detect in flocks of closely related species which differ chiefly in showing minor variation of a common structural theme, especially when the individual differences between species have resulted from parallelism. Similarly, the precise relationships of taxonomically isolated species or groups of species will be difficult to establish when extinction has destroyed vital evidence of relationships. In Chrysobalanaceae these two situations can be illustrated by *Maranthes* and *Licania* respectively.

In *Maranthes* the differences between the species are slight (see §16.12 and figure 33) and are of the kind that might be expected to show parallelism. *Maranthes* pervades the Palaeotropics and is also represented in the Neotropics. Of its 12 species it is rarely possible to pick out any one as being the sister species of another with a high degree of confidence. For instance, on ecogeographical grounds the sister species of the Zambezian savanna woodland species, *M. floribunda*, could be *M. polyandra*, its ecological counterpart in the Sudanian Region in West Africa. But it could equally well be one of the Guineo-Congolian rainforest species, or the geographically isolated sub-Afromontane rainforest species, *M. goetzeniana*. Our taxonomic work has not enabled us to decide which of these possibilities is most likely to be correct. Similarly, among the African species we have not been able to find sister species for the single American or the single Asiatic species, even though in theory they must exist. This means that on present knowledge *Maranthes* has nothing to offer either to cladistics or to vicariance biogeography, and effectively disproves the more extreme claims made for either.

In *Licania* all but three of the 171 species occur in America and belong to three subgenera endemic to the Neotropics. The single African species is sufficiently distinct to require its own subgenus, *Afrolicania*, and the two Asiatic species comprise the subgenus *Angelesia*. The few, possibly advanced, characters that the African and Asiatic species share could have arisen independently. This does not mean that they are not sister species, merely that no convincing evidence has been established. Nor has it been possible to find sister species for the Old World species among the American species. The Old World Licanias are so different from those of the New World that their taxonomic isolation must have involved considerable extinction. Bremer & Wanntorp (1978) say that sister groups exist independently of extinction. In theory they may, but in practice, even a moderate degree of extinction can destroy the evidence necessary for their detection.

It seems that cladistic methods are equally difficult to apply in other families. One of us (G.T.P.) considered the application of cladistics to the Lecythidaceae, but encountered the same problems as we have found in Chrysobalanaceae, namely parallelism and failure to identify sister groups. The monographer of *Parkia* (H. C. Hopkins, personal communication) tells us that she is unable to detect 'sisters' among the African species.

(*d*) *Historical biogeography*

(i) *Introduction*

Most taxonomists who write monographs are puzzled by some of the distribution patterns their work reveals, especially wide disjunctions in range. They are often tempted to offer some kind of historical explanation of an extremely hypothetical nature but would admit that it is easier to ask questions than to answer them, especially if their evidence comes from a single taxonomic group. They would also admit that the solution of problems in historical biogeography is only possible within a framework of actual knowledge of earth history.

In recent years, concomitant with a rapid increase in our understanding of earth history, especially in the field of plate tectonics, but also in other aspects of geomorphology and in palaeoclimatology, there has been a renewed interest in historical biogeography. Taxonomists are now more inclined to speculate about the history of their groups. Some do so in fairly general, though biologically meaningful, terms, as Johnson & Briggs (1981) have done for the three Southern Hemisphere angiosperm families Myrtaceae, Proteaceae and Restionaceae, and the history of scleromorphic floras in general.

Others, however, are more specific in their objectives and freely speculate on the centres of origin of plant and animal taxa and attempt to explain contemporary distributions in terms of wandering continents and past climatic events. Although the methods used may be relevant in some situations, their application has sometimes been inappropriate and important lines of evidence have often been ignored. In our work on Chrysobalanaceae we have found the methods of vicariance biology of little value, and we are led to believe that the importance of long-distance dispersal in the shaping of contemporary biota has been underestimated.

(ii) *Cladistics and vicariance biogeography*

Some biogeographers (e.g. Platnick & Nelson 1978; Rosen 1978), who refer to their special interest as 'vicariance biogeography', have developed a general method of biogeographic analysis which claims to sort out replicated distribution patterns due to fragmentation of range of an ancient biota (vicariance) from those that require unique explanations such as long-distance dispersal. The method is said to be applicable at any level (Wiley 1981). It is dependent, however, on the construction of cladograms, and hence is of limited usefulness where parallelism is known or suspected.

Although the methods of vicariance biogeography can be applied to disjunctions of any age or geographical pattern, in practice they are easier to apply at the continental level (Wiley 1981), and most vicariance biogeographers have been concerned with the biogeographical implications of continental drift. For land masses which were formerly together and have drifted apart, vicariance biogeography is only relevant to taxa which existed in the now separated areas before the time of their separation. For some plates and most contemporary taxa, at least below the level of family and sometimes higher rank, the time of separation appears to be too early for the vicariance approach to be relevant. Although each disjunction must be considered on its merits, there seems to be a tendency for vicariance biogeographers to overestimate the age of taxa and to underestimate the efficacy of long-distance dispersal. They also seem to assume that the geographical ranges of disjunct taxa have often been stable for immense periods of geological time.

In discussing considerations such as these, in a review of the zoogeography and phylogeny of mammal and bird faunas, the zoologist Keast (1977) found much to question in the fundamental tenets of the vicariance school.

As pointed out by Keast (1977, p. 263),

> in cases where a range of species have a common distribution pattern, a common distributional history is not necessary. Some groups may be relictual; others recent colonizers'. And (p. 282) – 'Except *possibly* [our italics] in the case of specialized peripheral relicts like the "southern cold temperate disjuncts" (e.g. *Nothofagus*) it is doubtful if contemporary patterns can be expected to reflect late Mesozoic historic patterns in more than a few cases. In 60 million years of evolution since the late Cretaceous, for example, ranges must have been repeatedly disrupted by climatic shifts, and the origin, radiation and extinction of new competitors. The whole question of dispersal is inadequately resolved.

Our own experience reinforces these views.

(iii) *Transoceanic disjunctions, centres of origin, and long-distance dispersal*

The idea that many angiosperm disjunctions are the consequences of continental drift, often involving vicariance events which happened more than 70 Ma BP, is not confined to vicariance biogeographers of the cladistic school. Thus, Raven & Axelrod (1974, p. 585), using the best evidence then available, have suggested that the Chrysobalanaceae originated in South America and subsequently migrated more or less directly overland to Africa and Asia and eventually Australia. At that time, we would not have seriously questioned that opinion, and one of us has even suggested (White 1976*c*) that *Parinari* existed as a genus before the breakup of Gondwanaland. In the light of our increased knowledge of the Chrysobalanaceae, especially its dispersal ecology and some recent significant discoveries in palaeobotany, we no longer hold those views.

We believe that most families and many genera of higher organisms during their history have undergone such extensive and complicated changes in their distribution that it is no longer possible to deduce their place of origin from contemporary evidence alone. Species richness *per se*, also, does not necessarily provide a sufficient clue. It is true that the overwhelming majority of species of Chrysobalanaceae occur in the Neotropics, and if centre of origin can be located merely by 'counting heads' at the species level, then South America would be identified as that centre. However, the Old World tropics are much more diversified at the supraspecific level (table 6, see p. 45) and that suggests alternative explanations. The Chrysobalanaceae also appear to be good dispersers (see below) and the overall pattern of relationships is too diffuse to indicate a probable centre of origin.

The fossil evidence does not support an early origin of Chrysobalanaceae. Discounting a few doubtfully identified leaf impressions, the earliest recorded fossil of Chrysobalanaceae is a palynomorph from the Oligocene (Muller 1981). The fossil record of Chrysobalanaceae, however, is so exiguous that no firm conclusions can be based on it alone. Nevertheless, recent critical work on angiosperm fossils (see summaries by Hickey & Doyle (1977), Doyle (1978) and Muller (1981)) suggests that very few extant families of flowering plants originated before the Upper Cretaceous, by which time some of the fragments of Gondwanaland, including Africa and South America, were quite widely separated. According to Tiffney (1984) large, animal-dispersed diaspores, such as those of Chrysobalanaceae, originated in the earliest Tertiary, associated with a radiation of fruit-eating birds and mammals.

Since Chrysobalanaceae appear to be good dispersers (see §11*c*) their contemporary distribution could easily be recent rather than ancient. The fruits of at least four genera, namely *Acioa*, *Exellodendron*, *Licania* and *Parinari*, float in fresh water and might be expected, at least occasionally, to be transported across the sea. For two species in other genera, *Chrysobalanus icaco* and *Atuna excelsa*, at least in parts of their range, the fruits are regularly transported by ocean currents and are known to germinate after immersion in salt water. In *Chrysobalanus*, which has an inland as well as a coastal distribution, we are probably witnessing the early stages in the evolution of what could possibly become an obligately ocean-transported strand plant. In other species such as *Licania splendens* and *Maranthes corymbosa* the fruits are eaten by strong-flying, gregarious, highly mobile birds, such as the fruit pigeon, *Ducula aenea*, which seem capable of effecting transport from island to island over moderate expanses of sea water.

(iv) *Intracontinental vicariance and refugia*

Both in tropical America and in tropical Africa several examples are known of closely related species of Chrysobalanaceae occupying discrete but widely separated areas. In some cases at least we are probably dealing with sister species. The disjunctions between some vicariads could be due to long-distance dispersal, but we believe that most are the consequence of disruption of former more continuous ranges, as a result of Quaternary, or in some cases possibly earlier, climatic change. At first sight it might appear that the methods of vicariance biogeography were applicable to this situation but, although we have prepared distribution maps for all species, we have not been able to detect a sufficiently consistent and clear-cut pattern of taxonomic and chorological relationships to confirm this. The pairs (and in some cases larger groups) of vicarious taxa were found to form part of a larger and very complex geographical pattern, for which we believe that, at least on present evidence, historical explanations of only a general kind can be offered, and that these must be based largely on methods of analysis other than those of vicariance biogeography.

Included in this wider pattern, in addition to true vicariance, the Chrysobalanaceae show other biogeographical features such as:

(i) the parapatric replacement of closely related species and subspecies, e.g. *Maranthes chrysophylla* (White 1976*a*, p. 295; 1976*b*, maps 315–317);

(ii) disjunctions in the ranges of phenetically uniform taxa, e.g. *Magnistipula zenkeri* (White 1976*a*, p. 293; 1976*b*, map 312);

(iii) endemic species of restricted geographical range for which sister species cannot be detected, e.g. *Licania elaeosperma* (White 1976*a*, p. 280; 1976*b*, map 293);

(iv) ecological and chorological transgressors, e.g. *Parinari excelsa* (White 1976*a*, p. 333; 1976*b*, map 334).

There is now an extensive literature which describes and attempts to explain these phenomena, much of it associated with 'refugia theory'.

A belief that throughout the Quaternary there has been an alternation of pluvial and arid phases, which has had a profound effect on the distribution and taxonomic relationships of plants and animals, has long been a commonplace of African biogeography (for an early historical summary see Moreau (1966)). Such views were more slowly accepted for the American and Eastern tropics, where the idea of a uniform and unchanging climate was more persistently upheld, as by Fedorov (1966).

In recent years attention has been focused largely on the detection of centres of endemism, especially in lowland rainforest, which have frequently been identified as refugia dating from an earlier phase in the climatic cycle. This is a highly controversial subject which has generated many publications, especially from the Neotropics. It has recently been comprehensively reviewed (Prance (ed.) 1982*c*).

On the basis of plant distributions in several families including Chrysobalanaceae, Prance (1982*a*) has identified 26 areas of lowland forest endemism in South America which may have been forest refugia at a time of reduced forest cover. He argues, however, against simply equating centres of endemism with refugia and explaining them exclusively in terms of the most recent climatic events. He notices that: some parts of South America are poorly collected and others are botanically unknown; areas of floristic diversity are often ecologically diverse; species differ greatly in their dispersal capacity and generation time and would respond differently to change; climatic instability possibly extended back for at least two million years and different biogeographical features might be due to different palaeoclimatic (and geomorphological) causes. In view of this, historical reconstruction cannot be easy.

The present-day restricted distribution of some forest organisms is often cited as evidence of drier conditions in the past, but, as pointed out by Hall & Swaine (1981), this is illogical, especially when the organisms are confined to areas of high rainfall. By contrast, such refugia provide evidence for the more widespread occurrence of a wetter climate. Drier conditions might have contributed to the shaping of refugia but they cannot be their only cause. Although there is much evidence to support the occurrence of dry phases in the Pleistocene, claims for their extent and severity, at least for some parts of the tropics, are often exaggerated. Much of the published evidence for 'Ice Age aridity', biological, geomorphological and palaeoclimatic, is controversial and some is erroneous (White 1981). Most attempts to explain contemporary distribution patterns are greatly oversimplified.

The complexity of present-day distribution patterns is well exemplified by the important investigations of Hall & Swaine (1981), who have published maps of the distribution in Ghana of 624 species of vascular plant (which include four Chrysobalanaceae), as part of what is probably the most detailed study of its kind. Many species were found to have ecologically anomalous distributions which seem to require historical explanations. They suggest that their maps could be regarded as a 'palimpsest on which are superposed the writings of innumerable climatic changes' but that it would be naive to suggest 'a simple scheme of two or three dry and wet phases to explain distribution patterns'.

The chorological patterns of Chrysobalanaceae throughout the tropics likewise seem to be the consequence of a long and complex history. Interpretation of these patterns will depend on a wider and deeper knowledge than we have at present, both of the plants themselves and past environmental change, preferably supported by fossils like the beautifully preserved assemblage from Lake Bosumtwi described by Hall *et al.* (1978) in which, unfortunately, Chrysobalanaceae are not represented.

(*f*) *The detection and relationships of monophyletic groups*

For reasons given above, the construction of cladograms by using Hennigian methods, as advocated by Bremer & Wanntorp (1978), is not possible in the Chrysobalanaceae. It is not possible therefore to distinguish between mono- and paraphyletic groups as defined by Hennig and his folllowers.

We believe that the genera we recognize are monophyletic in the sense of Mayr (1974, p. 104) in that their component species are one another's nearest 'relatives' and have descended from the same common ancestor, and we believe that this traditional usage serves biology better than the redefinitions of the cladists.

We do not, however, agree with Mayr (1974, p. 123) that 'a sound classification of a group of organisms cannot be devised without a well-considered reconstruction of its phylogeny' in that he places too much emphasis on branching patterns, which in a group like Chrysobalanaceae can rarely be inferred. As Keast (1977) observes 'most phylogenetic writings... are directed only at the highest, and therefore most distinct, taxonomic categories. It remains to be seen how effective the approach will be in resolving problems at the family/genus level.'

The main conclusions which we draw from our monograph are as follows.

(*a*) The Chrysobalanaceae form a tightly-knit family. Each species we include has many more features in common with other members than it has with any species in any other family. Hence the family is monophyletic in the sense of Mayr, and it is reasonable to assume that all Chrysobalanaceae have descended from the same common ancestor. We know of no evidence which contradicts that assumption.

(*b*) Similar considerations apply to each of the 17 genera. A few species (see §6*f*) occupy isolated positions within their genera or are otherwise anomalous. Arguments could be made on theoretical grounds for both increasing and decreasing the number of genera, but that is a matter of judgement, and ultimately of practical utility. The evidence we have presented, in so far as it is complete, supports the view that each of the 17 genera is monophyletic.

(*c*) The Chrysobalanaceae, however, is so different from all other families (see §5) that we are unable to suggest a close phylogenetic relationship with any of them.

(*d*) The distribution of character states within the Chrysobalanaceae is so reticulate (see §10*d*) that we are unable to produce an arrangement of the genera which we believe would faithfully reflect their phylogeny.

(*e*) It is for these reasons that we have found both the cladistic and other approaches to phylogeny unworkable at the family–genus level.

Conclusions such as these are not new but are the common experience of those who know their plants intimately as living organisms rather than as bran tubs of lifeless, codified character states. Over 50 years ago Gilbert-Carter (1936, p. x) said that, although the similarity in structure of members of most genera and even of most families leads us to believe that they are genetically related, structure provides no key to the nearest relatives of the higher categories. More recently, Davis (1978) has doubted the value of time and effort devoted to the creation of suprafamilial edifices and phylogenetic schemes, and suggests that the need for good generic monographs and tropical floras is greater.

Our failure to contribute anything positive to the phylogenetic relationships of the Chrysobalanaceae does not mean that it has nothing to offer to the evolutionary biologist, but merely that aspects of evolution other than branching patterns are of greater interest and are more amenable to study. Evolution is more than a matter of family trees. It encompasses all the 'changes in the diversity and adaptation of populations of living organisms' (Mayr 1976, p. 1). Such changes in populations within species ultimately lead to the differentiation of communities and whole floras and faunas and not merely of taxa. Much biological change since the angiosperms orginated has been moulded by environmental change associated with moving continents and other geomorphological events, and by climatic change associated with Pleistocene and earlier glaciations. As we learn more about earth history and the distribution, ecology and taxonomic relationships of organisms, evolutionary reconstruction becomes easier, and a knowledge of earth history can sometimes be used as an indicator of the direction of evolutionary change. Only limited conclusions can be drawn from a single family, but Johnson & Briggs (1981) have shown how interesting hypotheses concerning the origin and differentiation of regional vegetation types can be drawn from a detailed study of as few as three families of flowering plants.

In the following section some examples of major trends in the differentiation of communities are illustrated with examples from Chrysobalanaceae.

11. Evolutionary stability and change

(*a*) *Introduction*

In the field, members of the Chrysobalanaceae are easy to recognize as belonging to the family, even without close inspection. This implies that they have only a relatively limited range of variation in some features of their basic structure. In other features the range of variation is wide and is more clearly related to function, including pollination and dispersal. This interplay between stability and diversity needs to be fully understood in functional terms before anti-selectionist explanations of stability, such as the doctrine of constraints as expounded by Gould & Lewontin (1979), can be accepted.

The growth form of Chrysobalanaceae is uniform. They all apparently conform to the model of Troll (Hallé & Oldeman 1975) (see §3), but in Lecythidaceae, which often shares the same habitats as Chrysobalanaceae, there are nine models. Within the Chrysobalanaceae there is a very wide range in floral structure, much greater than that in several much larger families, but most genera have their own distinctive inflorescence architecture (see §§3 and 6). Ecology may help us to understand how such contemporary patterns came about. Little is known, because the subject has been little investigated, but we can begin by discussing a few situations where quite striking changes appear to be taking place at the present time.

(*b*) *Change in habit in response to climatic and geomorphological change*

The overwhelming majority of Chrysobalanaceae occur in lowland rainforest on well-drained soils. This does not necessarily mean that the group originated in rainforest, but it is reasonable to assume that it has undergone most of its differentiation under a rainforest climate or something similar. In the absence of other evidence it can be assumed that species occurring in other vegetation types represent relatively recent adaptations.

The range in habit and ecology shown by Chrysobalanaceae is outlined in the chapters on morphology and ecology. Despite the wide range of habitats occupied by the family, and, superfically at least, the diversity of its growth form, there is a remarkable underlying structural uniformity. Only a single architectural model has been recorded.

The most striking shift in habit in relation to a specialized environment is that of the geoxylic suffrutex. There are no herbs in Chrysobalanaceae but geoxylic suffrutices superficially resemble them and they occur predominantly in herbaceous communities. In reality they are 'trees which have gone underground'. The change from tree to suffrutex has involved relatively little structural and developmental change, although the difference in appearance and the ecological changes are pronounced. This transformation has been brought about by the suppression of the main stem and the production of low, short-lived, precociously flowering shoots from a massive system of shallow, extensively radiating subterranean axes. In Africa two species of Chrysobalanaceae, *Magnistipula sapinii* and *Parinari capensis*, show this unusual growth form. The latter is the most widespread and abundant African geoxylic suffrutex.

Geoxylic suffrutices in the sense of White (1976*c*) are almost confined to the tropics, where they occur under a savanna climate. They are not, however, uniformly distributed throughout the tropical savannas but are concentrated chiefly on certain soils where the rooting environment is severely restricted. They appear to reach their best development in Africa where there are at least 110 species in 31 families, but are also an extremely important element of the cerrados of Central Brazil. In common with *Magnistipula sapinii* and *Parinari capensis*, they all belong to genera of large woody plants which include no truly herbaceous members.

Although in area and climate the two great savanna regions of Africa, the Sudanian and Zambezian, are broadly similar, geoxylic suffrutices are very poorly represented in the former. In the latter they are concentrated in and near the Kalahari sand-covered Upper Zambezi basin, which can be referred to as 'Greater Barotseland'. In much of this area the rooting environment is restricted owing to unfavourable edaphic conditions provided by extremely oligotrophic, seasonally waterlogged sandy soils in a region of extremely low relief. White (1976*c*) has suggested that many geoxylic suffrutices first evolved in response to such edaphic conditions, and not as an adaptation to fire as had been previously supposed, although fire might have played an important role in the later stages.

The peculiar edaphic conditions of Barotseland are more extensively developed there than anywhere else in Africa, and are the consequence of its unique geological history. When the relatively recent geomorphological history of Barotseland and other parts of Africa has been more completely elucidated it should be possible to explain the origin of the geoxylic suffrutex and other ecogeographical elements in the African flora in greater detail, and possibly to fit their evolution into a timescale. This, it seems to us, is a much more interesting subject than the cladistic relationships of individual suffruticose species and their putative closest relatives. It is, however, one of some complexity. Because of the great concentration of suffrutices in Barotseland, the latter would appear to be the place to pursue this subject further. Some suffrutices, however, occur elsewhere, and others, including *Parinari capensis*, extend beyond Barotseland. The geographical variation of *P. capensis* suggests that its different phenotypes might have originated in more than one place and at more than one time, and that speciation might not be complete.

The relationships of *P. capensis* to *P. curatellifolia*, a tree of savanna woodland, from which it has probably been derived, are such as to suggest that the former is still in the process of recruiting populations from the latter. White (1976*a*) believes that *P. capensis* may have originated, not from a single founder population of *P. curatellifolia*, but from a succession of founder populations. This is supported, *inter alia*, by the following observations. The geographical location and somewhat intermediate nature of *P. capensis* subsp. *incohata* suggest a relatively recent origin from *P. curatellifolia* (see White 1976*a*, p. 317 for a full discussion). Other possible indications of polyphylesis can be seen on the Nyika Plateau in Zambia. Here, on shallow, stony soils, at its altitudinal limit at 2075 m, *P. curatellifolia* assumes the habit of *P. capensis*, but its stems are 1–2 m high (F. Dowsett-Lemaire, personal communication, 3 June 1982; F. White, unpublished observations).

Among African geoxylic suffrutices there is a complete gradation between taxonomically isolated obligate suffruticose species, through pairs of possible 'sister species' like *Parinari capensis* and *P. curatellifolia* with rare intermediate populations, to species which contain both arborescent and suffruticose populations.

Geoxylic suffrutices are also a conspicuous feature in the cerrados of the unrejuvenated land surface of the planalto of Central Brazil. They have evolved independently there but less is known about them, and factors other than a restricted root environment might be more important. In this region two species of Chrysobalanaceae have adopted the suffruticose growth form, although only facultatively. Both species, *Licania dealbata* and *Parinari obtusifolia*, are taxonomically isolated within their genera. The same is true for the third New World suffrutex, *Licania michauxii*, which is confined to the pine barrens of the southeast United States.

(*c*) *Biological consequences of long-distance dispersal across faunistic barriers*

Apart from a recent review (Pannell & White 1988), which is solely concerned with vertebrate dispersal, this important subject has received little attention.

The distribution of certain genera and individual species or groups of closely related species in Chrysobalanaceae is such that one might expect to find differences in the fruits in different parts of a taxon's range that are related to the structure, feeding behaviour and nutritional requirements of the animals that disperse their seeds. Although this subject has not been studied in detail there are indications that this is so. Further work might be expected to reveal how switches in major modes of dispersal are brought about.

The chrysobalanaceous fruit, despite differences in detail, varies little in basic structure. It is a drupe with a large edible seed protected by a hard endocarp. The mesocarp is usually, at least in part, fleshy and edible. More rarely it is wholly fibrous and inedible. In some species the fruit is buoyant. Notwithstanding this monotonous uniformity, the group pervades the moister tropics and is absent only from some of the remoter islands in the Pacific. Its fruits are dispersed by a wide range of agents (see §8*f*).

Atuna (§16.13) and *Chrysobalanus* (§16.1) are dispersed by seawater but also by animals. The fruit of *Parinari* is easily recognized but few specific differences are apparent in the herbarium, yet it is dispersed in many ways: by river, and possibly, at least occasionally, by oceanic currents (though the evidence for this is only circumstantial), by bats, primates, squirrels, elephants, fishes, flightless birds (rheas and emus) and volant birds (hornbills and fruit pigeons). *Parinari* occurs throughout the tropics, extending eastwards to Samoa, but little is known of the properties of the fruits of its 44 species in different parts of its range. For some species at least, the fruit shows specific features associated with a particular type of animal disperser, such as the orange colour and sugary mesocarp of *P. canarioides*, but such subtle distinctions can only be detected in the field.

When an animal-dispersed species is transported across a faunal barrier, such as at the Mozambique Channel or Wallace's Line, it will be presented with new evolutionary opportunities which may be determined in part by the behaviour and feeding habits of its new potential dispersers. The immigrant's response may lead to important and unsuspected taxonomic consequences. Until the reproductive biology of animal-pollinated and animal-dispersed seeds has been studied on both sides of a faunal boundary, it might not be possible to reach satisfactory taxonomic conclusions.

The woodland species *Parinari curatellifolia* is widespread on the African mainland, where it is dispersed mainly by mammals, including elephants and primates. Fruits are also occasionally taken by the green pigeon (*Treron australis*). Both *P. curatellifolia* and the pigeon also occur in Madagascar and it is possible that the former was transported there by the latter. The mammalian faunas (except for introductions and a few bats) are almost totally different on the two sides of the Mozambique Channel. What effects this may have had on the fruits of *Parinari* is unknown. In *Hirtella* there does seem to have been a significant response.

Hirtella zanzibarica occurs in the forests of East Africa and is widespread in Madagascar. In the genus *Hirtella* the fruit is characteristically small and has a thin juicy mesocarp, which appears to be easily separated from the thin bony endocarp. The fruit of the Madagascar plant, however, is larger than that from the mainland and is much more fibrous, with a less clear distinction between the layers. It has more in common with the fruit of *Couepia* (see §6*c*iii) than with the rest of *Hirtella*. Compared with the African mainland, the frugivorous avifauna of Madagascar is impoverished (Moreau 1966); the agents of dispersal may well be different on the two sides of the Mozambique Channel, and we are probably witnessing a response of the kind suggested above. Furthermore, on Madagascar there are four well-defined geographically replacing subspecies of *H. zanzibarica* (White 1976*a*) based mainly on differences in leaf shape.

On the mainland, however, it is essentially uniform despite its greater geographical range. These differences in patterns of variation may be related to differences in the mobility of the plant's dispersers in the two places. In this connection it is interesting to note that the most widespread lemur in Madagascar, the brown lemur (*Lemur fulvus*), has seven races which ring the island. Little is known about the feeding behaviour of lemurs, but at least half of the 26 species eat at least some fruit (Jolly *et al.* 1984). There may therefore be a connection between the low vagility of lemurian dispersers (territories can be as small as 100 ha or less) and the large amount of local endemism among Malagasy plants with fleshy fruits.

In the eastern tropics the taxonomy of *Atuna* and *Parinari*, both of which cross Wallace's Line, is largely unresolved at the species level. The apparent taxonomic complexity might, at least in part, be related to the different characteristics of their dispersers in different parts of their range.

(*d*) *The origins of adaptations to dispersal by ocean currents*

Because of their wide range of modes of dispersal, further study of the Chrysobalanaceae might yield useful information on this subject, as is suggested by the following considerations.

In *Couepia*, *Exellodendron*, *Licania* and *Parinari* some South American species are abundant on the banks of rivers and are dispersed by fishes. In *Couepia*, *Licania* and *Parinari* other species are known to be dispersed by bats, although it is not known whether any species in these genera is dispersed by both bats and fishes. It is not, however, unlikely. The fruits of *Exellodendron barbatum* float when they fall in the water. It is known to be dispersed by both fishes and bats. Patterns of taxonomic relationship in the family suggest that the group is easily dispersed across water barriers. In some cases birds (see above) may be implicated. Other species, however, e.g. *Chrysobalanus icaco* (see below) and *Atuna racemosa*, are known to be water-dispersed and this may have been the predominant mode of long-distance dispersal in the past.

It is possible that some species in becoming adapted to dispersal by fishes have acquired features, e.g. buoyancy combined with protection of the seed by a hard and thick endocarp, which have enabled them to cross the ocean. If such a species were also adapted to dispersal by, for example, bats, the possibility of successful establishment following successful dispersal might be enhanced. A study of dispersal of African *Parinari* and their closest American relatives might be used to test this hypothesis.

(*e*) *Stages in the evolution of ocean-dispersed obligate strand plants*

In several families there are species which have coastal distributions and are ocean-dispersed in some parts of their range, but elsewhere occur in swamp forest in the interior of continents and are dispersed there by rivers and other agents. *Chrysobalanus icaco* is such a species (see §16.1). The subspecies *icaco* is widely distributed as a strand plant on both sides of the Atlantic and, more locally, on the Pacific coast of Mexico and central America. It also occurs in savannas up to 200 km inland in Africa and 600 km in America, where it is bird-dispersed. The subspecies *atacorensis* is widely distributed on riverbanks in tropical Africa. Wherever subsp. *icaco* and subsp. *atacorensis* are in contact, intermediates are found. They so effectively bridge the morphological gap between these taxa that the latter must be regarded as conspecific. Thus within a single species we might be able to detect the early stages in the origin of adaptations to an extremely specialized habitat. In other families specialization has gone further. In the Meliaceae, for example, *Xylocarpus* is a small Old World genus of obligate strand (including mangrove) plants. It is most closely related to *Carapa*, the most characteristic habitat of which is fresh-water swamp on both sides of the Atlantic. The seeds of *Carapa* are transported by ocean currents, although the plant itself occurs only very locally in coastal habitats (White 1983*c*).

12. PRACTICAL CONSIDERATIONS

(*a*) *The role of fine structure and chemistry in taxonomy*

In §4 we have briefly described what is known of the anatomy, ultrastructure and chemistry of Chrysobalanaceae and have indicated the extent to which we have found this information useful in our taxonomic work. We found it particularly valuable concerning the rank and circumscription of the group, but in only a few cases did it help to resolve problems of generic delimitation.

Monographers, as our own work clearly shows, cannot afford to ignore fine structure and chemistry, although we think they are less useful than some of their advocates claim. We do not believe that fine structure and chemistry (at least in a practical sense) are somehow more fundamental in taxonomy than other sources of information. Evidence from Chrysobalanaceae, considered in relation to other families, shows that parallelism is as likely to affect the fine structure and chemistry of taxa as much as it does their morphology. It is also more difficult and expensive to detect.

On present knowledge it is uncertain whether the secondary compounds we mention in §4*k* are of any great significance in taxonomy, although for some of them the indications are otherwise. Gornall *et al.* (1979) have summarized the known distribution of 39 structural classes of flavonoid in the angiosperms. Their results, which are presented in the form of 20 diagrams, show that nearly all flavonoids, or groups of closely related flavonoids, occur in a wide range of totally unrelated orders, that no order is strikingly distinct in its flavonoid complement, and that a majority of compounds occur in some, but not all, of the members of most of the higher taxonomic groups in which they are known to occur. It is apparent that most of these chemicals have been either gained or lost (or both) repeatedly during the history of angiosperm evolution, and that as a tool in taxonomy they are of limited value. Gornall *et al.* (1979, p. 4) admit that many of their 'flavonoid structural classes are polyphyletic and therefore their systematic importance at the supra-familial level is lessened'. Nevertheless, they do draw several, at least tentative, taxonomic conclusions. Their suggestion (p. 10) that the relationships of the Chrysobalanaceae could lie with the Proteales finds little support from our own investigations. Many of the compounds of more restricted distribution discussed by Dahlgren *et al.* (1981) also seem to have limited taxonomic value. It seems that very few classes of compound show the compact distribution and high degree of correlation with other characters exemplified by the betalains. However, even with the betalains, there are still unresolved taxonomic problems (Bendz & Santesson 1974).

At a lower taxonomic level, Du Plessis & Vladár (1974) have compared the fatty acid composition of the oil from the seeds of *Parinari capensis* sensu stricto (Sand Apple), *P. curatellifolia* (Mobola tree), and a somewhat intermediate taxon which White (1976*a*) has described as *P. capensis* subsp. *incohata* (Mobola shrub). They say that the placing together of Mobola tree and Mobola shrub is supported by their results. The latter, however, are difficult to evaluate, because their work was limited in scope and lacked controls. Chemical analysis is beset with so many difficulties that it should be used with caution.

(*b*) *Priorities in monographic research*

> '*Don't be silly, it isn't a nettle. Anyone can see that it's a kind of mint*'. (Six-year-old child on being told the vernacular name of *Lamium purpureum* ('dead nettle', Labiatae))

We conclude from our experience of Chrysobalanaceae (and other families) that several currently fashionable approaches to taxonomy are of limited relevance to the tropics, at least at the present time. It is much more important to develop objective methods of visual analysis for dealing with the copious material that monographic work entails. It is equally necessary to understand the central role of ecology. Without ecological understanding taxonomy is lifeless and dull, and taxonomically important information goes undetected (White 1971). In practical terms our views could be summarized as follows:

1. At the beginning of a monographic study many species will be imperfectly known. This should not necessarily preclude a tentative assessment of relationships, but from the start it should be understood that the quality of the final synthesis will depend on the extent to which is is based on complete material. At present, for most tropical plant families, botanical exploration is more important than numerical and chemical analysis and the study of ultrastructure.
2. Many genera, at least, can be provisionally recognized intuitively by eye (see §6*e*).
3. The objectivity of such tentative groupings can be rapidly but rigorously tested, by using intelligent and well-motivated but relatively untrained personnel (see §6*e*).
4. The visual analysis of overall resemblance can reveal complexes of highly correlated minor characters which have previously escaped detection. Individually the characters may not be absolutely diagnostic, though the character-complex itself is highly diagnostic (see §6*e* and Appendixes 1 and 2).
5. The extent to which such character complexes can be used for identification or in the assessment of relationships largely depends on the precise way in which the character states are formulated (see Appendix 1) and on the quality of the associated iconography.
6. The character complexes such as inflorescence architecture seem to be functional syndromes which determine, for instance, the precise way in which polliniferous and stigmatic surfaces are exposed in space and time to potential pollen vectors (see §10*c*). The reproductive biology of few Chrysobalanaceae has been studied in detail in the field, but there are indications that such studies would reveal a plenitude of taxonomically important features, which can only be dimly perceived in museum specimens. Pannell & White (1988) give several examples, including some from Chrysobalanaceae, of taxonomically significant cryptic variation in the fruits of vertebrate-dispersed tropical plants.
7. Artificial keys are of limited use in monographs (White 1980). This is partly because of the prevalence of parallelism. When functional syndromes have been identified and understood, they should be exploited for classification. Synopses and illustrations should be more widely used. If genera and species can be identified by eye it should be possible to describe and illustrate their diagnostic differences.

PART II. TAXONOMIC CONSPECTUS

13. FAMILY DESCRIPTION

CHRYSOBALANACEAE R. Br.

Chrysobalanaceae R. Br., in Tuckey, *Narr. Exp. Congo*: 433 (1819). – Bartling, *Ord. Nat. Pl.*: 405 (1830). – Mart. & Zucc., in Zuccarini, *Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. (München)* **1**: 372 (1832); *Flora* **2**, *Beibl.*: 78 (1832). – Lindley, *Nat. Syst. Bot.*, ed. 2: 158 (1836). – Benth., in Hook., *Lond. J. Bot.* **2**: 210 (1840). – Endl., *Gen. Pl.* **2**: 1251 (1840), suppl. 2 (*Mantissa botanica*): 95 (1842). – C. Muell., Walp., *Ann. Bot. Syst.* **4**: 640 (1857). – Fritsch, *Verh. K. K. Zool.-Bot. Ges. Wien* **38**: 93 (1888). – Wettstein, *Handb. Syst. Bot.*, ed. 4: 771 (1935). – Gundersen, *Fam. Dicot.*: 109 (1950). – Prance, A taxonomic study of the Chrysobalanaceae; unpublished D.Phil. thesis, pp. 232 + xlix, Bodleian Library, University of Oxford (1963). – Schulze-Menz in Melchior (Editor), Engl., *Syllab. Pflanzenfam.*, ed. 12, **2**: 219 (1964). – Takhtajan, *Systema Phyl. Magnoliophytarum*: 267 (1966). – Cronquist, *Evol. Classif. Fl. Pl.*: 235 (1968). – Prance, *Fl. Neotrop.*, **9**, *Chrysobalanaceae*, 1–410 (1972). – Cronquist, *Integr. Syst. Fl. Pl.*: 580 (1981).

ROSACEAE: CHRYSOBALANOIDEAE Focke, in Engl. & Prantl, *Nat. Pflanzenfam.*, **3** (3): 55 (1981). – Hauman, *Bull. Jard. Bot. État Brux.* **21**: 167 (1951).

ROSACEAE: CHRYSOBALANEAE DC., *Prodr.* **2**: 525 (1825). – Meisner, *Pl. Vasc. Gen.* **1**: 101 (1837). – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1** (2): 607 (1865). – Hook. f., in Mart., *Fl. Bras.* **14** (2): 5 (1867). – Hutch., *Gen. Fl. Pl.*, **1**: 190 (1964); *Evol. Phyl. Fl. Pl.*: 50 (1969).

ROSACEAE tribus *Prockieae* pro parte, tribus: *Amygdaleae* pro parte, Jussieu, *Gen. Pl.*: 339 (1789).

HIRTELLACEAE Horaninow, *Charact. essent. fam.*: 152 (1847) pro parte.

Trees, shrubs or suffrutices. *Leaves* simple, entire, alternate, often coriaceous; undersurface glabrous or hairy. Stipules small and caducous to large and persistent. *Inflorescence* racemose, paniculate or cymose; flowers bracteate and usually 2-bracteolate. *Flowers* actinomorphic to zygomorphic, bisexual, rarely polygamous or unisexual, markedly perigynous. *Receptacle* short to elongate, sometimes gibbous at the base. *Disc* always present, forming a lining to the receptacle or an annular or shortly tubular structure at its mouth. *Calyx-lobes* 5, imbricate, often unequal, erect or reflexed. *Petals* 5, occasionally absent, commonly unequal, imbricate, usually caducous, rarely distinctly unguiculate. *Stamens* variable, 2–100 (300), inserted on the margin or the surface of the disc, or basally adnate to it, forming a complete circle or, in zygomorphic flowers, unilateral, all fertile or some without anthers and then often reduced to small staminodes; filaments filiform, free, connate at the base or ligulately connate, included to far exserted; anthers small, dorsifixed, longitudinally dehiscent, glabrous. *Gynoecium* basically of three carpels and gynobasic, but usually with only one carpel fully developed, attached to the base, middle or mouth of the receptacle-tube, sessile or with a short gynophore, pubescent or villous, each carpel unilocular with two ovules or bilocular (owing to a false partition) with one ovule in each compartment. *Style* filiform, arising from the receptacle at the base of the carpel(s); stigma distinctly or indistinctly 3-lobed. *Ovules* erect, epitropous, with micropyle directed towards the base. *Fruit* a dry or fleshy drupe; endocarp various, thick or thin, fibrous or bony, often with a special mechanism for seedling escape, often densely hairy inside. *Seed* erect, almost exalbuminous; cotyledons planoconvex, fleshy, sometimes ruminate.

14. ARTIFICIAL KEY TO THE GENERA

1. Ovary inserted at or near the base of the receptacle:
2. Endocarp with distinct longitudinal ridges . . . . 1. *Chrysobalanus*
2. Endocarp not distinctly ridged:
3. Endocarp without lateral plates which allow the seedling to escape . . . . 3. *Licania*
3. Endocarp dehiscing on germination by means of a pair of large lateral plates . . . . . 4. *Parastemon*
1. Ovary inserted laterally at or near the mouth of the receptacle:
4. Endocarp with two small basal 'plugs' (obturators):
5. Receptacle turbinate–campanulate; fertile stamens 6–8 . . . . 9. *Parinari*
5. Receptacle saccate; fertile stamens 12–17 . . . . 8. *Neocarya*
4. Endocarp without two basal 'plugs' but sometimes dehiscing on germination by means of two large lateral plates:
6. Endocarp with two lateral plates:
7. Ovary inserted at mouth of receptacle-tube; carpels bilocular; inflorescence corymbose or thyrsoid. . . . . 12. *Maranthes*
7. Ovary inserted laterally; carpels unilocular; inflorescence racemose . . . . 2. *Grangeria*
6. Endocarp without lateral plates:
8. Endocarp opening by longitudinal lines of weakness which allow the seedling to escape:
9. Stamens far-exserted; ovary unilocular . . . . 15. *Hirtella*
9. Stamens included; ovary bilocular . . . . 7. *Hunga*
8. Endocarp without lines of weakness:
10. Sepals very unequal in size, 3 large, 2 very small, the outer sepals with 1 or 2 large discoid glands on surface; filaments usually united . . . . 10. *Acioa*
10. Sepals subequal, without discoid glands on surface (except for 2 species of *Couepia*):
11. Two posterior petals unguiculate, enclosing stamens in the bud . . . . . 16. *Kostermanthus*
11. Posterior petals not unguiculate:
12. Filaments ligulately connate . . . . 14. *Dactyladenia*
12. Filaments free:
13. Receptacle ventricose or markedly curved and obliquely campanulate:
14. Leaf-undersurface with stomatal cavities; endocarp hard, with a smooth surface; epicarp weakly verrucose . . . . 5. *Bafodeya*
14. Leaf-undersurface without stomatal cavities; endocarp with a rough surface or soft and fibrous; epicarp not verrucose . . . . 17. *Magnistipula*
13. Receptacle campanulate to cylindrical, neither ventricose nor curved and obliquely campanulate:
15. Endocarp with a bony ridge on one side at the base and with a smooth surface; stamens 6–8 . . . . 6. *Exellodendron*
15. Endocarp not ridged, with a rough surface; stamens 10–300:
16. Branching divaricate; stipules strongly keeled; ovary bilocular; cotyledons ruminate . . . . 13. *Atuna*
16. Branching not divaricate; stipules not keeled; ovary unilocular; cotyledons not ruminate . . . . 11. *Couepia*

15. SYNOPSES OF THE TRIBES, AND NATURAL KEYS TO THE GENERA

1. CHRYSOBALANEAE

Tribus *Chrysobalaneae* Prance & F. White stat.nov.

Rosaceae, Chrysobalanoideae subtribus Chrysobalaninae Focke, in Engl. & Prantl., *Nat. Pflanzenfam.*, **3** (3): 57 (1891) pro parte.

Flowers small, actinomorphic. Receptacle-tube shorter than the calyx, patelliform or cupuliform, not blocked at the throat by long retrorse hairs. Fertile stamens usually forming a complete circle, filaments free, or united only at the base; staminodes absent. Ovary 1-locular, inserted at centre or base of receptacle.

Exceptions: Flowers weakly zygomorphic in *Grangeria* and *Licania licaniiflora* because of laterally inserted ovary, and in *L. splendens* because of asymmetric development of calyx and receptacle. Receptacle-tube longer than calyx in a few species of *Licania*. Staminal circle incomplete in a few species of *Licania*, *Grangeria porosa* and *Parastemon urophyllus*; this feature is usually but not always associated with the presence of inconspicuous staminodes.

1. Style deeply lobed at apex; endocarp dehiscing on germination by means of a pair of large lateral plates . . . . 4. *Parastemon*
1. Style scarcely lobed at apex:
  2. Ovary inserted at mouth of receptacle-tube; endocarp dehiscing by means of large lateral plates; influorescence a simple or, rarely, branched raceme . . . . 2. *Grangeria*
  2. Ovary inserted in centre of patelliform receptacle or at base of cupuliform receptacle-tube (or laterally in *Licania licaniiflora*); endocarp without lateral plates; inflorescence various, racemose only in a few species of *Licania*:
    3. Endocarp with 4–8 prominent longitudinal ridges corresponding to the lines of fracture that allow the seedling to escape . . . . 1. *Chrysobalanus*
    3. Endocarp without longitudinal ridges . . . . 3. *Licania*

2. PARINARIEAE

Tribus Parinarieae Prance & F. White trib.nov.

Hirtellaceae sectio (sic) Parinariinae Hauman, *Bull. Jard. Bot. État, Brux.* **21**: 170 (1951) sine descr. lat.

Flores leviter zygomorphi. Tubus receptaculi calycem aequans vel superans, faucibus pilis longis retrorsis obsaeptus. Stamina fertilia 7–17 posteriora; filamenta libera, calyce breviora vel paullo longiora; staminodia denticulata usque claviformia, in annulo faucali inserta. Ovarium 2-loculare, in ipso ore vel prope os tubi receptaculi insertum.

Flowers weakly zygomorphic. Receptacle-tube equalling or longer than the calyx, blocked at the throat by long retrorse hairs. Fertile stamens 7–17, posterior; filaments free, shorter or slightly longer than the calyx; staminodes denticulate to claviform, inserted on a faucal annulus. Ovary 2-locular, inserted at or near mouth of receptacle-tube.

Exceptions: Flowers strongly zygomorphic in *Bafodeya* and *Neocarya*. Receptacle short, saccate and gibbous in *Neocarya*. Ovary laterally inserted in lower half of receptacle-tube in *Hunga*.

1. Flowers strongly zygomorphic:
  2. Receptacle-tube obliquely campanulate, ventricose, as long as the sepals, hairy throughout inside; sepals hairy on adaxial surface; stamens *ca.* 7; staminodes well-developed, fleshy, claviform; endocarp without obturators . . . . 5. *Bafodeya*
  2. Receptacle-tube saccate, much shorter than the sepals, glabrous inside except at the throat; sepals glabrous on adaxial surface; stamens 12–17; staminodes minute, subulate; endocarp with 2 small basal obturators . . . . 8. *Neocarya*
1. Flowers weakly zygomorphic:
  3. Endocarp rough, with 2 small basal obturators; lower leaf surface nearly always with stomatal crypts; filaments almost equalling sepals; ovary inserted in upper half of receptacle-tube . . . 9. *Parinari*
  3. Endocarp smooth, without obturators; lower leaf-surface without stomatal crypts:
    4. Endocarp with two prominent bony ridges; filaments equalling sepals; staminodes forming a denticulate rim; ovary inserted at mouth of receptacle-tube . . . . 6. *Exellodendron*
    4. Endocarp unridged; filaments much shorter than the sepals; staminodes subulate; ovary inserted in lower half of receptacle-tube . . . . 7. *Hunga*

3. COUEPIEAE

Tribus Couepieae Prance & F. White trib. nov.

Flores vulgo leviter zygomorphi. Tubus receptaculi plerumque calyce longior, faucibus pilis longis, retrorsis obsaeptus. Sepala suborbicularia, concava, insigniter imbricata. Stamina vulgo ultra (15) 20, plerumque circulum plenum formantia; filamento vulgo libera et bi- vel pluriseriata in annulo faucali inserta, sepalis multo longiora, in alabastro plerumque undulata; staminodia nulla, parva et denticulata, vel filiformia. Ovarium 1–3-carpellare, carpello quoque 1–2-loculari, ore tubi receptaculi insertum.

Flowers usually weakly zygomorphic. Receptacle-tube mostly longer than the calyx, blocked at the throat by long retrorse hairs. Sepals suborbicular, concave, markedly imbricate. Stamens usually more than (15) 20, usually forming a complete circle; filaments usually free and inserted in two or more rows on the faucal annulus, much longer than the sepals, usually undulate in bud; staminodes absent or small and denticulate or filiform. Ovary 1–3-carpellary, each carpel 1–2-locular, inserted at mouth of receptacle-tube.

Exceptions: Flowers strongly zygomorphic in *Acioa*. Receptacle-tube shorter than the calyx in *Maranthes corymbosa* and also in *Couepia platycalyx*, which has a solid receptacle. Fertile stamens fewer than 20 in *Acioa* and a few species of *Couepia*, forming a markedly incomplete circle only in *Acioa*; filaments coiled in bud in *Acioa*, united in *Acioa* except in *A. edulis*.

1. Sepals unequal, 2 very small and 3 much larger, the outer sepals with conspicuous discoid glands; endocarp very thick and woody, without obturators; germination phanerocotylar . . . . 10. *Acioa*
1. Sepals subequal, eglandular (except in *C. dolichopoda* and *longipendula*); endocarp thinner:
    2. Receptacle-tube narrowed into the elongate 'pedicel'; style glabrous; ovary bilocular; endocarp with obturators; germination phanerocotylar . . . . 12. *Maranthes*
    2. Receptacle-tube sharply differentiated from the short pedicel; style hairy; ovary unilocular; endocarp without obturators; germination cryptocotylar . . . . 11. *Couepia*

4. HIRTELLEAE

Tribus Hirtelleae Prance & F. White stat. nov.

Rosaceae, Chrysobalanoideae, subtribus Hirtellinae Focke, in Engl. & Prantl, *Nat. Pflanzenfam.*, **3**(3): 58 (1891) pro parte.

Hirtellaceae sectio (sic) Hirtellinae Hauman, *Bull. Jard. Bot. État Brux.* **21**: 170 (1951).

Flowers strongly zygomorphic. Receptacle-tube usually blocked at the throat by long retrorse hairs. Fertile stamens 3–75, posterior; filaments free or ligulately connate, usually much longer than the sepals, usually coiled in bud. Staminodes usually forming a short ligule or a denticulate rim to the faucal annulus. Ovary 1–3-carpellary, usually unilocular, inserted at or near the mouth of receptacle-tube.

Exceptions: Retrorse hairs absent in *Kostermanthus* and *Magnistipula cerebriformis* and *M. tamenaka*. Filaments scarcely longer than the sepals in *Kostermanthus* and *Magnistipula*. Ovary bilocular in *Atuna* and *Magnistipula tessmannii*.

1. Filaments ligulately connate or at least united in lower third:
    2. Sepals strongly imbricate; petals very unequal, the 2 posterior long-unguiculate; filaments shorter than the sepals . . . . 16. *Kostermanthus*
    2. Sepals slightly imbricate; petals subequal, not or slightly unguiculate:
        3. Filaments ligulately connate for most of length, far-exserted . . . . 14. *Dactyladenia*
        3. Filaments united only in lower third, scarcely exserted . . . . 17. *Magnistipula*
1. Filaments free:
    4. Stipules large, prominently keeled; ovary bilocular; epicarp verrucose, mesocarp fibrous; endocarp thick, breaking up irregularly at germination; cotyledons strongly ruminate . . . . 13. *Atuna*
    4. Stipules not keeled; ovary unilocular; epicarp smooth; mesocarp juicy, endocarp thin, breaking up at germination along 4–7 longitudinal lines of weakness; cotyledons not ruminate . . . . 15. *Hirtella*

16. GENERIC DESCRIPTIONS

1. *Chrysobalanus* (*figure* 15)

(Greek: 'golden acorn', an allusion to the fruit)

Chrysobalanus L., *Gen. Pl.*: 365 (1737); *Sp. Pl.*: 513 (1753); *Gen. Pl.* ed. 5: 229 (1754). – DC., *Prodr.* **2**: 525 (1825). – Focke, in Engl. & Prantl, *Nat. Pflanzenfam.* **3**(3): 57, t. 30 fig. A–C (1894). – Hutch., *Gen. Fl. Pl.* **1**: 190 (1964). – Prance, *Fl. Neotr.* **9**: 14, t. 2 (1972). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 272 (1976); *Distr. Pl. Afr.* **10**: 283–286 (1976); *Fl. Zamb.* **4**: 34 (1978). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 60, t. 19 (1978).

Icaco Plum., *Nov. Pl. Amer. Gen.*: 43, t. 5 (1703) nom.illegit.

Small or medium-sized trees or shrubs. *Leaves* with two or more glands on lower surface; petiole eglandular; lower surface of lamina glabrous or with a few stiff, appressed hairs; stipules absent (*fide* de Souza 1979*a*). *Inflorescence* few-flowered, a short raceme of cymules or cymose throughout, or a false raceme, or a subsessile fascicle. Bracts small, eglandular. *Flowers* bisexual,

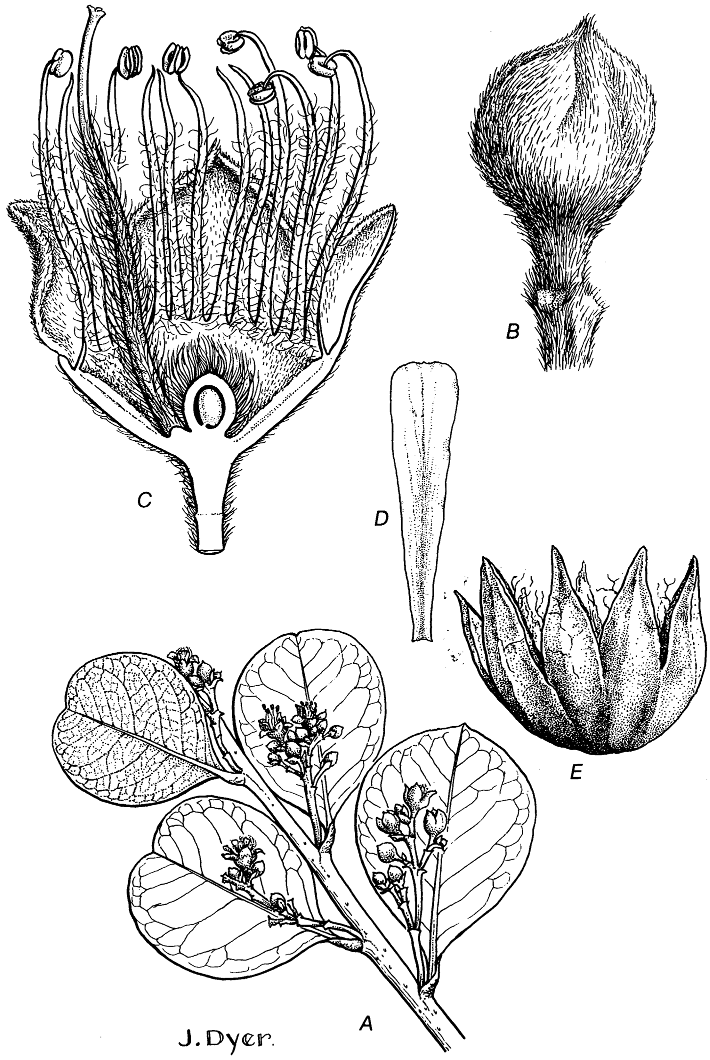


FIGURE 15. *Chrysobalanus icaco*: A, habit ($\times \frac{3}{4}$); B, flower bud ($\times$ 10); C, half flower ($\times$ 10); D, petal ($\times$ 10); E, fruit ($\times 1\frac{1}{4}$). (A–D from Prance & Pennington 1304; E from Prance & Silva 58762).

actinomorphic. Receptacle-tube cupuliform, interior and exterior puberulous. Sepals 5, acute, subequal. Petals 5, longer than the sepals. Stamens 12–26, forming a complete circle; filaments hairy, approximately twice as long as sepals, appearing slightly united at the base. Ovary monocarpellary, 1-locular, inserted at base of receptacle-tube, covered with a dense mass of hairs; style puberulous; stigma slightly expanded, shallowly 3-lobed. *Drupe* small, glabrous; endocarp thin, hard, interior glabrous, exterior smooth, with 4–8 prominent longitudinal ridges corresponding to the lines of fracture that allow the seedling to escape.

Germination: cryptocotylar; cataphylls *ca.* 15, minute; eophylls alternate, laminate; the lamina with a pair of glands at the base on the upper surface (Mensbruge 1966: 124–130, cum.ic.; Duke 1965: 315, t. 4., fig. 35).

Chromosome number: $2n = 22$ (*C. icaco* L. ('*orbicularis* Schumach.') Mangenot & Mangenot 1962).

Type species: *C. icaco* L.

Distribution and ecology: one widespread species in tropical America and tropical Africa, and a localized endemic in the West Indies (see individual species below).

Reproductive biology: the fruit is fleshy and normally purple, although yellow and purple fruits often occur in the same population, as in Trinidad and Pará, Brazil. The fruit of *C. cuspidatus* is said to be attractive to birds (*Beard* no. 492). *C. icaco* is dispersed by ocean currents and also apparently by bats (Ridley 1930, quoting Guppy; Greenhall 1956; van der Pijl 1957). According to Guppy the fruit is buoyant because the seed does not entirely fill the cavity of the endocarp. The seed remains viable after the fruit has floated for two months. Large numbers of apparently water-transported fruits can be found on the shore-line flotsam of Jamaica, Trinidad, Brazil, etc. (G.T.P., personal observations).

In Bénin, de Souza (1979*a*) found piles of endocarps containing viable seeds of *Chrysobalanus icaco* subsp. *icaco* beneath the feeding perches of bats of the genus *Eidolon*. The same author mentions various rodents and monkeys as being dispersal agents and states that the fruits of subsp. *atacorensis* are capable of water transport for short distances along the banks of rivers. In Brazil the flowers of *C. icaco* are visited by small bees, especially *Trigona* and *Melipona* (B. W. Nelson, personal communication).

Taxonomic history and relationships: *Chrysobalanus* and *Licania* are probably more closely related than any two genera in the family (see under *Licania*). Nevertheless they have been kept apart in all major systems of classification, and very few species have ever been misplaced. The more important are listed below. Others are given by Prance (1972).

(i) *Licania oligantha* A.C.Sm. is a synonym of *Chrysobalanus cuspidatus* Duss.

(ii) *Licania incana* Aubl., the type species of *Licania*, was transfered to *Chrysobalanus* by Gómez de la Maza (*Fl. Cub.*: 39 (1887)), who thereby implied that the remaining species should be transferred. No subsequent author has followed him in this. Because Gómez de la Maza also transferred species of *Hirtella* and *Parinari* to *Chrysobalanus* he appears to have had unusual ideas on generic delimitation.

(iii) *Licania humilis* Cham. & Schlecht. was transferred to *Chrysobalanus* by Kuntze (*Rev. Gen.* 3(2): 76 (1891)), one of his many erratic judgments.

(iv) *Chrysobalanus racemosa* Roxb. is an *Atuna*. These two genera have only the family characters in common.

(v) *Licania michauxii* Prance (1970), a North American geoxylic suffrutex, has three synonyms in *Chrysobalanus*. It is the only *Licania* which provides a connecting link to *Chrysobalanus*, although it stands closer to the former. It is remarkably similar to *Chrysobalanus* in general appearance, especially in the colour of its leaves, and its inflorescence. It differs, however, in its method of seedling escape which, in Chrysobalanaceae, is usually constant within a genus, and in several floral characters, such as its shorter, hairy, non-spathulate petals and its glabrous filaments and style.

Conspectus of the species

1. Inflorescence 1–5-flowered; flowers terminating a stalk 0.4–0.6 cm long, which bears 2 conspicuous bracteoles without flower-buds in their axils; receptacle-tube and sepals strigulose–puberulous outside; leaves lanceolate and acuminate and often also mucronulate . . . . 1. *C. cuspidatus*

1. Inflorescence usually with 7 or more sessile or subsessile flowers; receptacle-tube and sepals grey–tomentellous outside; leaves orbicular to lanceolate–acuminate . . . . 2. *C. icaco*

1. ***Chrysobalanus cuspidatus*** Griseb. [*Fl. Brit. W. Ind.*: 711 (1864) nom. nud.] ex Duss., *Fl. Phan. Antill. Fr.*: 258 (1897). – Prance, *Fl. Neotrop.* **9**: 20, t. 2 fig. G (1972). Type: Guadeloupe, fl., *Duss.* 3633 (B, destroyed, holotype; NY, lectotype of Prance 1972).

Licania oligantha A. C. Smith, *J. Arn. Arb.* **28**: 333 (1947). Type: St. Lucia, fl., *Beard* 492 (A, holotype; K, LE, MO, NY).

Only known from St. Kitts in the Leeward Islands, and Dominica, Martinique and St. Lucia in the Windward Islands. On St Lucia (Beard, reported by Smith 1947) it is almost confined to a stunted, windswept type of rainforest, only 10 m high, which occurs on the crests of all but the highest ridges and *pitons* between 490 and 670 m. It is one of the principal species, forming up to 30% of the stand and is associated with *Micropholis chrysophylloides*, *Myrica* sp., and *Tovomita plumieri.*

The differences between *C. cuspidatus* and *C. icaco* are slight. In its leaves *C. cuspidatus* is barely distinguishable from an African subsp. of *C. icaco*, subsp. *atacorensis*. Because the latter is connected to *C. icaco* subsp. *icaco* by intermediates, wherever they come into contact, it cannot be kept up as a species. At present, no intermediates are known between *C. cuspidatus* and *C. icaco* and, at least provisionally, specific rank seems justified.

2. ***Chrysobalanus icaco*** L., *Sp. Pl.*: 514 (1753) – Guill., Perr. & A. Rich., *Fl. Sénég. Tent.*: 272 (1832). Hook. f. in Mart. *Fl. Bras.* **14**(2): 7 (1867). – Oliv. *F.T.A.* **2**: 365 (1871). – Prance, *Fl. Neotrop.* **9**: 14, t. 2 (1972). – White, *Bull. Jard. Bot. Nat. Belg.* **46**: 272 (1976); *Distr. Pl. Afr.* **10**: 282–286 (1976); *Fl. Zamb.* **4**: 34, t. 9, fig. A1–3 (1978). – Letouzey & F. White, *Fl. Cam.* **20**; Fl. Gab. **24**: 61, t. 19 (1978). Type: Jamaica, *P. Browne* in Herb. Linnaeus no. 641 (LINN, holotype).

Widespread in tropical America and tropical Africa, with a mainly coastal distribution, except for subsp. *atacorensis*, which is widespread in the interior of Africa.

Whether *C. icaco* occurs on both sides of the Atlantic or not has long been debated. Earlier workers such as de Candolle (1825), Guillemin *et al.* (1832), J. D. Hooker (1867) and Oliver (1971) believed the American and African plants to be conspecific, but most other workers on the African flora have kept them apart, and, indeed, have sometimes recognized three African species, *C. ellipticus*, *C. orbicularis* and *C. atacorensis*, although in some cases expressing doubts as to their distinctness.

We have failed to find any characters to keep *C. icaco*, *C. orbicularis* and *C. ellipticus* apart and regard them as belonging to the same subspecies. *C. atacorensis* has a distribution which is parapatric with that of *C. icaco* in Africa. Because it differs principally in leaf-shape and is connected by intermediates wherever it comes into contact with *C. icaco* we give it only subspecific rank.

C. icaco subsp. *icaco* is very variable in leaf-shape, branching of inflorescence, and in fruit shape, size and colour. Little of this variation is correlated with geography. The general pattern of variation in America is described by Prance (1972, p. 19). Variation in Bénin has been described in great detail by de Souza (1979*a*, *b*), who recognizes three subspecies: subsp. *orbicularis* (Schumach.) S. de Souza, with five varities and subsp. *ellipticus* (Soland. ex Sabine) S. de Souza, as well as subsp. *atacorensis*. Such a treatment is no doubt useful for some local purposes but, because the variation recorded for Bénin is largely continuous and most can be matched in parts of the range of subsp. *icaco* in the Neotropics, an informal treatment seems preferable for monographic purposes. Murray has recently (*Kalmia* **12**: 19, 1982) published the name *C. icaco* subsp. *pellocarpus* (G. F. W. Mey.) E. Murray for no apparent reason.

The distribution and ecology of the two subspecies are as follows.

(i) Subsp. *icaco* is widespread in coastal regions of tropical and subtropical America from Florida to southern Brazil and along the Atlantic seaboard of Africa from Senegal to Angola. In both America and Africa it occurs mainly in coastal thicket on sandy shores, often immediately above the strand line. But it is also found on the landward side of mangrove swamps and further inland (up to 200 km in Africa and 600 km in South America) on river banks, and in swampy subcoastal depressions or wooded grassland. Thus in Trinidad it is abundant in palm marsh dominated by *Mauritia setigera*; it also occurs as scattered bushes in the waterlogged Aripo savannas (Beard 1946). On the South American mainland it is found in savanna in the Guianas. It is naturalized in the Seychelles and Fiji.

(ii) Subsp. *atacorensis* (A. Chev.) F. White is widespread in the wetter parts of tropical Africa from Liberia to the Central African Republic and southwards to Zambia and Angola. It nearly always occurs in fringing forest.

Excluded species

(i) *Chrysobalanus luteus* Sabine, *Trans. Roy. Hort. Soc.* **5**: 453 (1824). Only the fruit was described from information supplied by a correspondent. Brignoli (1862) suggests that it belongs to Icacinaceae or Olacaceae.

(ii) *Chrysobalanus stuhlmannii* Engl., *Pflanzenw. Ost. Afr.* **C.**: 191 (1895). The holotype (*Stuhlmann* 430, B) was destroyed during the last war. Engler himself questions whether this species belongs to *Chrysobalanus*, as does Graham (*F.T.E.A. Rosaceae*: 48, 1960).

2. *Grangeria* (*figure* 16)

(after N. Granger, an 18th century traveller)

Grangeria Commers. ex Juss., *Gen.*: 340 (4 August 1789). – DC., *Prodr.* **2**: 527 (1825). – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 607 (1865). – Baill., *Adansonia* **8**: 200 (1868). – Focke, in Engl. & Prantl, *Nat. Pflanzenf.* **3**(3): 58, t. 30, fig. D (1891). – Hutch., *Gen. Fl. Pl.* **1**: 191 (1964).

Trees or shrubs. *Leaves* with a pair of small, discoid, marginal glands at base of lamina; petiole eglandular; lower surface of lamina glabrous; stipules small, lateral, caducous. *Inflorescence* a simple or, rarely, branched, axillary or terminal raceme. Pedicels slender, much longer than the receptacle-tube. Bracts and bracteoles minute, not enclosing the flower-buds, mostly with a single apical gland. *Flowers* bisexual, slightly zygomorphic. Receptacle-tube obliquely turbinate, slightly asymmetric, shorter than the sepals, completely glabrous inside. Sepals 5, subequal, reflexed, rounded or obtuse. Petals 5, slightly shorter than the sepals,

Rosemary Wise.

FIGURE 16. *Grangeria borbonica*: A, habit (× $\frac{1}{2}$, OXF s.n.); B, half flower and detached petal (× 10, OXF s.n.). *G. porosa*: C, habit (× $\frac{1}{2}$, Decary 8182) and stipules (× $7\frac{1}{2}$, Baron 5755); D, fruits (× 1, SFM 58).

caducous. Stamens 15 or 7–8, forming a complete or incomplete circle; filaments glabrous, slightly longer than the sepals, flattened and slightly expanded at the base, shortly united; staminodes, when present, 2–5, forming a denticulate ridge to the faucal annulus. Ovary 1-carpellary, 1-locular, inserted laterally at mouth of receptacle-tube, covered with conspicuous, white woolly hairs which block entrance to receptacle-tube; style somewhat shorter than the filaments, glabrous; stigma slightly 3-lobed. *Drupe* small, trigonous or irregularly angular; epicarp smooth; endocarp thin, hard, bony, smooth outside, hairy inside, with two large lateral plates which break away on germination and allow seedling to escape.

Type species: *G. borbonica* Lam.

Distribution and ecology: two species. *G. borbonica* is confined to Mauritius and Réunion, and *G. porosa* to Madagascar.

On Réunion (Rivals 1952) *G. borbonica* occurs in forest at low and medium altitudes on the east and southern sides of the island which are exposed to the SE monsoon and receive more than 3000 mm of rainfall per year. On very infertile soils the forest does not form a closed canopy, and pioneer species such as *Aphloia theiformis* and *Agauria salicifolia* are able to persist. In this community, forest species that can tolerate nutrient-deficient soils, including *Grangeria borbonica* and *Memecylon cordatum*, are much more abundant than on more fertile soils.

Reproductive biology: nothing appears to have been published.

Taxonomic history and relationships: *Grangeria*, based on a Commerson specimen from Réunion, was described by Jussieu in 1789. In the same year the type species, *G. borbonica*, based on the same gathering, was described by Lamarck. A second species, from Madagascar, *G. porosa*, was described by Baillon in 1868. *Grangeria* has been accepted as a distinct genus by all workers, except Drake (1895) who transferred *Grangeria porosa* to *Hirtella*.

Grangeria borbonica has relatively few (15) exserted stamens, which are all fertile and are inserted all the way round the rim of the receptacle-tube. This feature is rather rare in the family and is found elsewhere only in *Chrysobalanus*, and in some species of *Couepia* and *Licania* subgenus *Moquilea*. Although *G. porosa* agrees with *G. borbonica* in most features, it differs in having only 7 or 8 posterior fertile stamens and 2–5 anterior filiform or denticulate staminodes. Its androecium is thus not unlike that of *Hirtella*.

Both Jussieu and Lamarck, who only knew *G. borbonica*, thought that *Grangeria* was closely related to *Hirtella*. J. D. Hooker, however, believed it to be closer to *Licania* (*Moquilea*), a view also shared by Focke.

Grangeria differs from all species of *Licania* in the method of seedling escape from the endocarp: by means of well-defined lateral plates, rather than by irregular fragmentation. It also differs from all species of *Licania* in the lateral insertion of the ovary just below the mouth of the receptacle-tube. In all species of *Licania* except *L. licaniiflora* the ovary is centrally inserted at the base of the receptacle-tube. In *L. licaniiflora*, which is sufficiently isolated in the genus to require its own subgenus, the ovary is laterally inserted but only about halfway up the receptacle-tube. *L. licaniiflora* also differs from *Grangeria* in the construction of the inflorescence and several details of the flower.

Grangeria shares with *Parastemon*, another small satellite of *Licania*, the method of seedling escape, but differs in having more stamens with filaments longer than, not much shorter than, the sepals, the lateral insertion of the ovary and in its shallowly, not deeply lobed, stigma.

Hirtella differs from *Grangeria* in its more zygomorphic flowers with a gibbous receptacle-tube, long retrorse hairs arising from the throat of the receptacle-tube, much longer filaments, and the mechanism of seedling escape by means of 4–7 longitudinal lines of weakness.

Grangeria occupies a somewhat isolated position in Chrysobalaneae and possibly provides a connecting link with Hirtelleae.

Conspectus of the species

1. Leaves up to 4 × 2 cm, apex rounded or emarginate; inflorescence-axes and outside of the receptacle-tube and sepals densely setulose; fertile stamens 15, inserted all the way round the rim of the receptacle-tube . . . . 1. *G. borbonica*
1. Leaves 5 cm × 1.5 cm to 8 cm × 3 cm, apex bluntly acuminate; inflorescence-axes and outside of receptacle-tube and sepals very sparsely setulose; fertile stamens 7 or 8, inserted laterally at mouth of receptacle-tube . . . . 2. *G. porosa*

1. ***Grangeria borbonica*** Lam., *Encyc.* **3**: 21 (19 Oct. 1789); *Tabl. Encyc.* **3** (1), t. 427 (1794). – Type: Réunion, fl., fr., *Commerson*, (P-LAM, holotype; C-Herb Vahl; G).

Grangeria buxifolia Sm. in Rees, *Cyclop.* **16**: n.l. (without pagination) (1811). Type: unknown, not cited.

Mauritius and Réunion. Early collectors said this species was plentiful.

2. ***Grangeria porosa*** Boiv. ex Baill., *Adansonia* **8**: 200 (1868); Hist. Nat. Pl., in Grandidier, *Hist. Phys. Nat. Pol. Madag.* **28**: t. 14 (1887). Types: Madagascar, fl. *Richard* 220 (P); fl., *Richard* 582 (P); fl., *Pervillé* 354 (P); fr., *Pervillé* 507 (K, P); fl., *Boivin* 2210 (P, lectotype, here designated).

Grangeria madagascariensis O. Hoffmann, *Sert. Plant. Madag.*: 15 (1881). Type: Madagascar, coll. unknown (B, holotype, destroyed).

Hirtella porosa (Boiv. ex Baill.) Drake, *Hist. Pl. Madag.* **1**: 30 (1895). Type as for *G. porosa*.

Madagascar.

3. *Licania* (*figures* 17–20)

(an anagram of a local name in French Guiana)

Licania Aubl., *Hist. Pl. Guiane Fr.* **1**: 119, t. 45 (1775). – DC., *Prodr.* **2**: 527 (1825). – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 606 (1865). – Fritsch, *Ann. Naturhist. Mus. Wien* **4**: 33 (1889). – Focke, in Engl. & Prantl, *Nat. Pflanzenf.* **3**(3): 58 (1891). – Hutch., *Gen. Fl. Pl.* **1**: 191 (1964). – Prance, *Fl. Neotrop.* **9**: 21, t. 3–27 (1972). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 280 (1976); *Distr. Pl. Afr.* **10**: 293 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 67, t. 20 (1978).

Moquilea Aubl., *Hist. Pl. Guiane Fr.* **1**: 521, t. 208 (1775). – DC., *Prodr.* **2**: 526 (1825). – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 606 (1865). – Focke, in Engl. & Prantl, *Nat. Pflanzenf.* **3** (3): 58 (1891). – Hutch., *Gen. Fl. Pl.* **1**: 191 (1964).

Dahuronia Scop., *Introd.*: 217 (1777) nom.illegit.

Hedycrea Schreb., Linn. *Gen. Pl.* ed. 8, **1**: 160 (1789) nom.illegit.

Angelesia Korth., *Ned. Kruidk. Arch.* **3**: 384 (1854). – Hutch, *Gen. Fl. Pl.* **1**: 192 (1964).

Trichocarya Miq., *Fl. Ind. Bat.* **1** (2): 258 (1855), **6**: 1084 (1858) quoad *T. splendens* tantum.

Geobalanus Small, *Fl. Miami*: 80 (1913). – Hutch., *Gen. Fl. Pl.* **1**: 192 (1964).

Coccomelia Ridl., *J. Roy. Asiat. Soc. Straits Branch* **82** (1920).

Afrolicania Mildbr., *Notizbl. Bot. Gart. Berlin* **7**: 483 (1921).

Trees up to 35 m tall or shrubs, rarely suffruticose. *Leaves* often with an ill-defined glandular area on upper surface at junction of lamina and the eglandular petiole; lower surface of lamina glabrous, lanate or strigose, or (in 25 species) with stomatal crypts filled with densely matted hairs; stipules small, free, subulate or narrowly deltate, lateral or intrapetiolar, usually persistent. *Inflorescence* usually a simple or, more frequently, a branched raceme of sessile or subsessile cymose glomerules of sessile or subsessile flowers, more rarely a simple or branched raceme of shortly stalked cymose glomerules with subsessile or shortly pedicellate flowers, very rarely a simple or compound raceme or spike, or a raceme of many-flowered, rather lax cymes. Bracts and bracteoles usually eglandular and not enclosing the flower-buds. *Flowers* bisexual, actinomorphic or weakly zygomorphic. Receptacle-tube 0.1–0.8 cm long, variable in shape, usually cupuliform, campanulate or urceolate, rarely turbinate or patelliform, or (*L. splendens*) obliquely patelliform, always hairy inside, but throat without long retrorse hairs. Sepals 5, subequal, acute. Petals 5, more or less equalling sepals, or absent. Stamens 3–40; filaments forming a complete circle or unilateral; included and much shorter than the sepals to exserted and about twice as long, usually united at base, usually glabrous; staminodes usually absent, rarely represented by a short denticulate ridge. Ovary 1-carpellary, 1-locular, inserted at or near base of receptacle-tube; style filiform, indistinctly 3-lobed at apex. *Drupe* 1.2 cm × 0.8 cm to 10 cm × 5 cm, dry or fleshy; epicarp tomentose, glabrous or verrucose; endocarp thick, hard and woody, or thin and fibrous, without any special mechanisms for seedling escape, interior hairy or glabrous.

Exceptions: *L. dealbata* and *L. michauxii* are rhizomatous geoxylic suffructices. The latter is unique in the family in having crenulate leaves. In *L. licaniiflora* (subgenus *Parinariopsis*) the petiole has two large, alternate glands on its upper surface. Bracts and bracteoles are glandular in *L. alba*, *L. longistyla*, *L. octandra* and *L. sprucei*; they enclose the flower-buds in *L. licaniiflora* and *L. densiflora*. The flowers are unisexual in *L. elaeosperma* (subgenus *Afrolicania*) and strongly zygomorphic in *L. splendens* (subgenus *Angelesia*). Filamentous staminodes occur in *L. arachnoidea* and *L. macrophylla*. The ovary is laterally inserted in *L. licaniiflora*.

Germination: cryptocotylar, eophylls alternate.

Chromosome number: $2n = 22$ (*L. elaeosperma* ('*Afrolicania elaeosperma*' Mangenot & Mangenot 1962).

Type species: *L. incana* Aubl.

Distribution and ecology: 192 species, of which one occurs in Africa, three in tropical Asia, and the remainder in America.

Of the 188 American species all but 12 occur in South America, though a few of them also extend further north. Thus, of the four West Indian species, three, *L. leucosepala*, *L. pyrifolia*, and *L. cruegerana*, also grow on the mainland. Similarly, five of the 15 species which grow in Central America and Mexico, namely *L. affinis*, *L. arborea*, *L. glabriflora*, *L. hypoleuca* and *L. platypus*, also occur in South America. One of them, *L. affinis*, shows a wide disjunction between Costa Rica, Panama and the Guiana forests. Some species in other genera, e.g. *Aspidosperma macrosperma* (Apocynaceae) and *Caryocar nuciferum* (Caryocaraceae), show a similar distribution. Of the northern endemics four are confined to lowland forest in Panama. Only one species, *L. michauxii*, grows beyond the tropics in North America.

Licania is predominantly a genus of moist forests, but a few species have adapted to other habitats. Some of the Central American species, e.g. *L. arborea*, which extends from Mexico to Peru, grow in dry forests. The remarkable North American species, *L. michauxii*, is a rhizomatous geoxylic suffrutex which is abundant in pinelands, oak scrubland and on sand dunes in Florida, and extends westwards to Louisiana and northeast to South Carolina.

FIGURE 17. *Licania licaniiflora*: A, habit (× ½), axillary bud (× 1) and half flower and petal (× 7½), all from Prance *et al.* 15745. *L. michauxii*: B, habit (× ½, Small); C, drupe (× 1, Curtiss 5779); D, interior of endocarp (× 1, Curtiss 5779).

Although it grows no more than 30 cm high it has been described as an 'underground tree'. Its subterranean stems, which are up to 8 cm thick, have a spread of more than 30 m (Prance 1970).

Of the South American species 23 occur in non-forest vegetation, as follows.

(i) Seven species, including *L. incana*, occur in the savannas of Colombia, Venezuela and Amazonia.

(ii) Five species, namely *L. glazioviana*, *L. littoralis*, *L. salzmannii*, *L. tomentosa* and *L. turbinata*, occur in coastal scrub (restinga) behind sand bars in eastern Brazil, and *L. maritima* occurs in a similar habitat in Pacific Colombia.

(iii) One species, *L. rigida*, is a member of the caatinga formation of northeast Brazil, which is an open scrub forest characterized by the abundance of cacti and spinous Leguminosae.

(iv) Seven species are found in the cerrado, the open woodlands of the planalto of central Brazil. Among them, *L. dealbata* is a geoxylic suffrutex, and *L. humilis* is sometimes suffruticose but otherwise grows as a small, gnarled tree with thick corky bark.

(v) Two species, *L. joseramosii* and *L. stewardii*, are characteristic members of scrub forest on sandstone rock (campina rupestre), which occurs in a few places in the Amazon basin.

All other South American Licanias are forest species and the genus is represented in all main types of forest below 1500 m as follows.

(i) Nine species occur in the isolated lowland forests of the west coast of Colombia.

(ii) Six species occur in the almost equally isolated coastal forests of Brazil.

(iii) Nine species are characteristic of montane forests between 1000 and 1500 m. Among them, *L. chiriquiensis* is endemic to the mountains in Panama, *L. tepuiensis* to the Guyana Highlands of Venezuela, *L. subrotundata* to the coastal range of Venezuela, *L. aracaensis* to the isolated sandstone Serra de Araca in Northern Amazonas, Brazil. Three species, *L. cabrerae*, *L. durifolia* and *L. macrocarpa*, occur in different parts of the Andes.

(iv) One species is endemic to Bolivia.

(v) Two species occur in forest patches in the cerrado region.

The remaining species, approximately 100 in all, belong to the evergreen rainforest of the great Hylaea region of the Amazon and Orinoco basins. About one third are confined to inundated forest fringing the main watercourses; the remainder occur on well-drained sites, but some of the latter also extend into flooded areas.

The genus is well represented in wallaba (*Eperua falcata*) forest, one of the most distinctive dry-land forest types, which occurs on the bleached white sands of the Essequibo basin in Guyana. Some Licanias, e.g. *L. laxiflora*, which occur in wallaba forest, also grow in other forest types.

Different *Licania* species vary greatly in abundance. A few are very rare but others are abundant. For example, in Guyana, *L. alba* (*L. venosa*) is one of the most abundant subordinate species in mixed forest, and in greenheart (*Ocotea rodiaei*) forest near Moraballi Creek (Davis & Richards 1933–4; Richards 1952). In the same area, *L. buxifolia*, next to *Eperua falcata* itself, is, together with *Catostemma fragrans*, the most abundant tree species in wallaba forest. In the Hylaea, the widely distributed *L. heteromorpha* is locally abundant in inundated forests, and *L. apetala* is one of the most numerous trees on river beaches, especially those of the Rio Negro. In Trinidad *L. heteromorpha* (*L. biglandulosa*) is also locally abundant in the canopy of montane rainforest between 760 and 850 m. *L. ternatensis*, an endemic of the Lesser Antilles, is plentiful in various types of montane forest and thicket (Beard, 1949).

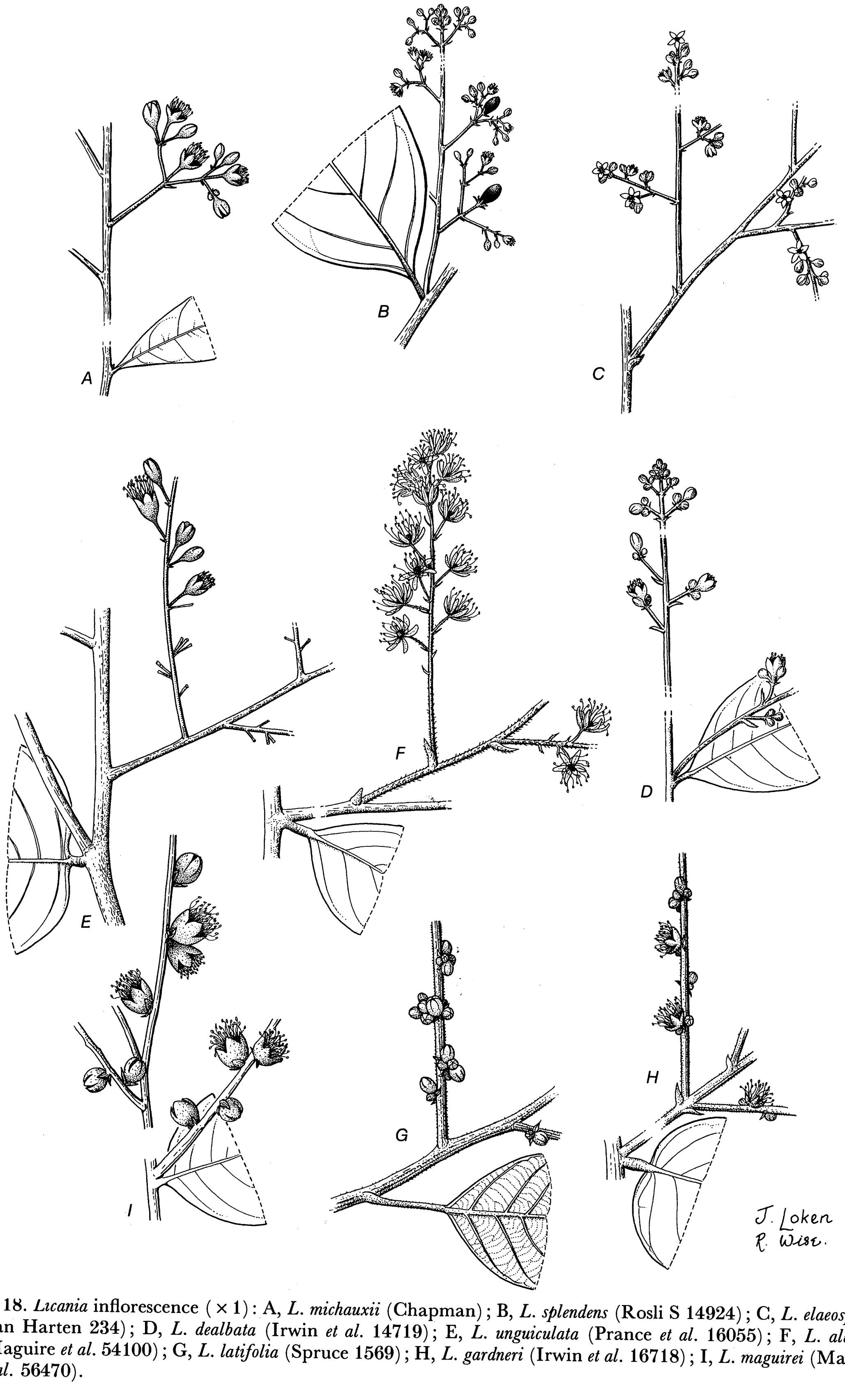


Figure 18. *Licania* inflorescence (× 1) : A, *L. michauxii* (Chapman) ; B, *L. splendens* (Rosli S 14924) ; C, *L. elaeosperma* (van Harten 234) ; D, *L. dealbata* (Irwin *et al.* 14719) ; E, *L. unguiculata* (Prance *et al.* 16055) ; F, *L. albiflora* (Maguire *et al.* 54100) ; G, *L. latifolia* (Spruce 1569) ; H, *L. gardneri* (Irwin *et al.* 16718) ; I, *L. maguirei* (Maguire *et al.* 56470).

Details of the distribution and ecology of the African species are given under the individual species below.

Reproductive biology: nothing appears to have been published on pollination. The sweet-scented flowers of *L. apetala* are visited by innumerable small bees of the genera *Apis* and *Trigona* (G.T.P., personal observations).

The fruits of some species are dispersed by bats (Huber 1909; G.T.P., personal observations). Those of other species are dispersed by fishes (Huber 1909; Gottsberger 1978; Goulding 1980; G.T.P., personal observations). Huber found germinable seeds of several species belonging to different families in the stomach of a fish; among them were endocarps of *L. macrophylla*. The fruits of three other riverine species, *L. leptostachya*, *L. parviflora* and *L. longipetala*, fall into the water and almost immediately are swallowed by fish (G.T.P., personal observations). The stomachs of a large fish, *Lithodoras dorsalis*, have been found to be stuffed full of the fruits of *Licania longipetala*, which are capable of floating for two or three days. When the fruit-skin is perforated or is penetrated by water the fleshy mesocarp, which acts like an air sac, disintegrates and the fruit sinks. It is believed that the fish feeds at night and is an important dispersal agent. Endocarps, stripped of their fleshy covering, pass through the fish unharmed; those removed from the lower intestines germinated in experimental pots (Goulding 1980). The fruits of the only African species, *L. elaeosperma*, are said to be dispersed by water (F. C. Deighton, MS in Herb. Kew), but it is not known whether they are eaten by fish. The seed of *L. splendens* is dispersed by the fruit pigeon *Ducula aenea* (M. Leighton, personal communication) and is eaten by the squirrel *Ratufa affinis*.

Taxonomic history and relationships: *Licania* and *Moquilea* were described by Aublet in the same publication (1775). The former, based on *L. incana*, was placed in Pentandria Monogynia, and the latter, based on *Moquilea guianensis*, was placed in Icosandria Polygynia next to *Couepia*. Because Aublet was using the sexual system of Linnaeus and thereby giving undue weight to stamen number, and probably also because he interpreted the bracteoles of *L. incana* as calyx, and the calyx as corolla, he apparently did not realize the close relationship of *Licania* and *Moquilea*. Jussieu (1789) brought them close together for the first time in his subfamily Amygdaloideae of the Rosaceae.

Aublet's herbarium was dispersed after his death and this led to the widespread misinterpretation of his genera (see §6*b*). Thus the name *Moquilea* was used for *Couepia* by most botanists until the matter was put right by Bentham in 1840. Since then, several workers have suggested that the true *Moquilea* and *Licania* are synonymous, although others (e.g. Hutchinson 1964), albeit in decreasing numbers, have kept them apart until the present time.

Grisebach (1857) was familiar with species which in stamen number are intermediate between *Licania* and *Moquilea*, and was the first to suggest they should be united, a view accepted by Baillon (1869) and Fritsch (1889*b*) although Focke (1891) continued to keep them apart. During the present century opinion on the status of *Moquilea* has been divided. However, when the present study began, only three species of *Moquilea* had not already been transferred to *Licania*, and of these we regard two as synonymous with already established *Licania* species. Reasons for sinking *Moquilea* are given in full elsewhere (Prance 1972). The relationships with *Chrysobalanus* are discussed under the latter.

Prance (1972) has placed the American species in three subgenera. Two other subgenera are needed to accommodate the African and Asiatic species, which until recently were placed in separate genera, *Afrolicania* and *Angelesia* respectively.

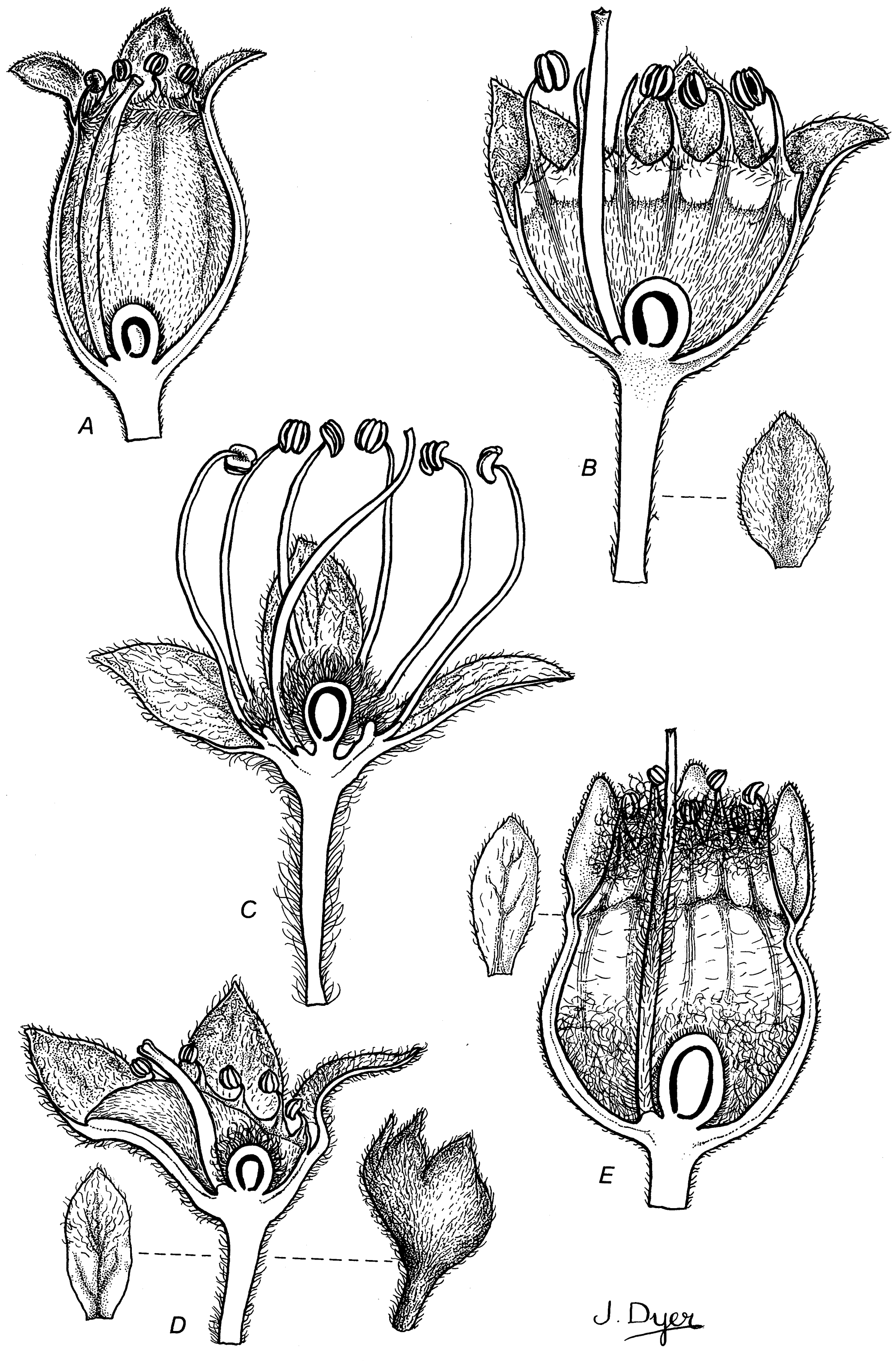


Figure 19. *Licania* flowers: A, *L. kunthiana* (× 13$\frac{1}{3}$, Prance & Silva 58643); B, *L. michauxii* (× 13$\frac{1}{3}$, Curtiss 727); C, *L. sclerophylla* ((× 13$\frac{1}{3}$, Pires & Cavalcante 52276); D, *L. splendens* (× 20, SAN 41196); E, *L. macrophylla* (× 20, Prance & Pennington 1752).

Conspectus of the subgenera and non-American species

SUBGENUS 1. ***Moquilea*** (Aubl.) Prance, *Atas do Simpósio Sobre a Biota Amazônica*, **4**: 224 (1967).

Moquilea Aubl. *Hist. Pl. Guiane Fr.*, **1**: 521 (1775).

Flowers actinomorphic, bisexual. Receptacle usually shallowly cyathiform, rarely longer than wide, densely hairy and without a conspicuous disc inside. Filaments usually 10–20, inserted in a complete circle, shortly united at the base, longer than, and usually much longer than, the sepals. Petals present or absent. Ovary inserted at base of receptacle. Sixty-four species. Confined to America.

Type species: *Licania* (*Moquilea*) *guianensis* (Aubl.) Griseb.

SUBGENUS 2. ***Parinariopsis*** Huber, *Bol. Mus. Emílio Goeldi* **5**: 368 (1909).

Flowers actinomorphic, bisexual. Receptacle deeply cyathiform, longer than wide, densely hairy near the throat inside, otherwise glabrous, without a conspicuous disc. Filaments *ca.* 20, inserted in a complete or incomplete circle, shortly united at the base, slightly longer than the sepals. Petals present. Ovary inserted laterally on receptacle-tube. One species in South America.

Type species: *L. licaniiflora* (Sagot) Blake.

SUBGENUS 3. ***Licania***

Flowers actinomorphic or slightly zygomorphic, bisexual. Receptacle usually deeply cyathiform, usually distinctly longer than broad, densely hairy throughout inside, without a conspicuous disc. Filaments usually 10 or fewer, united at the base or for at least half of length, distinctly shorter than the sepals, sometimes alternatively long and short, sometimes inserted unilaterally; petals present or absent. Ovary inserted at base of receptacle-tube. One hundred and two species in America.

SUBGENUS 4. ***Afrolicania*** (Mildbr.) Prance & F. White, in Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 67 (1978).

Afrolicania Mildbr., *Notizbl. Bot. Gart. Berlin* **7**: 483 (1921) – Dalziel, *Useful Pl. W. Trop. Afr.*: 167 (1937).

Flowers actinomorphic, unisexual. Receptacle patelliform, covered with a minutely puberulous conspicuous disc inside. Petals absent. Filaments *ca.* 20, inserted in a complete circle, not united at base but arising from base of margin of disc, much shorter than the sepals. Ovary inserted at base of receptacle. Drupe large, 5 cm × 3.5 cm, pericarp verruculose. Seed filling the locule; cotyledons thick, fleshy, oleaginous, strongly concave, connate at their margins and enclosing a large internal cavity. One species in Africa.

1. ***Licania elaeosperma*** (Mildbr.) Prance & F. White, in White, *Bull. Jard. Bot. Nat. Belg.* **46**: 280 (1976); F. White, *Distr. Pl. Afr.* **10**: 293 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; Fl. Gab. **24**: 67, t. 20 (1978). Type: Cameroun, fl., *Zenker* 1629 (B, lectotype of Prance & White 1976; K, M, P).

Small or medium-sized tree up to 15 m tall, sometimes flowering when only 4 m high. In West Africa from Guinea to Gabon. In coastal forest, especially on the landward side of mangrove swamps, and further inland in periodically flooded riparian forest.

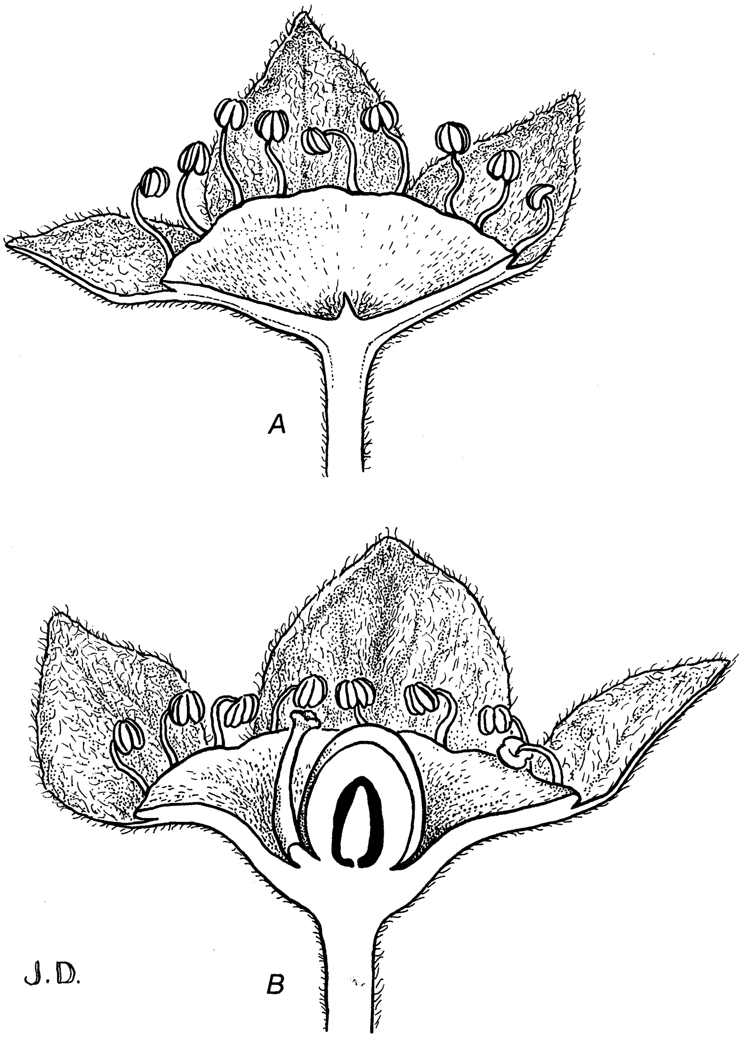


FIGURE 20. *Licania elaeosperma*: A, male flower (×20, Ainslie 8); B, hermaphrodite flower (×20, Talbot 3098).

Afrolicania was thought to differ from other Chrysobalanaceae in its secondary xylem (Prance 1972). It appears that the wood samples (F.P.R.L. 12616 and I.F.I. 12844) were incorrectly labelled and belong to Euphorbiaceae (A. M. W. Mennega, personal communication, 15 April 1975).

SUBGENUS 5. ***Angelesia*** (Korth.) Prance & F. White, stat.nov.

Angelesia Korth., *Ned. Kruidk. Arch.* **3**: 384 (1854).

Flowers strongly zygomorphic, bisexual, sepals very unequal. Receptacle obliquely patelliform, with a minutely puberulous conspicuous disc. Petals present. Filaments *ca.* 9, unilateral, slightly united at base, much shorter than the sepals. Ovary inserted at centre of receptacle. Drupe small, 1.2 × 0.8 cm, narrowed to a shortly stipitate trigonous base, otherwise unridged; epicarp glabrous; mesocarp thin and fleshy; endocarp thin, hard and bony, smooth but closely invested with a reticulate vascular supply. Two, possibly three, species in tropical Asia.

Type species: *L. splendens* (Korth.) Prance.

1. Leaves elliptic to oblong-elliptic, apex acute to rounded and emarginate; inflorescence 3–4 cm long, rhachis sparsely puberulous. . . . . 1. *L. palawanensis*
1. Leaves oblong, apex acuminate; inflorescence 1.5–14 cm long; rhachis densely puberulous. . 2. *L. splendens*

1. ***Licania palawanensis*** Prance, *Brittonia* **31**: 94, t. 7 (1979). Type: Philippines, Palawan, Queza, fl., *Mendoza & Espirita* PNH 91305 (BM, holotype; L).

Shrub 3 m high. Only known from Palawan and Luzon, where it occurs in forest on rocky seashores.

2. ***Licania splendens*** (Korth.) Prance, *Fl. Neotrop.* **9**: 172 (1972). Type: Borneo, fr., *Korthals* s.n. (L, holotype).

Angelesia splendens Korth., *Ned. Kruidk. Arch.* **3**: 384 (1854).

Tree up to 25 m tall. Extending from Thailand, Sumatra and the Malay Peninsula eastwards through Borneo to the Philippines and Sulawesi (Celebes). In lowland rainforest.

(*Note*: Kostermans (1965*c*) was apparently the first to publish this name, but because he failed to cite the bibliographic reference of the basionym his combination is illegitimate.)

Taxonomic history and relationships: *Angelesia splendens*, the type species, was published by Korthals in 1854. Very soon afterwards Blume (1855) in a rare and little-known work, his '*Mélanges botaniques*', suggested that it should be transferred to *Licania*, but the name he proposed (*Licania angelesia*) is illegitimate. Hallier (1903), using the anatomical work of Küster (1897), suggested that *Licania*, *Moquilea* and *Angelesia* should be united, but did not make any new combinations. Until recently *Licania splendens* was known as *Angelesia splendens* or went under the name of one or other of its synonyms in *Parinari* or *Coccomelia*.

Korthals published another new genus of Chrysobalanaceae, *Diemenia* (*D. racemosa*), in the same paper as *Angelesia*. These two genera were combined by Miquel in 1855 to form the illegitimate *Trichocarya*. *Diemenia racemosa* was transferred to *Angelesia* by Kuntze (1891) and was regarded as a synonym of *Licania* by Blume (1855), but it is a synonym of *Parastemon urophyllus* (Wall. ex A.DC.) A.DC. The only other *Angelesia* to be described, *A. papuana* Bak.f., is a *Hunga*.

Excluded species

Licania myrsinoides (Schlechter) Kosterm., *Reinwardtia* **7**: 185 (1965) = *Hunga myrsinoides* (Schlechter) Prance, *Fl. Nouvelle-Cal.* **12**: 122 (1983).

Licania tontoutense (Guillaumin) Kosterm., Reinwardtia **7**: 185 (1965) = *Hunga minutiflora* (Bak.f.) Prance.

4. *Parastemon* (*figure* 21)

(referring to the laterally inserted stamens)

Parastemon A.DC., *Ann. Sci. Nat. Bot.*, sér. 2, **18**: 208 (1842). – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 607 (1865). – Focke, in Engl. & Prantl *Nat. Pflanzenfam.* **3** (3): 60 (1894). – Merrill, *Philipp. J. Sci. Bot.* **10**: 307 (1915). – Merrill & Perry, *J. Arn. Arb.* **21**: 197 (1940). – Hutch., *Gen. Fl. Pl.* **1**: 193 (1964).

Diemenia Korth., *Ned. Kruidk. Arch.* **3**: 388 (1854).

Trichocarya Miq., *Fl. Ind. Bat.* **1** (1): 357 (1855) pro parte quoad *T. racemosa* tantum.

Tree or shrubs. *Leaves* with two small discoid glands at base of lamina; petiole eglandular; lower surface of lamina glabrous; stipules minute, triangular, caducous. *Inflorescence* an axillary, or rarely terminal, simple or sparsely branched raceme. Bracts and bracteoles small, eglandular. *Flowers* actinomorphic. Receptacle-tube patelliform or shallowly cupuliform, shortly hairy inside. Sepals 5, subequal, acute. Petals 5, more or less equalling sepals. Stamens 5 and all fertile, or 2 fertile with 3 staminodes; filaments glabrous, much shorter than the sepals. Ovary 1-carpellary, 1-locular, centrally inserted; style filiform, puberulous towards the base, with 3 large undivided lobes at apex, or with 1 obscure lobe and 2 large deeply divided lobes. *Drupe* 1.5 cm long; epicarp smooth; endocarp thin, hard, bony, smooth outside; glabrous inside; with 2 large lateral plates which break away on germination and allow the seedlings to escape.

Germination: cryptocotylar; cotyledons fleshy; cataphylls absent; first two eophylls opposite, with 1 or 2 stipules; the next 4–5 leaves are spiral and bistipulate; the stem then becomes curved and shows a plagiotropic tendency with alternate distichous leaves; new shoots that arise from the straight basal part repeat the plagiotropic process and the development of a bole is long retarded (F. S. P. Ng, personal communication, 16 August 1978).

Type species: *P. urophyllus* (Wall. ex A.DC.) A.DC.

Distribution and ecology: two species extending from the Nicobar Islands and the Malay Peninsula to New Guinea (see individual species below).

Reproductive biology: *P. urophyllus* is said to be polygamodioecious. Otherwise nothing appears to have been published.

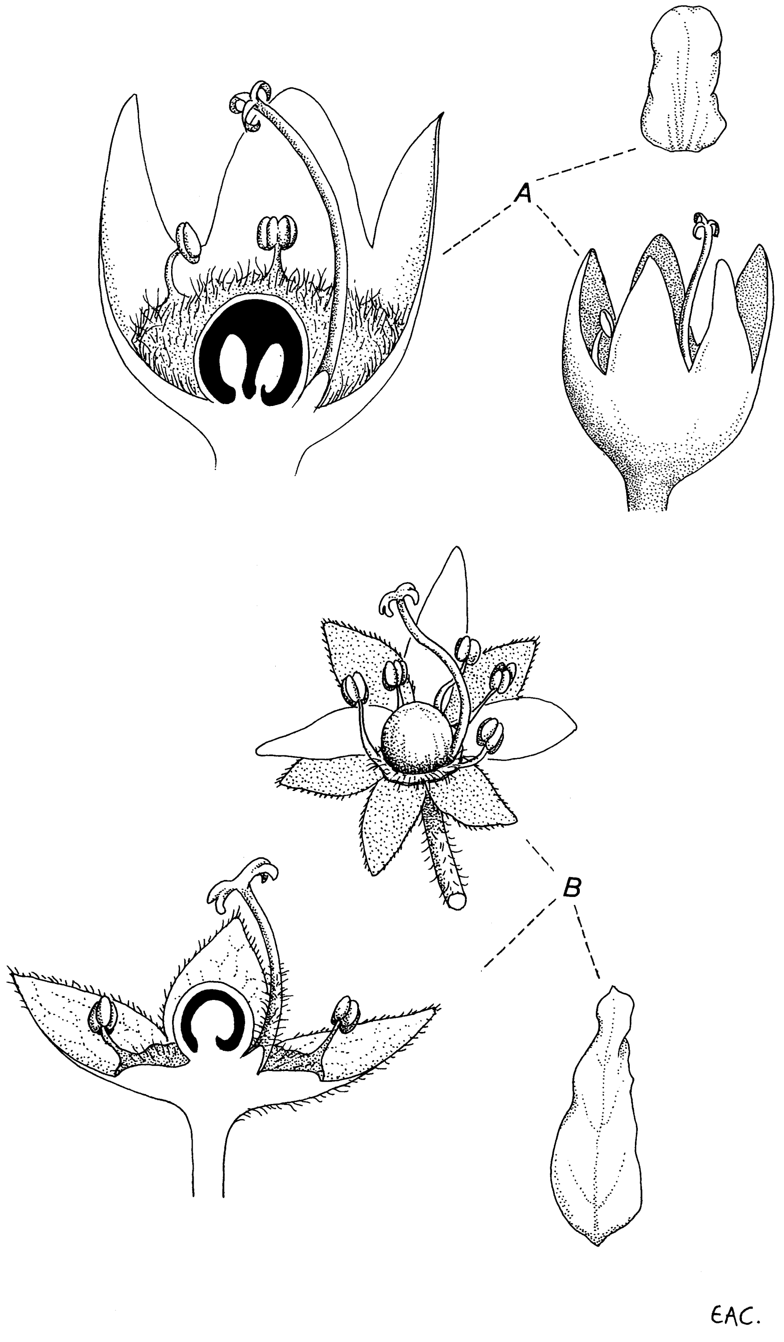
Taxonomic history and relationships: *Parastemon* was described by A. de Candolle (1842) to accommodate *Embelia urophylla*, which he had mistakenly placed in Myrsinaceae a few years earlier (1837). de Candolle was still uncertain of the relationships of his new genus and tentatively included it in Olacaceae. It was transferred to Rosaceae: Chrysobalaneae by J. D. Hooker in the *Genera plantarum* (1865).

In much of the literature, *Parastemon* is said to differ from other Chrysobalanaceae in having two stamens and polygamodioecious flowers. Merrill & Perry (1940), in describing *P. versteeghii*, which has neither of these characters, placed it in *Parastemon* with some hesitation. They also suggested that *Parastemon* and *Angelesia*, now *Licania* subgenus *Angelesia*, are closely related, echoing the opinion of Miquel, who united, under *Trichocarya*, *Diemenia racemosa* (a synonym of *Parastemon urophyllus*) with *Angelesia splendens* (treated in this work as *Licania splendens*). *Licania* and *Parastemon* are indeed closely related and the latter must be regarded as a satellite of the former. Because, however, both species of *Parastemon* have two features, namely a large, conspicuous, deeply lobed stigma, and endocarp dehiscence by means of two lateral plates, which are unknown in *Licania*, generic rank is justified. Other features of *Parastemon*, which are rare in *Licania* and scarcely ever occur in combination there, are the simple racemose inflorescence, flat or very shallowly cup-shaped receptacle and the small number (2–5) of stamens.

Conspectus of the species

1. Receptacle shallowly cup-shaped, glabrous outside; fertile stamens 2; style 3-lobed at apex . 1. *P. urophyllus*
1. Receptacle saucer-shaped, puberulous outside; fertile stamens 5; style with one obscure and two large bifid apical lobes . . . . 2. *P. versteeghii*

1. ***Parastemon urophyllus*** (Wall. ex A.DC.) A.DC., *Ann. Sci. Nat. Bot.* sér. 2 **18**: 208 (1842). – Boerlage & Koorders, *Ic. Bog.* **1**: 61, t. 97 (1901). Type: Malay Peninsula, *Wallich* 2309, fl. (BM, holotype).



Parastemon flowers: A, *P. urophyllus*, flower ($\times 16\frac{2}{3}$), half flower ($\times 26\frac{2}{3}$) and petal ($\times 16\frac{2}{3}$) all from Meijer SAN 19197); B, *P. versteeghii* ($\times 16\frac{2}{3}$, Versteegh & Kalkmann BW 4694).

Embelia urophylla [Wall., Cat. no. 2309 (1830) nom.nud.ex] A.DC., *Trans. Linn. Soc.* **17**: 131 (1837). Type as above.

Diemenia racemosa Korth., *Ned. Kruidk. Arch.* **3**: 388 (1854). Type: Sumatra. *Korthals* s.n., fr. (L, holotype).

Trichocarya racemosa (Korth.) Miq., *Fl. Ind. Bat.* **1** (1): 358 (1855), nom.illegit.

Licania diemenia Blume, *Mélanges Bot.* **2**: 10 (1855); Hasskl., *Flora* **41**: 256 (1858) nom.illegit.

Parastemon spicatus Ridley, *J. Roy. Asiat. Soc. Straits Branch* **75**: 29 (1917) synon.nov. Type: *Haviland & Hose* 3240, Borneo, fl., (K, lectotype; L, SAR).

Tree up to 40 m tall but often much smaller. Trunk often buttressed. Common in lowland forest, especially swamp and secondary forest, from the Nicobar Islands through the Malay Peninsula and Sumatra to Borneo. The only record from Java (*Blume* s.n., L) is dubious.

P. urophyllus is a characteristic species of peat-swamp forest (Anderson 1961, quoted by Whitmore 1975). It occurs in forest more than 45 m tall dominated by enormous *Shorea albida* but becomes much more abundant towards the centre of the peat swamp. There it is codominant with *Tristania maingayi* and *Palaquium cochleariifolium* in 18 m tall forest. It is also plentiful in shorter more open scrub forest characterized by *Combretocarpus rotundatus* and *Dactylocladus stenostachys*.

Note: The only differences between *P. spicatus* and *P. urophyllus* that Ridley mentions are that the former is a shrub with sessile flowers. However, some forms of *P. urophyllus* may have extremely short pedicels, and most sessile-flowered individuals are recorded as being small trees. There appears to be insufficient reason for maintaining *P. spicatus* as a distinct species. R. Anderson, however, (personal communication) says that in Sarawak the sessile-flowered plant has a distinctive bark and differs ecologically. Further work is needed to clarify its status.

2. ***Parastemon versteeghii*** Merrill & Perry, *J. Arn. Arb.* **21**: 197 (1940).
Type: West Irian, fl., fr. (A, holotype).

Tree up to 30 m tall. Mostly in drier forest than *P. urophyllus*. In eastern Indonesia from the Moluccas through West Irian to Papua and the Admiralty Islands.

5. *Bafodeya* (*figure* 22)

(from the Bafodeya Hills, the type locality)

Bafodeya Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 271 (1976). – F. White, *Distr. Pl. Afr.* **10**: 282 (1976).

Parinari auct. non Aubl. pro parte quoad *P. benna* Scott Elliot tantum.

Small trees. *Leaves* appearing eglandular on herbarium specimens; lower surface of lamina with small stomatal crypts filled with densely matted hairs; stipules small, deltate. *Inflorescence* a terminal cymose panicle. Bracts and bracteoles small, eglandular, not enclosing the flower buds. *Flowers* bisexual, markedly zygomorphic; flower-buds sigmoid. Receptacle-tube curved, obliquely campanulate, much swollen on one side, markedly oblique at throat, hairy inside throughout, throat blocked by long retrorse hairs. Sepals 5, acute, unequal in size. Petals 5, about as long as sepals, caducous. Stamens *ca.* 7; filaments white, more or less equalling sepals, slightly curved in bud and during anthesis, laterally expanded at the base; staminodes 4–10, claviform, fleshy, variable in length but some almost as long as filaments. Ovary monocarpellary, 2-locular, inserted laterally just below mouth of receptacle-tube; style arcuate, included. *Drupe* somewhat dry; epicarp sparsely verrucose; endocarp hard, smooth, without basal obturators.

Type species: *Bafodeya benna* (Scott Elliot) Prance.

Distribution and ecology: a single species in West Africa (see below).

Taxonomic history and relationships: superficially *Bafodeya* looks like *Parinari* and has similar

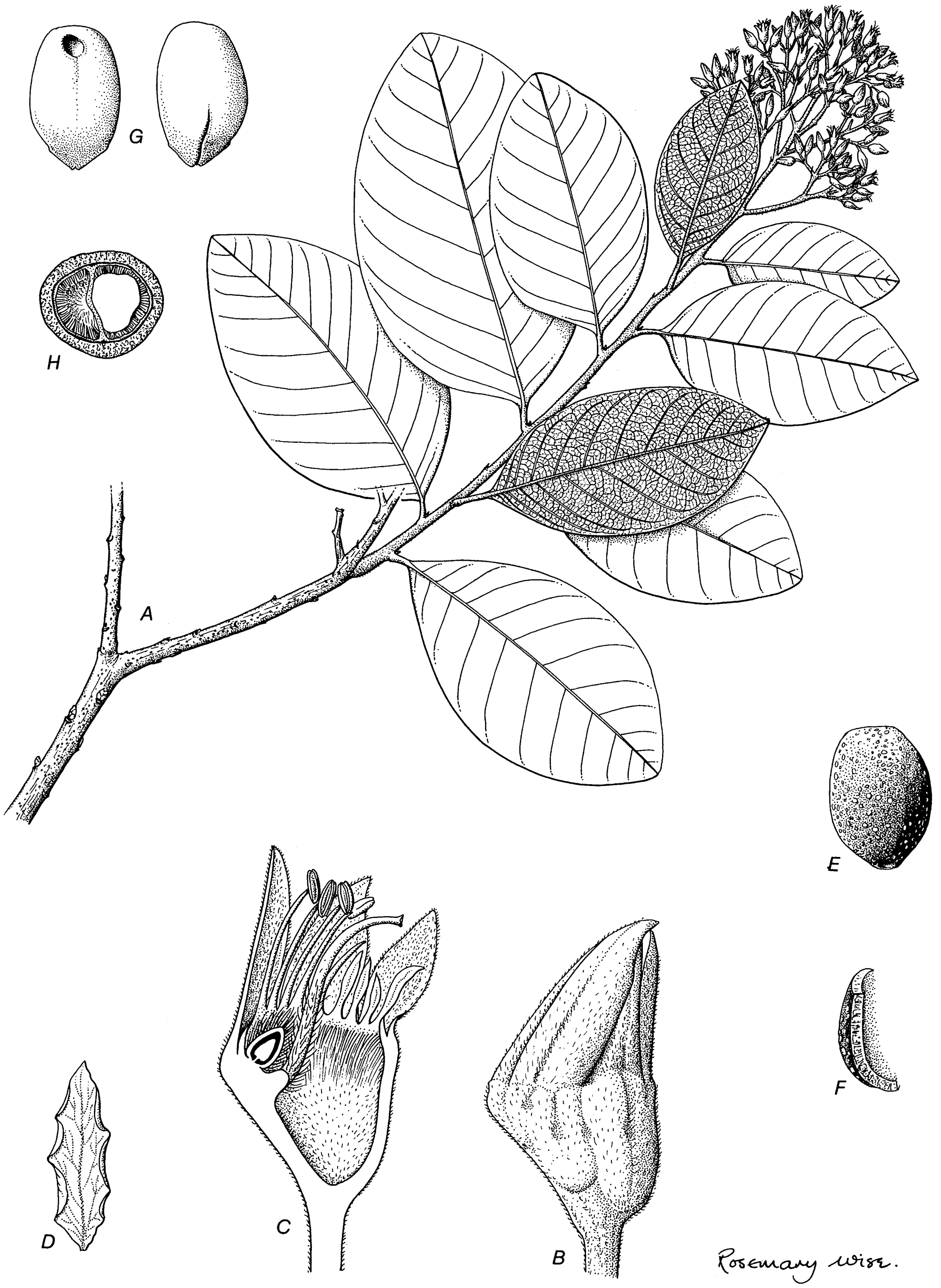


Figure 22. *Bafodeya benna*: A, habit (× ½, Deighton 5445); B, flower bud (× 5, Deighton 5445); C, half flower (× 5, Chevalier 13164); D, petal (× 5, Chevalier 13164); E, drupe (× 1, Chevalier 13068); F. section of exocarp (× 1, Chevalier 13068); G, two views of endocarp (× 1, Schnell 6807); H, ts drupe (× 1, Chevalier 13068).

leaves, but quite different flowers and fruits. The flowers, which are not enclosed by bracts in the bud, differ from those of *Parinari* in their markedly asymmetric, obliquely ventricose receptacle-tube and fleshy claviform staminodes. This type of receptacle is only found elsewhere in some species of *Magnistipula*. The endocarp is perfectly smooth and the seedlings do not escape by means of basal plugs or stoppers.

1. ***Bafodeya benna*** (Scott Elliot), Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 271 (1976). Type: Sierra Leone, fl., *Scott Elliot* 5480 (K, holotype; P).

Parinari benna Scott Elliot, *J. Linn. Soc. Bot.* **30**: 78 (1894). Type as above.

Small tree *ca.* 9 m tall. Only known for certain from Fouta Djalon in Guinea and adjacent upland areas in Sierra Leone at altitudes of about 900–1000 m. Little is known of its ecology. *Fleurydora felicis* and *Diospyros feliciana* have similar distributions.

6. *Exellodendron* (*figure* 23)

(after A. W. Exell, student of African botany)

Exellodendron Prance, *Fl. Neotrop.* **9**: 195, t. 31–32 (1972).

Parinari sensu Hook. f., in Mart., *Fl. Bras.* **14** (2): 49–53 (1867) pro parte quoad *P. cordata*, *P. coriacea* et *P. gardneri* tantum.

Parinari subgenus *Pellegriniella* Hauman, *Bull. Jard. Bot. État Brux.* **21**: 188 (1951) pro parte, *P. tessmannii* exclusum.

Trees or shrubs. *Leaves* with a pair of small glands or ill-defined glandular areas on upper surface at junction of lamina and the eglandular petiole; lower surface of lamina glabrous or with a dense arachnoid indumentum which is easily rubbed off; stipules small, lateral, narrowly deltate, caducous. *Inflorescence* a simple or branched raceme of small, congested cymes. Bracts and bracteoles eglandular, small, not enclosing the young flowers in small groups. *Flowers* bisexual, slightly zygomorphic. Receptacle-tube subcampanulate, slightly swollen on one side, hollow, hairy inside throughout. Sepals 5, deltate, acute. Petals 5, as long as sepals, subpersistent. Stamens *ca.* 7; filaments more or less equalling sepals, slightly expanded at the base; staminodes *ca.* 7, minute, forming a denticulate rim to the faucal annulus. Ovary monocarpellary, 2-locular, inserted at mouth of receptacle-tube. *Drupe* fleshy; epicarp smooth; endocarp smooth, with a bony ridge on one side at base, without basal obturators, sparsely to densely hairy inside.

Type species: *Exellodendron coriaceum* (Benth.) Prance.

Distribution and ecology: five species, confined to tropical South America. Two sympatric species, *E. coriaceum* and *E. barbatum*, extend from Venezuela and the Guianas southwards into northern Brazil. The former occurs in open places such as savanna and savanna margins as well as open inundated forest, especially on river beaches, whereas the latter is a species of both flooded and non-flooded closed forest. Two shrubby species, *E. cordatum* and *E. gardneri*, occur sympatrically in the cerrados of the planalto of central Brazil; *E. gracile* is only known from the coastal riverine forest of Espírito Santo.

Reproductive biology: the flowers of *E. barbatum* are visited abundantly by small bees (G.T.P, personal observations). On the Rio Negro in Brazil its fruits fall into the water at the high flood season and are immediately taken by fishes; they are also eaten by bats (G.T.P., personal observations).

Taxonomic history and relationships: the 5 species were originally described in *Parinari* as *P. coriacea* Benth., *P. cordata* Hook. f., *P. barbata* Ducke, *P. gardneri* Hook. f. and *P. gracilis* Kuhlm. When Ducke described *P. barbata* he commented on its isolated position in that genus. In 1937 Hill, who had studied the fruits of certain *Parinari* sensu lato, mentioned that those of *P. coriacea* are so different from those of *P. curatellifolia* that the former species should be placed in a separate genus, stating that Dr Ducke agreed with him; neither author, however, acted on this.

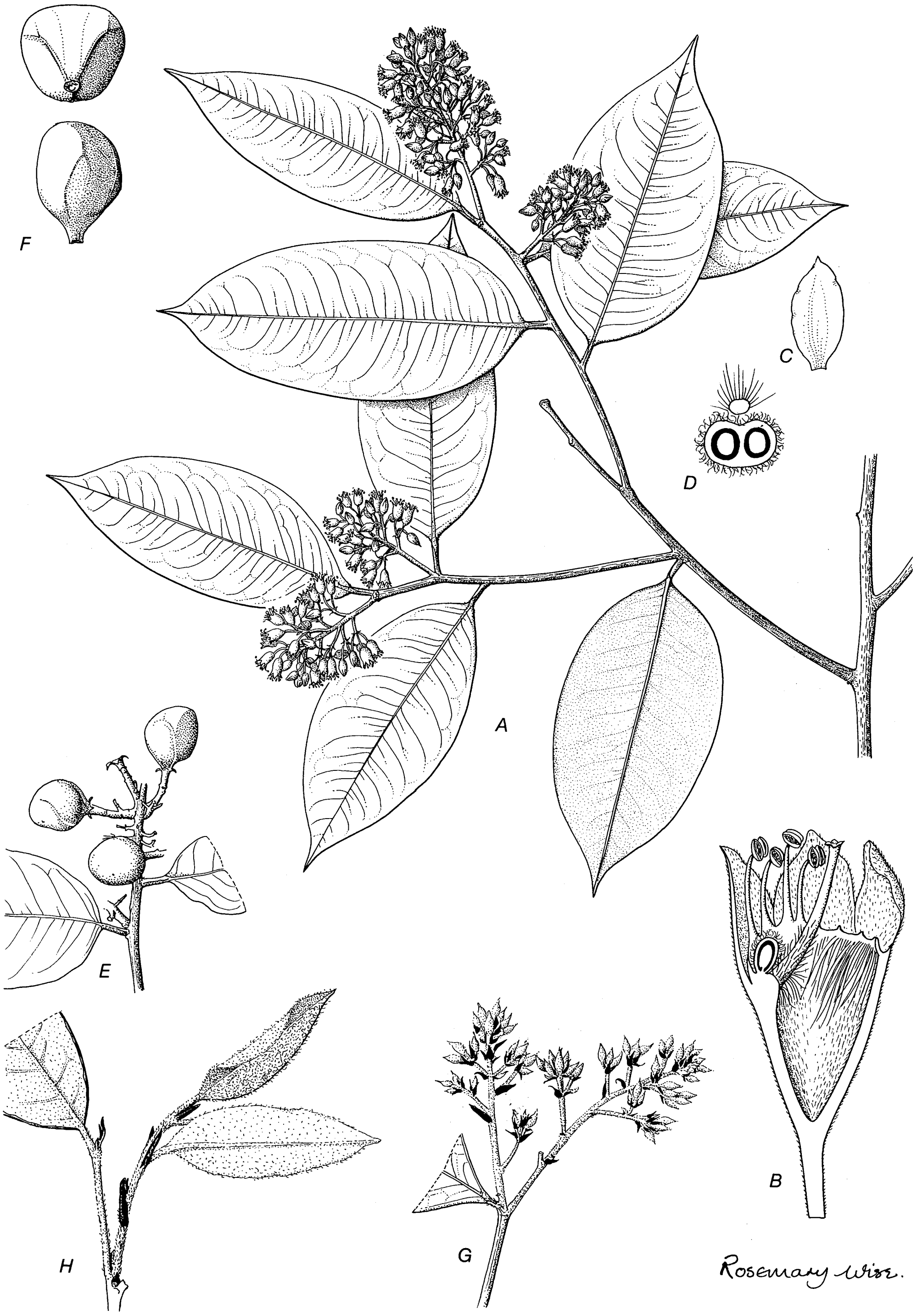


FIGURE 23. *Exellodendron coriaceum*: A, habit (×$\frac{1}{2}$, Prance *et al.* 23131); B, half flower (×5, Maguire *et al.* 31039); C, petal (×5, Maguire *et al.* 31039); D, TS ovary (×5, Maguire *et al.* 31019); E, infructescence (×$\frac{1}{2}$, Prance *et al.* 11471); F, two views of fruit (×1, Prance *et al.* 11471). *E. barbatum*: G, young inflorescence showing bracts and flower buds (×$\frac{1}{2}$, Prance & Silva 58727). *E. gardneri*: H, young shoot showing bud scales and stipules (×$\frac{1}{2}$, Irwin *et al.* 14591).

7. *Hunga* (*figure* 24)

(from a vernacular name in New Caledonia)

Hunga Pancher ex Prance, *Brittonia* **31**: 79 (1979).

Shrubs or small trees. *Leaves* with a pair of, often obscure, marginal glands towards the base; petiole eglandular; lower surface of lamina glabrous or lanate, with stomata visible at a magnification of ×25; stipules apparently absent in New Caledonian species, linear and persistent in New Guinea species. *Inflorescence* a few-flowered, terminal or axillary raceme of cymules. Bracts and bracteoles small, persistent, not enclosing the flowers in small groups. *Flowers* bisexual, slightly zygomorphic. Receptacle-tube subcampanulate, slightly asymmetric, shortly puberulous outside, hairy inside throughout, but most densely hairy at the throat. Sepals 5, acute. Petals 5, small, not exceeding the calyx-lobes. Stamens 5–9, included; filaments much shorter than the sepals, unilateral; staminodes 3–7, subulate. Ovary monocarpellary, bilocular, inserted midway up the receptacle, densely hairy outside; style truncate but distinctly 3-lobed at the apex, base hairy. *Drupe* small, fleshy, bilocular or often with one loculus under-developed; epicarp smooth; mesocarp thin, fleshy; endocarp hard, thin, bony with a smooth surface, interior very hairy, with 4–6 longitudinal lines of weakness which allow the seedling to escape.

Type species: *H. rhamnoides* (Guillaum.) Prance.

Distribution and ecology: 11 species, some of which appear to be very closely related. Three species occur in Papua New Guinea, and 8 in New Caledonia and the nearby Loyalty Islands. Three of the New Caledonian species are found on serpentine.

Taxonomic history and relationships: the species now gathered together in *Hunga* were originally described in three different genera, *Licania*, *Angelesia* and *Parinari*, but we regard the first two as synonymous. Because, at least in floral structure, *Hunga* is intermediate between *Licania* and *Parinari*, it is perhaps not surprising that some of its species have been described in both genera, sometimes even by the same author, e.g. *Licania balansae* Guillaumin (1921) and *Parinari tontoutensis* Guillaumin (1959), which we place in synonymy with *Hunga minutiflora* (Baker f.) Prance. At the onset of the present study nine species had been described in the three genera mentioned above. They were transferred to *Hunga* by Prance (1979*c*) who considered them to represent only six species. Three new species of *Hunga* were described in the same paper. Prance (1983*b*) described a further two new species from New Caledonia and recognized *Parinari myrsinoides* Schlechter as a good species of *Hunga*. Kostermans (1985) described *Hunga fusicarpa* from New Guinea but we have not yet studied material of that species.

Hunga differs from all species of *Licania* in its bilocular carpel. It also differs from the great majority of *Licania* species in its partly staminodial androecium, and from all except one species (*L. licaniiflora*) in its laterally inserted gynoecium. The very large stomata of *Hunga* are also distinctive. The differences between *Hunga* and *Parinari* are summarized in §6*d*.

Conspectus of the species

1. Leaf-apex rounded to retuse or rarely subacute, lower surface frequently lanate:
  2. Leaf-base rounded to cuneate:
    3. Leaves elliptic to ovate, apex often subacute, lower surface glabrous:
      4. Exterior of flowers entirely glabrous; leaf base rounded and decurrent onto petiole 10. *H. guillauminii*
      4. Exterior of flowers grey–pubescent; leaf base subcordate, not decurrent . . . . . 4. *H. mackeeana*
    3. Leaves oblong to oblong–elliptic, apex always rounded to retuse, lower surface lanate or glabrous:
      5. Lower leaf surface lanate; petiole smooth; inflorescence and flowers densely pubescent . . . . 1. *H. gerontogea*

FIGURE 24. *Hunga rhamnoides*: A, habit (× ½), drupe and TS drupe (× 1) from Balansa 3549. *H. gerontogea*: B, habit (× ½), inflorescence (× 1½) and half flower (× 15), all from Le Rat 460.

5. Lower leaf surface glabrous; petiole rugose; inflorescence and flowers glabrous to puberulous. . . . . 5. *H. minutiflora*
2. Leaf base distinctly cordate; lamina otherwise deltate in outline . . . . 11. *H. cordata*
1. Leaf apex acute or acuminate, the lower surface glabrous when mature:
  6. Inflorescence branches puberulous to lanate; flowers pubsecent outside; leaves without conspicuously anastomosing venation; fruit ellipsoid, without stipe:
    7. Leaves lanceolate to oblong–lanceolate, 7–13 cm long, stipules 0.5–0.65 cm, filamentous. 3. *H. longifolia*
    7. Leaves oblong to ovate, 3–9 cm long, stipules 0.1–0.2 cm long, lanceolate:
      8. Petioles 0.6–1 cm long; leaves coriaceous, acuminate at apex . . . . 8. *H. rhamnoides*
      8. Petioles 0.3–0.5 cm long; leaves membranaceous, acute at apex . . . . 2. *H. lifouana*
  6. Inflorescence branches glabrescent; flowers glabrescent on exterior; leaves with conspicuously anastamosing venation; fruit sagittate with a long stipe (not seen in *H. myrsinoides*):
    9. Leaves elliptic, 7.5–8.5 cm broad . . . . 6. *H. novoguineensis*
    9. Leaves oblong to oblong–elliptic, 3–6.5 cm broad:
      10. Petioles 0.2–0.4 cm long; stipules persistent; leaf-apex finely acuminate . . . . . .7. *H. papuana*
      10. Petioles 1–1.5 cm long; stipules caducous; leaf-apex subacute to acuminate . . . 9. *H. myrsinoides*

1. ***Hunga gerontogea*** (Schlechter) Prance, *Brittonia* **31**: 81, t. 1 fig. A–E (1979). Type: New Caledonia, fl., *Le Rat* 460 (P, lectotype of Prance 1979).

Shrub or small tree. Endemic to northwestern New Caledonia where it is frequent beside creeks and in riverine woodland in serpentine terrain and on serpentine alluvia.

2. ***Hunga lifouana*** (Däniker) Prance, *Brittonia* **31**: 86, t. 1 fig. J–M (1979). Type: Loyalty Islands, fl., *Däniker* 2470 (Z, holotype; P). Tree. Loyalty Islands and northern New Caledonia.

3. ***Hunga longifolia*** Prance, *Brittonia* **31**: 84, t. 2 fig. G–J (1979). Type: Papua, fl., *Brass* 27462 (L, holotype: K).

Tree to 15 m tall. Only known from the type locality. In rainforest.

4. ***Hunga mackeeana*** Prance, *Brittonia* **31**: 81 (1979). Type: New Caledonia, 600–800 m, fl., *McKee* 19573 (P, holotype).

Shrub 3 m high. Only known from northern New Caledonia.

5. ***Hunga minutiflora*** (Baker. f.) Prance, *Brittonia* **31**: 83, t. 1 fig. F–I (1979). Type: New Caledonia, fl., *Compton* 2245 (BM, holotype).

Shrub *ca.* 4 m high. New Caledonia, widespread, but commoner in the south. In riverine communities on serpentine.

6. ***Hunga novoguineensis*** Prance, *Brittonia* **31**: 88, t. 3 fig. G–H (1979). Type: New Guinea, fr., *Hartley* 12645 (L, holotype; C, K).

Shrub 4 m high. Only known from the type locality. In oak forest.

7. ***Hunga papuana*** (Baker f.) Prance, *Brittonia* **31**: 88, t. 3 fig. A–F (1979). Type: Papua, fl., *Forbes* 204 (BM, holotype; K).

Small tree. Papua. In understorey of rain forest.

8. ***Hunga rhamnoides*** (Guillaumin) Prance, *Brittonia* **31**: 84, t. 2 fig. A–F (1979). Type: New Caledonia, fl., *Deplanche* 519 (P, lectotype of Prance 1979; GH, K, L, NY, P, Z).

Shrub or small tree up to 10 m tall. In forests on serpentine in southern New Caledonia (including Île des Pins), and Lifou in the Loyalty Islands.

9. ***Hunga myrsinoides*** (Schlechter) Prance, *Fl. Nouv. Cal.* **12**: 122 (1983). Type: New Caledonia, fl., *Schlechter* 15687 (B, holotype, destroyed; P, lectotype).

Shrub, up to 4 m high. New Caledonia.

10. ***Hunga guillauminii*** Prance, *Fl. Nouv. Cal.* **12**: 107, t. 22 (1983). Type: New Caledonia, *Webster & Hildreth* 14653 (P, holotype; DAV).

Shrub 1–2 m. 'Maquis' of northwestern New Caledonia.

11. ***Hunga cordata*** Prance, *Fl. Nouv. Cal.* **12**: 116, t. 24 (1983). Type: New Caledonia, *Mackee* 23007 (P, holotype; NY).

Shrub to 1 m. 'Maquis' of northwestern New Caledonia.

8. *Neocarya* (*figures* 25 *and* 26)

(Greek: new nut)

Neocarya Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 308 (1976). – F. White, *Distr. Pl. Afr.* **10**: 326 (1976).

Parinari sectio *Neocarya* DC., *Prodr.* **2**: 527 (1825) pro parte quoad *P. senegalensis* tantum. – Benth., in Hook., *Niger Fl.*: 335 (1849). – C. Muell., in Walp., Ann. Bot. Syst. **4**: 645 (1857).

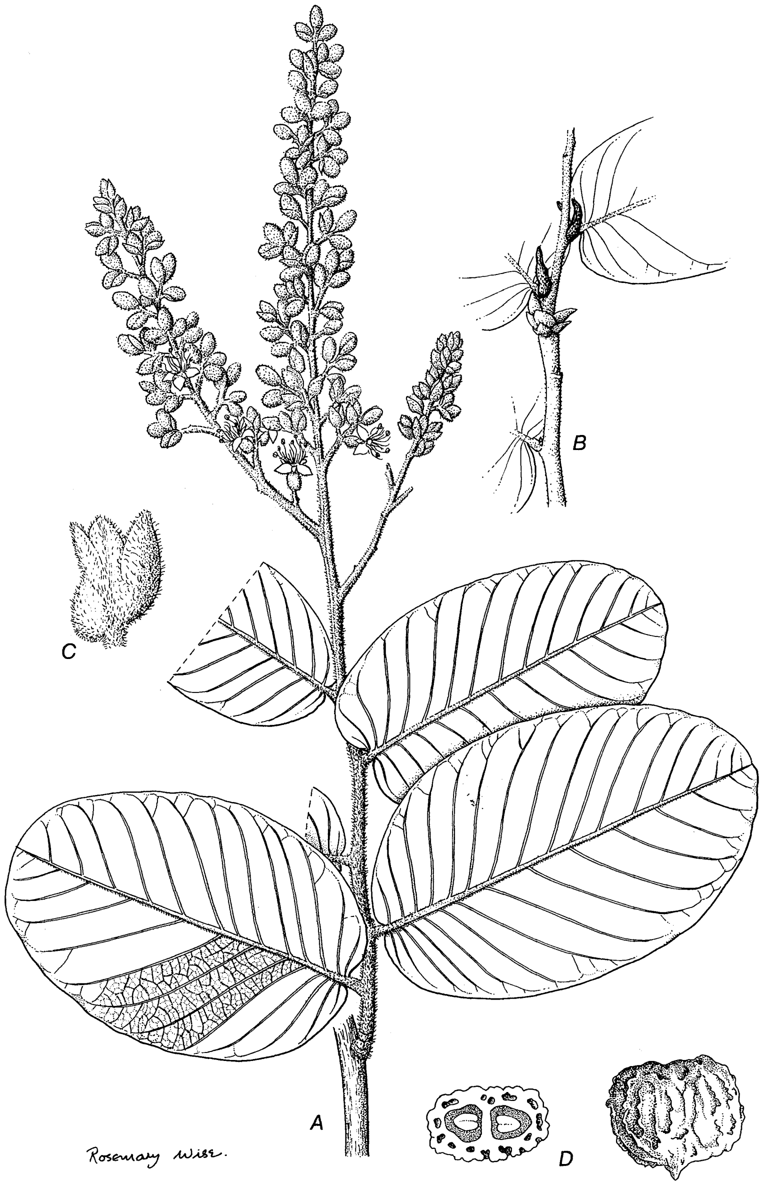


FIGURE 25. *Neocarya macrophylla*: A, habit ($\times\frac{1}{2}$, Perrotet 303); B, bud scales and stipules ($\times\frac{1}{2}$, Fox 82); C, flower bud ($\times 2$, Fox 82); D, endocarp ($\times 1$, after Guillemin *et al.* (1832, t. 61).

Parinari subgenus *Neocarya* (DC.) Blume, *Mélanges Bot.* **2**: 10 (1885). – Hasskl., *Flora* **16**: 225 (1858). – Hauman, *Bull. Jard. Bot. État Brux.* **21**: 189 (1951).

Shrubs or small trees. *Leaves* with several small, sessile, marginal glands especially near base of lamina; petioles eglandular; lower surface of lamina with small stomatal crypts filled with densely matted hairs; stipules small, deltate, caducous. *Inflorescence* a terminal raceme of almost sessile cymules, sometimes unbranched, but more frequently with one or more short to elongate branches at the base. Bracts and bracteoles eglandular, usually enclosing a single flower-but sometimes also an additional rudimentary bud. *Flowers* bisexual, zygomorphic. Receptacle-tube much shorter than the sepals, very asymmetric, saccate, gibbous, hollow, hairy at the throat, otherwise glabrous inside. Sepals 5, spreading, obovate, apex rounded or broadly acute, hairy outside, inner surface glabrous and contrasting with the densely ciliolate margin. Petals 5, shorter than the sepals, caducous. Stamens 12–17; filaments white, slightly longer than the sepals, slightly curved in bud and during anthesis, slightly expanded at the base; staminodes *ca.* 6, minute, subulate, inserted on the faucal annulus. Ovary monocarpellary, 2-locular, inserted laterally at the mouth of the receptacle-tube. *Drupe* fleshy; epicarp sparsely verrucose; endocarp hard, thick and with a rough fibrous surface, with 2 basal obturators.

Germination: cryptocotylar; cataphylls absent (Hill 1937, p. 247, t. 9).

Type species: *Parinari senegalensis* DC., a synonym of *Neocarya macrophylla* (Sabine) Prance.

Distribution and ecology: 1 species in West Africa (see below).

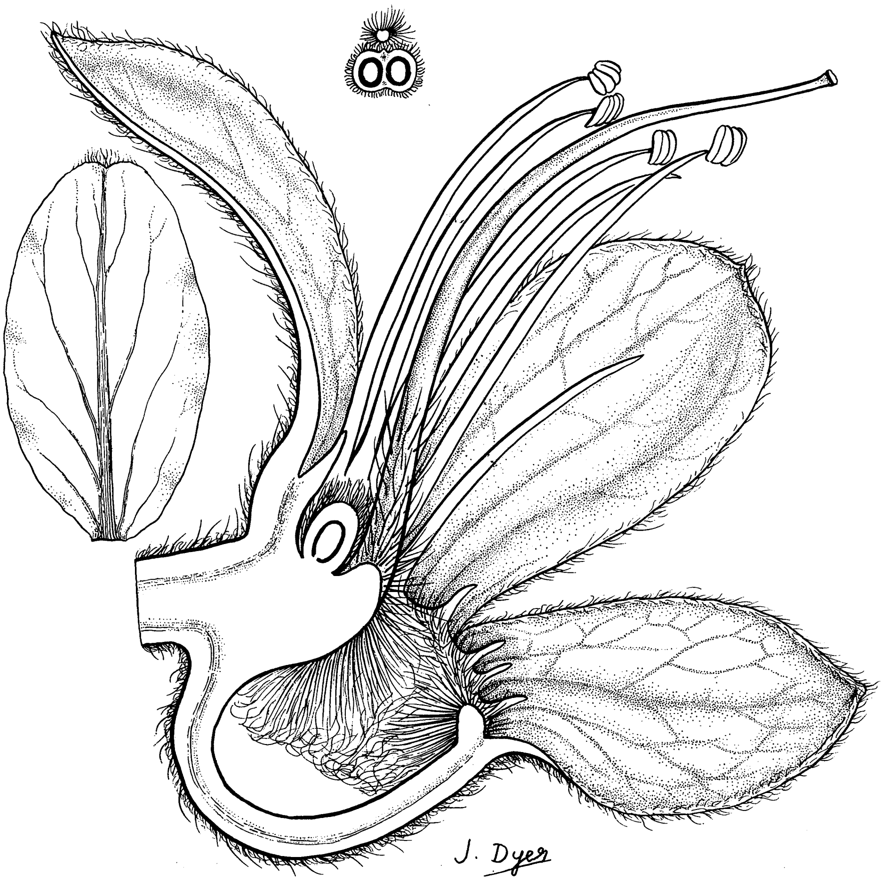


FIGURE 26. *Neocarya macrophylla*: half flower and TS ovary (×10, Fox FHI 5305).

Taxonomic history and relationships: *Neocarya* has been recognized as a distinct entity by most authors from the beginning. Adanson (1763), who discovered it in Senegal, referred to it by its vernacular name *Neou* but did not formally propose it as a genus. Jussieu (1789) cites *Neou* as a synonym of *Parinari*.

Within *Parinari*, most authors following de Candolle have placed it in its own section or subgenus, *Neocarya*. de Candolle, however, also included in his section *Neocarya* a true *Parinari*, *P. excelsa* Sabine, probably because the type description of the latter is inadequate to characterize it properly, and he had not seen material. The differences between *Neocarya* and *Parinari* are summarized in §6*d*.

1. ***Neocarya macrophylla*** (Sabine) Prance, in F. White, *Bull. Jard. Bot. Nat. Belg*. **46**: 308 (1976). – F. White, *Distr. Pl. Afr.* **10**: 326 (1976). Type: Sierra Leone, fl., *Don* s.n. (K, holotype).

Small bushy tree rarely more than 9 m high. Common in West Africa in a coastal strip, in places up to 300 km wide, from Senegal to Liberia. It also has a scattered east–west distribution in the much drier and more continental northern half of the Sudanian region 700–1000 km inland. It seems to be confined to sandy soils.

9. *Parinari* (*figures* 27 *and* 28)

(a vernacular name in French Guiana)

Parinari Aubl., *Hist. Pl. Guiane Fr.* **1**: 514, t. 204–206 (1775). – Hauman, *Bull. Jard. Bot. État Brux.* **21**: 184 (1951) quoad subgenus *Euparinari* tantum. – Hutchinson, *Gen. Fl. Pl.* **1**: 192 (1964) excl.syn. *Maranthes* etc. – Kostermans, *Reinwardtia* **7**: 147 (1965) excl.syn. *Thelira*, *Ferolia* et *Neou*. – Prance, *Fl. Neotrop.* **9**: 178, t. 28, 29, 30 fig. A–E (1972). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 310 (1976); *Distr. Pl. Afr.* **10**: 327–334 (1976); *Fl. Zamb.* **4**: 36, t. 10 (1978). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 122, t. 37–40 (1978).

Dugortia Scop., *Introd.*: 217 (1777).

Parinarium Juss., *Gen.*: 342 (1789). – C. Muell., in Walp., *Ann. Bot. Syst.* **4**: 644 (1857) quoad sectio *Euparinarium* tantum. – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 607 (1865) excl.syn. *Maranthes* et *Exitelea*. – Focke, in Engl. & Prantl, *Nat. Pflanzenfam.* **3** (3): 60 (1894).

Petrocarya Schreb., Linn. *Gen. Pl.* ed. 8, **1**: 245 (1789) nom.illegit. (superflu.).

Balantium Desv.ex Buch.-Ham., *Prodr. Pl. Ind. Occid.*: 34 (1825).

Parinarium sectio *Petrocarya* DC., *Prodr.* **2**: 526 (1825). – Benth., in Hook., *Niger Fl.*: 335 (1849) excl. *P. glaberrima* et *P. scabra*.

Parinarium subgenus *Petrocarya* (DC.) Miquel, *Fl. Ind. Bat.* **1** (1): 352 (1855).

Parinarium sectio *Neocarya* DC., *Prodr.*, **2**: 526 (1825) quoad *P. excelsum* tantum.

Lepidocarya Korth., *Ned. Kruidk. Arch.* **3**: 385 (1855).

Ferolia sensu Kuntze, *Rev. Gen.* **1**: 216 (1891) pro parte quoad *Parinari* sensu nobis tantum non *Ferolia* Aubl.

Small or large trees, or, more rarely, shrubs or rhizomatous geoxylic suffrutices. *Leaves* with 2 circular glands on upper surface of petiole and often with several small marginal or submarginal discoid glands along entire length of lamina; lower surface of lamina nearly always with small stomatal crypts filled with densely matted hairs; stipules 0.5–7 cm long, caducous or persistent. *Inflorescence* a many-flowered complex cyme or cymose panicle. Bracts and bracteoles eglandular, nearly always completely concealing flower-buds, both individually and in small groups. *Flowers* bisexual, slightly zygomorphic; flower-buds straight. Receptacle-tube longer than the sepals, subcampanulate, slightly swollen on one side, hollow, hairy inside throughout. Sepals 5, deltate, apex acute, densely hairy on both surfaces, eglandular, except in *P. congolana*. Petals 5, as long as or shorter than the sepals, caducous. Stamens 6–10; filaments white, shorter than the sepals, slightly curved in bud and during anthesis, slightly expanded at the base; staminodes *ca.* 6, minute, subulate. Ovary monocarpellary, 2-locular, inserted in upper half of receptacle-tube below the mouth; style arcuate, included. *Drupe* fleshy; epicarp verrucose; endocarp hard, thick, with a rough, fibrous surface, with 2 basal obturators.

Exceptions: *P. congolana* has a few-flowered inflorescence. *P. canarioides* and *P. argenteosericea* do not have stomatal crypts, but a smooth, glabrous lower leaf-surface.

Germination: cryptocotylar; cataphylls 6–15; eophylls alternate, with lanceolate persistent stipules.

Chromosome number: $2n = 20$ (*P. excelsa* ('*holstii*'); Mangenot & Mangenot 1957, 1962).

Type species: *P. campestris* Aubl. (lectotype of Hauman 1951).

Distribution and ecology: pantropical. Forty-four species are currently accepted, of which 18 occur in tropical America, 6 in tropical Africa and 21 in tropical Asia and the Pacific region, where they extend to northern Queensland (*P. nonda*) and Fiji, Tonga and Samoa (*P. insularum*).

In South America *Parinari* extends from the Pacific-coast forests of Colombia and Ecuador across Amazonia to the Atlantic-coast forests of Brazil. One of the 18 species, *P. campestris*, also occurs in Trinidad. Apart from *P. maguirei*, a species endemic to the savannas of the Kaieteur Plateau, and *P. obtusifolia*, a geoxylic suffrutex or small shrub of the cerrado of the planalto of Central Brazil, all species occur in various types of forest, but the genus is absent from the caatinga of northeast Brazil. *P. campestris* is characteristic of marsh forest (Beard 1946) and savanna margins, and *P. pachyphylla* occurs in deciduous forest in Colombia and Venezuela. The other species are chiefly found in evergreen rainforest; among them, *P. parilis* and *P. sprucei* occur in inundated, várzea forest. The most widespread species, which extends from Colombia to southeast Brazil, is usually referred to as '*P. excelsa* Sabine', which also occurs in Africa. This identification, however, may require some modification after further study (White 1976*a*).

The African species collectively extend throughout tropical Africa except for the driest parts. Although very similar in the structure of their leaves, flowers and fruits, they occupy a wide range of vegetation types, and in growth form vary from dwarf geoxylic suffrutices to lofty rainforest trees (White 1976*a*, *b*).

P. hypochrysea is confined to the wetter Guineo-Congolian rain forest adjoining the Atlantic littoral, whereas *P. excelsa* is widely distributed in the drier forests and extends far beyond the limits of the Guineo-Congolian region in various other types of forest. *P. congensis* and *P. congolana* are confined to swamp and riparian forest. *P. curatellifolia* is one of the most widespread savanna trees in Africa; *P. capensis* is the most widely distributed African geoxylic suffrutex.

Much less is known about the Asiatic species, several of which appear to be very closely related.

Reproductive biology: in Africa the flowers of *P. curatellifolia* are much visited by honey bees (*Meikle* no. 1045). Small bees also visit the flowers of the American *P. campestris* and *R. rodolphii* (G.T.P., personal observations). The fruits of *P. excelsa* are dispersed in Africa by bats of the genus *Eidolon* (Kingdon 1971, p. 31) and by elephants (Aléxandre 1978). In Ghana endocarps

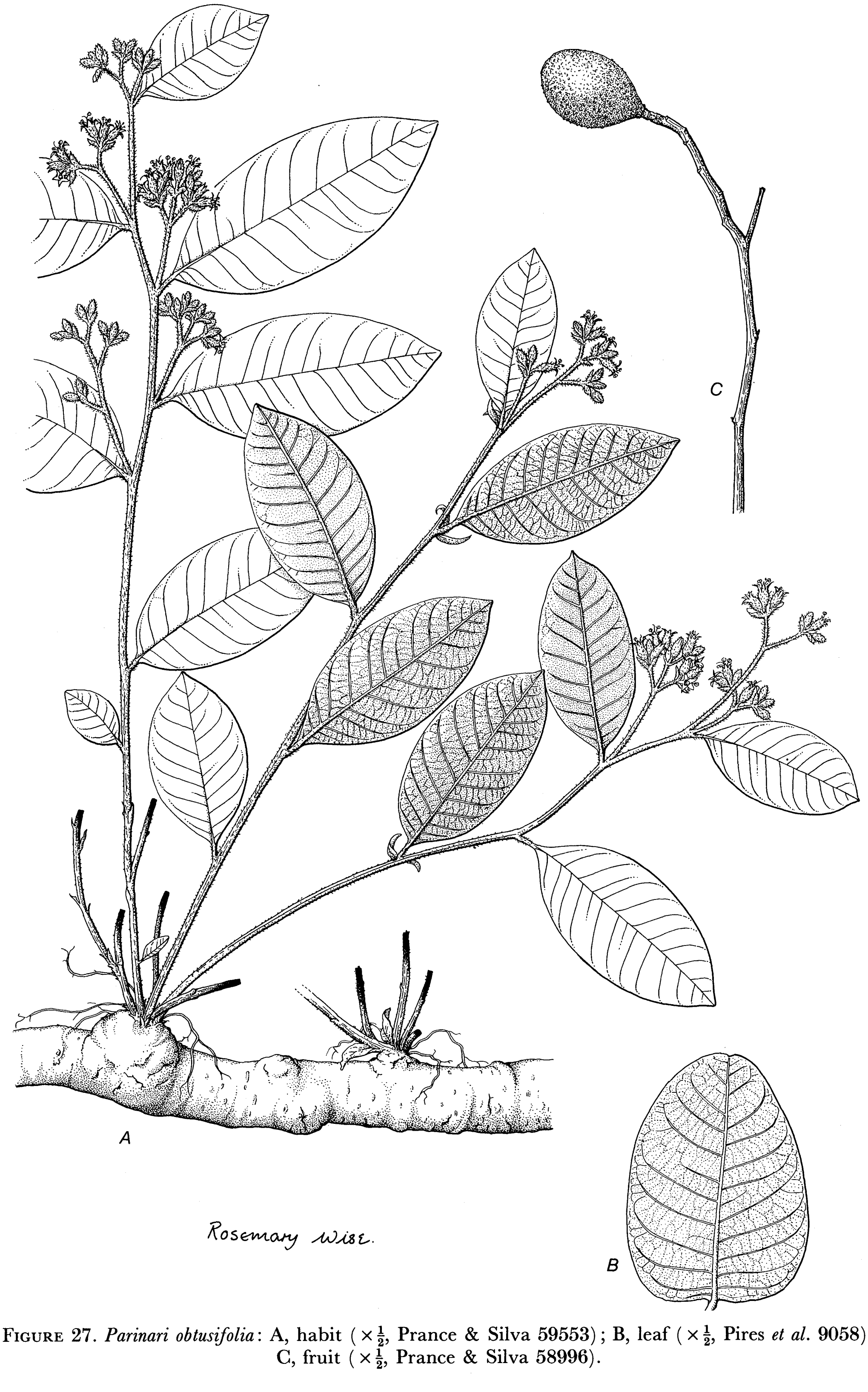


FIGURE 27. *Parinari obtusifolia*: A, habit ($\times\frac{1}{2}$, Prance & Silva 59553); B, leaf ($\times\frac{1}{2}$, Pires *et al.* 9058); C, fruit ($\times\frac{1}{2}$, Prance & Silva 58996).

of *P. curatellifolia* have been found in the dung of baboons (J. B. Hall, personal communication). In Bénin elephants and various kinds of monkey disperse this species (de Souza 1979*a*). In Malawi its fruits are eaten, and presumably it is dispersed, by the green pigeon, *Treron australis* (F. Dowsett-Lemaire, personal communication). *P. insularum* is said to be dispersed by fruit pigeons (Ridley 1930, p. 208). The fruit of the geoxylic suffrutex *P. obtusifolia* of the Brazilian cerrado is eaten by rheas, hence its local name, 'fruta de ema'. The birds do not destroy the endocarp (G.T.P., personal observation), which is voided unharmed. In Kalimantan (M. Leighton, personal communication) the orange fruit of *P. canarioides*, which has a white sugary mesocarp, is dispersed by three primates, Müller's gibbon (*Hylobates muelleri*), the orang utan (*Pongo pygmaeus*) and the pig-tailed macaque (*Macaca nemestrina*). It has the widest endocarp known to be swallowed and passed by primates. A squirrel, *Sundasciurus hippurus*, scatter-hoards the fruit. In Australia, the endocarps of *P. nonda* have been found abundantly in the stomach of the emu (*Dromaius novaehollandiae*).

In Roraima Territory, Brazil, the fruits of the riverine *Parinari campestris* are instantly gobbled up by fish as they fall into the water (G.T.P, personal observations).

Taxonomic history and relationships: these topics are discussed at some length elsewhere (§§6*c* and 6*d*).

Conspectus of the African species

The American species are dealt with by Prance (1972) and the Asiatic species by Kostermans (1965*c*). Because published information on the African species is widely scattered they are briefly reviewed below. Their synonymy and suggestions on relationships are given by White (1976*a*).

1. Rhizomatous suffrutex, usually less than 30 cm in height, rarely up to 2 m . . . . 1. *P. capensis*
1. Trees more than 4 m in height:
  2. Receptacle-tube *ca.* 0.8 cm long, twice as long as sepals, longitudinally ribbed; sepals with 1–3 marginal glands . . . . 3. *P. congolana*
  2. Receptable-tube up to 0.5 cm long, about as long as sepals, not ribbed; sepals eglandular:
    3. Savanna tree; leaves rounded or emarginate at apex, rarely subacute, base scarcely ever cordate . . 4. *P. curatellifolia*
    3. Forest trees; leaves acuminate at apex, rarely subacute, but then base cordate:
      4. Leaves not cordate at the base . . . . 5. *P. excelsa*
      4. Leaves cordate or subcordate:
        5. Indumentum of lower leaf-surface grey . . . . 2. *P. congensis*
        5. Indumentum of lower leaf-surface ferruginous . . . . 6. *P. hypochrysea*

1. ***Parinari capensis*** Harv., in Harv. & Sond. *F.C.* **2**: 596 (1862). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 310 (1976); *Distr. Pl. Afr.* **10**: 328–330 (1976); *Fl. Zamb.* 4: 36, t. 10 fig. c. (1978). Type: South Africa, fl., *Zeyher* 537 (TCD, lectotype here designated; K, OXF).

Extensively rhizomatous geoxylic suffrutex with massive, woody, underground axes; subaerial stems 5 cm to 2 m tall, usually less than 25 cm tall.

Throughout the greater part of the Zambezian region, and extending southwards to Natal and northwards into the Guineo-Congolian region, in which it crosses the equator in the Congo Republic.

2. ***Parinari congensis*** F. Didr., *Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn* **1854**: 197 (1854). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 321 (1976); *Distr. Pl. Afr.* **10**: 331 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 124, t. 37 (1978). Type: Zaire, fl., *C. Smith* 67/366 (C, lectotype here designated).

Evergreen tree up to 25 m tall. In some parts of its range the trunk supports a girdle of much-

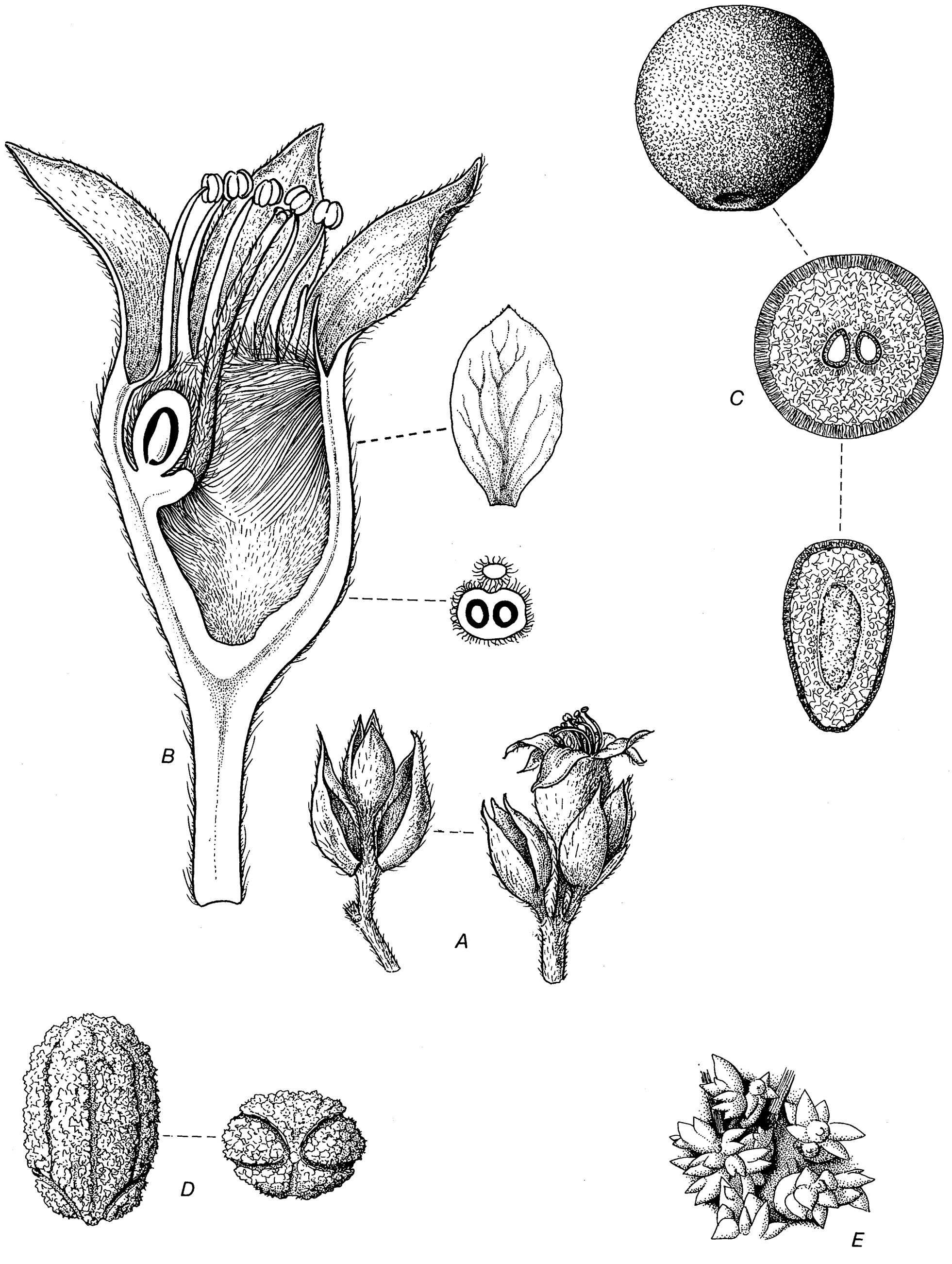


Figure 28. *Parinari rodolphii*: A, flower bud ($\times 2\frac{1}{2}$, Kuhlman & Jimbo 328); B, half flower and ts ovary ($\times 10$, Kuhlman & Jimbo 328). *Parinari curatellifolia*: C, fruit, ts and ls ($\times 1$, Styles 274); D, two views of endocarp ($\times 1$, Angus 1622); E, surface of endocarp ($\times 5$, Angus 1622).

branched adventitious roots about 2 m from the base. They function as pneumatophores and are exposed when the floodwater recedes.

Widespread in West Africa from Guinea to Cameroun. It is also abundant on the banks of the River Zaire and the lower courses of its major tributaries. An interval of 900 km separates these two main areas. It always occurs near water.

3. ***Parinari congolana*** Th. & H. Durand, *Syll. Fl. Congo*: 189 (1909). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 323 (1976); *Distr. Pl. Afr.* **10**: 332 (1976). Type: Zaire, fl., *Camp* 691 (BR, holotype).

Evergreen tree up to 20 m tall.

Confined to the banks of the River Zaire and the lower courses of its tributaries.

4. ***Parinari curatellifolia*** Planch. ex Benth., in Hook., *Niger Fl.*: 333 (1849). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 323 (1976); *Distr. Pl. Afr.* **10**: 333 (1976); *Fl. Zamb.* **4**: 38, t. 10 fig. a (1978). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 126, t. 38 (1978). Type: Senegal, fl., *Heudelot* 362 (K, lectotype here designated; OXF).

Small or medium-sized evergreen tree up to 12 (20) m tall. Widespread in woodland on the African mainland from Senegal to Kenya and southwards to Namibia and the Transvaal, but absent from the forests of the Guineo-Congolian region. Also in coastal forest on the east side of Madagascar.

5. ***Parinari excelsa*** Sabine, *Trans. Roy. Hort. Soc.* **5**: 451 (1824). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 333 (1976); *Distr. Pl. Afr.* **10**: 334 (1976); *Fl. Zamb.* **4**: 40, t. 10 fig. b. (1978). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 130, t. 39 (1978). Type: Sierra Leone, fl., fr., *Don* s.n. (K, holotype).

Large evergreen forest tree up to 40 m tall.

Throughout most of the rainforests of the Guineo-Congolian region but absent from the wettest parts. It is also widely distributed on the mountains of tropical Africa and in the northern part of the Zambezian region. There is some doubt over its occurrence in South America (White 1976*a*).

6. ***Parinari hypochrysea*** Mildbr. ex Letouzey & F. White, *Adansonia*, sér. 2 **16**: 234, t. 3 (1976). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 348 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 134, t. 40 (1978). Type: Cameroun, st., *Mildbraed* 5023 (HBG, holotype).

Large evergreen tree up to 40 m tall.

In hygrophilous coastal evergreen rainforest in a relatively narrow band extending from southern Nigeria to Gabon. *P. excelsa* replaces it further inland.

Excluded species

Species now placed in other genera of Chrysobalanaceae but formerly included in *Parinari* are listed in table 5 (see §6*c*). In addition, the following belongs to another family.

Parinari emirensis Baker, *J. Linn. Soc. Bot.* **22**: 469 (1887). = *Dichapetalum pachypus* (Tul.) Engl. (Dichapetalaceae).

10. *Acioa* (*figure* 29)

(from the vernacular name 'acioua' in French Guiana)

Acioa Aubl., *Hist. Pl. Guiane Fr.* **2**: 698, t. 280 (1775). – DC., *Prodr.* **2**: 526 (1825). – Baill., *Adansonia*, **7**: 221 (1867) quoad *A. guianensis* tantum. – Focke, in Engl. & Prantl, *Nat. Pflanzenfam.* **3**(3): 60, t. 33, quoad relat. spec. Amer. tantum. – Hutch., *Gen. Fl. Pl.* **1**: 192 (1964) excl. syn. *Dactyladenia* Welw. et *Griffonia* Hook. f. – Prance, *Fl. Neotrop.* **9**: 357, t. 58 (1972) excl. syn. *Dactyladenia* et *Griffonia*. – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 6, quoad relat. spec. Amer. tantum.

Dulacia Neck., *Elem. Bot.* **2**: 414 (1790), nom.illegit., non *Dulacia* Vell. (1823) (Olacaceae).

Acia Schreb., *Linn. Gen. Pl.* ed. 8, **2**: 458 (1791) nom. illegit. pro parte excl. syn. *Couepia*.

Moquilea sensu Martius, *Nov. Gen. et Sp.*: 59 (1826) pro parte quoad syn. *Acioa* tantum.

Couepia sensu Hook. f., in Benth. & Hook. f., *Gen. Pl.* 1: 608 (1865) pro parte quoad syn. *Acioa* tantum.

Trees or shrubs. *Leaves* coriaceous, with 1 or 2 pairs of conspicuous glands at base of lamina and several smaller discoid glands; petiole eglandular; lower surface of lamina glabrous; stipules small, intrapetiolar. *Inflorescence* a rather lax thyrse with flattened axes. Bracteoles minute, persistent, eglandular. *Flowers* bisexual, strongly zygmorphic. Receptacle-tube obconic, slightly curved (cyathiform in *A. schultesii*). Sepals 5, glabrous outside except for the ciliolate margins, suborbicular, deeply concave, very unequal in size, 3 large, 2 very small, the 3 outer with one or two large, discoid glands towards the base. Petals 5, fimbriate. Stamens 10–20, ligulately connate (free in *A. edulis*), coiled in bud; staminodes absent or represented by minute denticulations on the faucal annulus. Ovary 1-carpellary, 1-locular, inserted laterally at mouth of receptacle-tube, glabrous or tomentose; style hairy at base or throughout, very slightly 3-lobed at apex. *Drupe* (only known in *A. edulis* and *A. guianensis*) 8 cm or more long, pericarp poorly differentiated into mesocarp and endocarp, thick, hard and fibrous, glabrous outside and inside, on germination breaking up irregularly.

Germination: phanerocotylar; cotyledons fleshy, without chlorophyll; eophylls with intrapetiolar stipules, the first two opposite, otherwise alternate.

Type species: *A. guianensis* Aubl.

Distribution and ecology: 4 species with restricted distributions in lowland tropical rainforest in northern South America. See also individual species below.

Reproductive biology: nothing is known about pollination. The fruit of *A. edulis* is apparently dispersed by agoutis. The vernacular name of *A. edulis* near the type-locality is 'castanha de cutia', which means 'agouti nut'. The local people consider it to be well named, because the agoutis carry away and eat the seeds in large numbers. They presumably effect dispersal by 'scatter-hoarding'. The hard woody endocarp of *A. edulis* is typical of many other fruits carried by agoutis, e.g. *Couepia longipendula* and *Bertholletia excelsa*. *A. guianensis* is dispersed by water. Ducke observed fruits floating in large quantities in the Rio Purus in Amazonian Brazil, and germinated some in the Rio de Janeiro Botanical Garden.

Taxonomic history and relationships: largely as a result of the confusion caused by the dispersal of Aublet's herbarium after his death (see §6*b*), *Acioa* was not accepted as a distinct genus by most authors until it was resurrected by Baillon in 1867. Baillon extended the concept of *Acioa* to Africa by uniting with it *Griffonia* Hook.f., which also has a staminal ligule. This view has been universally followed until now, but in our opinion (Prance & White 1979) the African species have so few characters in common with the American that the genus *Dactyladenia* Welw. (q.v.) should be revived to accommodate them.

Two Asiatic species of Chrysobalanaceae also have a staminal ligule. Kostermans (1965*a*) transferred one of them to *Acioa* from *Parinari* (*P. heteropetala* Scortech. ex King) and described the other (*Acioa malayana*) as new. In our opinion they represent a distinct new genus, *Kostermanthus* Prance (1979*c*) and are discussed further under that heading. Until recently *A. guianensis* was the only known American species, but in 1951 Maguire described two new species, *A. somnolens* and *A. schultesii*. The former is closely related to *A. guianensis*, but the latter is very distinct in having a shallowly cup-shaped, not narrowly obconic, receptacle and in having a short, much-branched staminal ligule. In other respects, including its fruit, it seems typical, but its distinctive flowers might justify creating a new subgenus to accommodate it. A

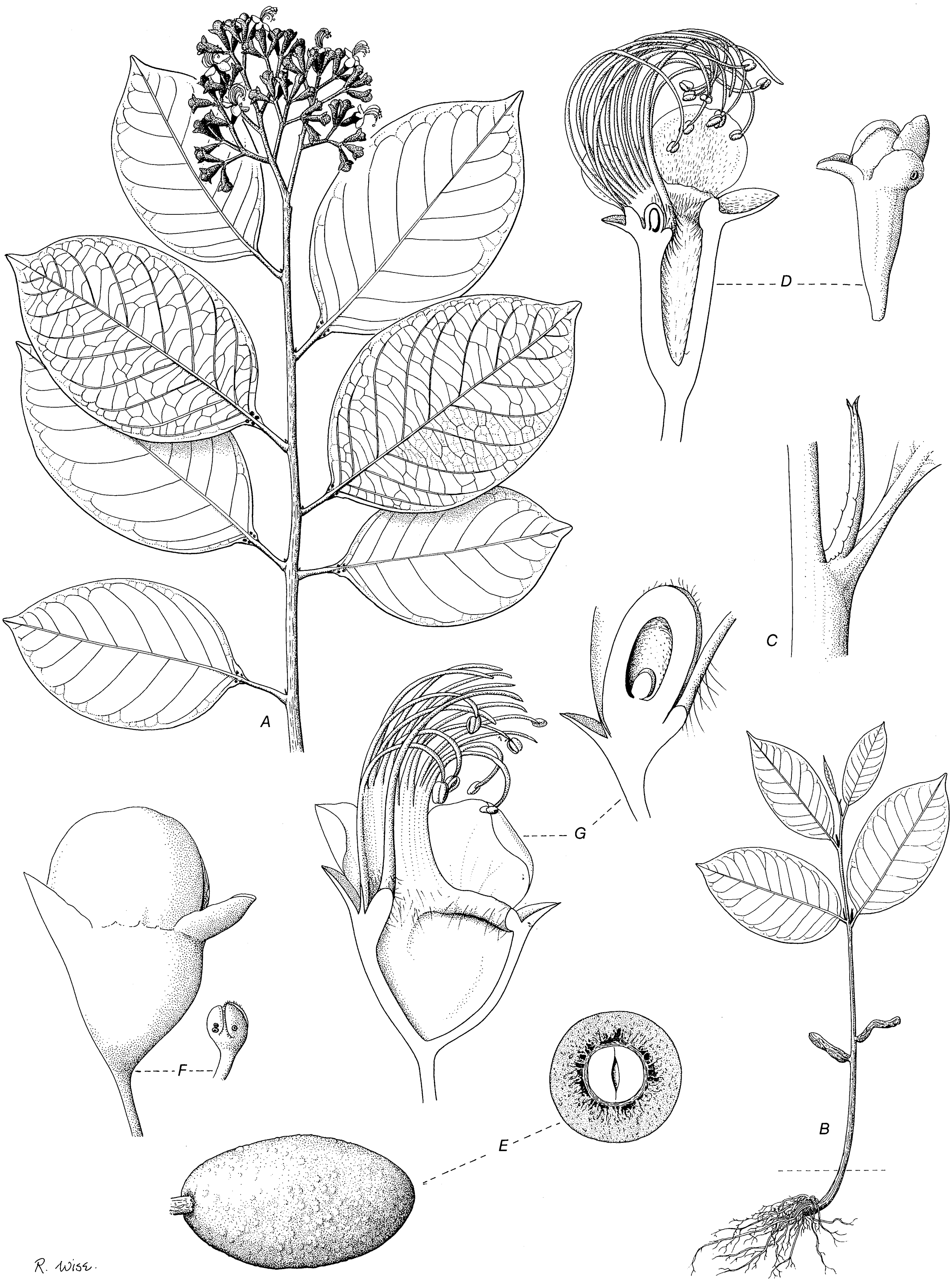


FIGURE 29. *Acioa edulis*: A, habit ($\times\frac{1}{2}$, Ramos P23251); B, seedling ($\times\frac{1}{6}$, Prance Bl. 13); C, stipules ($\times 4$, Prance Bl. 13); D, flower bud and half flower ($\times 4$, Ramos P 23251); E, fruit ($\times\frac{1}{2}$, Prance *et al.* 14015). *A. schultesii*: F, developing and fully developed flower bud ($\times 4$, Clark 6740); G, half male flower and developing fruit ($\times 4$, Clark 6740).

fourth American species, *A. edulis* Prance (1973*a*), was originally described from fruiting specimens. When flowers became available, it was transferred to *Couepia* (Prance 1975*a*) because it lacks a staminal ligule. A more recent reappraisal, however, has revealed so many characters which *A. guianensis*, *A. schultesii* and *A. edulis* have in common, as well as general appearance, that congeneric status seems to be justified. The striking differences between these species also need to be emphasized. It seems that in *Acioa* we are dealing with the last remnants of a genus which formerly might have been as diverse and species-rich as, say, *Hirtella* or *Couepia* is today. In view of the considerable changes to the circumscription of *Acioa* proposed since the publication of *Flora Neotropica* a brief conspectus of the species is appended.

Conspectus of the species

1\. Receptacle-tube obconic, much longer than the sepals, gradually narrowed into the pedicel; sepals tomentellous inside; filaments completely free, or united to form an unbranched staminal ligule:

  2\. Leaves with inconspicuous venation; receptacle-tube more than 5 times as long as broad, relatively thin-walled; faucal annulus relatively poorly developed, not blocking throat; filaments united to form a staminal ligule; ovary densely hairy; style hairy for most of length:

    3\. Leaves shortly cuspidate at apex, cuneate or decurrent into the petiole at base . . . 2. *A. guianensis*

    3\. Leaves rounded or emarginate at apex, rounded at base . . . . 4. *A. somnolens*

  2\. Leaves with prominently reticulate venation; receptable-tube less than 3 times as long as broad, almost solid; faucal annulus well developed, very thick and fleshy, almost blocking the throat; filaments completely free; ovary glabrous; style hairy only at the base . . . . 1. *A. edulis*

1\. Receptacle-tube cyathiform, as long as the sepals; sepals glabrous inside; staminal ligule with several branches at base . . . . 3. *A. schultesii*

1\. ***Acioa edulis*** Prance, *Acta Amazonica* **2**: 12, t. 5–6 (1973). Type: Brazil, fr., *Prance* et al. 14015 (NY, holotype; FHO, INPA, MG, US).

Couepia edulis (Prance) Prance, *Acta Amazonica* **5**: 143, t. 1 (1975).

Tree 25 m tall. Only known from a small area of Amazonas, Brazil, where, however, it is locally abundant in forest of non-flooded ground (terra firme). It is also cultivated outside its natural range, especially along the Rio Solimões in Amazonas, Brazil.

2\. ***Acioa guianensis*** Aubl., *Hist. Pl. Guiane Fr.* **2**: 698, t. 280 (1775). – Prance, *Fl. Neotrop.* **9**: 359, t. 58 fig. a–c (1972). Type: French Guiana, fl., *Aublet* (BM, holotype).

Medium-sized tree. French Guiana and Amazonian Brazil.

3\. ***Acioa schultesii*** Maguire, *Brittonia*, **7**: 272 (1951). – Prance, *Fl. Neotrop.* **9**: 361, t. 58 fig. d–e (1972). Type: Brazil, fr., *Schultes & López* 9958 (NY, holotype; K).

Small tree. Upper Rio Negro region of Venezuela and Brazil. Abundant in forests on white sand (bana and caatinga) (Howard Clark, personal communication).

4\. ***Acioa somnolens*** Maguire, *Brittonia* **7**: 272 (1951). – Prance, *Fl. Neotrop.* **9**: 359 (1972). Type: French Guiana, fl., *Melinon* 230 (P, holotype).

Very closely related to *A. guianensis* and possibly not distinct.

Only known from French Guiana.

Excluded species

Acioa goetzeana Engl., *Bot. Jahrb.* **30**: 315, t. 12 (1901) = *Hirtella zanzibarica* Oliv.

African species, other than *A. goetzeana*, which were formerly placed in *Acioa*, have been transferred to *Dactyladenia*, and Asiatic species to *Kostermanthus*.

11. *Couepia* (*figures* 30 *and* 31)
(a vernacular name in French Guiana)

Couepia Aubl., *Hist. Pl. Guiane Fr.* **1**: 519, t. 207 (1775). – DC., *Prodr.* **2**: 526 (1825). – Benth., in Hook., *London. J. Bot.* **2**: 215 (1840). – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 608 (1865) excl. syn. *Acioa*; Hook.f., in Mart., *Fl. Bras.* **14** (2): 40 (1867). – Focke, in Engl. & Prantl, *Nat. Pflanzenf.* **3** (3): 59 (1891). – Hutch, *Gen. Fl. Pl.* **1**: 192 (1964) excl. syn. *Dulacia*. – Prance, *Fl. Neotrop.* **9**: 202, t. 34–41 (1972).

Acia Schreb., *Linn. Gen. Pl.* ed. 8, **2**: 458 (1791), nom. illegit. (superfl.) pro parte quoad syn. *Couepia* tantum.

Grymania Presl, *Epim. Bot.*: 193 (1851) nom.nud. pro parte quoad *G. polyandra* tantum.

Pleragina Arruda de Camara ex Koster, *Trav.*: 499 (1816) nom.nud. pro parte quoad *P. rufa* tantum.

Moquilea auct. non Aubl.; sensu Mart., *Nov. Gen. et Sp. Pl.* **2**: 79, t. 166 (1827) – Martius & Zuccarini, *Abh. Akad. München*, **1**: 387 (1832). – Zuccarini, *Flora* **15**, Beibl. 2: 78 (1832). – Endl., *Gen.*: 1251 (1840). – Meisn., *Pl. Vasc. Gen.* **1**: 102 (1836) pro parte excl. *M. guianensis* et *Acioa guianensis*.

Trees or shrubs. *Leaves* often with 1 or 2 pairs of glands at base of lamina and sometimes with several small marginal glands especially near apex; petiole eglandular; lower surface of lamina glabrous or with an arachnoid indumentum; stipules subulate or deltate, usually persistent or sub-persistent. *Inflorescence* usually a congested thyrse, often with a few ascending branches, less often a few-flowered spike or raceme, very rarely flowers solitary, or densely crowded in a long-pedunculate compound corymb. Pedicels usually shorter than, and often much shorter than, the receptacle-tube. Bracts and bracteoles usually persistent, rarely enclosing flower-buds in small groups, eglandular. *Flowers* bisexual, slightly zygomorphic. Receptacle-tube turbinate to narrowly cylindric, often slightly curved, ventricose, rarely longer than the calyx, hollow, glabrous inside except at the throat; faucal annulus well developed. Sepals 5, subequal, spreading or reflexed, acute or rounded, usually eglandular. Petals 5, more or less equalling sepals, orbicular to lingulate, sometimes shortly unguiculate. Stamens usually 20–100 or more, only exceptionally less than 15: filaments undulate in bud with 3 or more bends; inserted on abaxial surface of faucal annulus, usually forming a complete circle, less frequently unilateral, far-exserted, but not much longer than the combined length of calyx and receptacle-tube; staminodes absent or short and filiform. Ovary 1 (2–3)-carpellary, 1-locular, inserted laterally at mouth of receptacle-tube; style filiform, far-exserted, indistinctly 3-lobed at apex, hairy for greater part of length. *Drupe* 2.5–12 cm or more long; endocarp hard, granular, shortly hairy inside, on germination breaking up irregularly, surface without longitudinal channels, rough and irregular owing to fusiform anticlinal aggregations of stone cells and fibres which penetrate the mesocarp more or less deeply.

Exceptions: Setulose hairs occur on the nerves and veins in a few species, e.g. *C. canomensis*. Bracts and bracteoles enclose the flower-buds in small groups in *C. belemii*, *C. bracteosa*, *C. eriantha* and *C. subcordata*. The receptacle of *C. platycalyx* is solid and shorter than the calyx. Two closely related species, *C. longipendula* and *C. dolichopoda*, have two sessile glands on the abaxial surface of the sepals. Fewer than 20 stamens occur in *C. canescens*, *C. cognata*, *C. exflexa*, *C. guianensis*, *C. impressa*, *C. obovata*, *C. ovalifolia*, *C. pernambucensis*, *C. polyandra*, *C. recurva*, *C. schottii* and *C. spicata*.

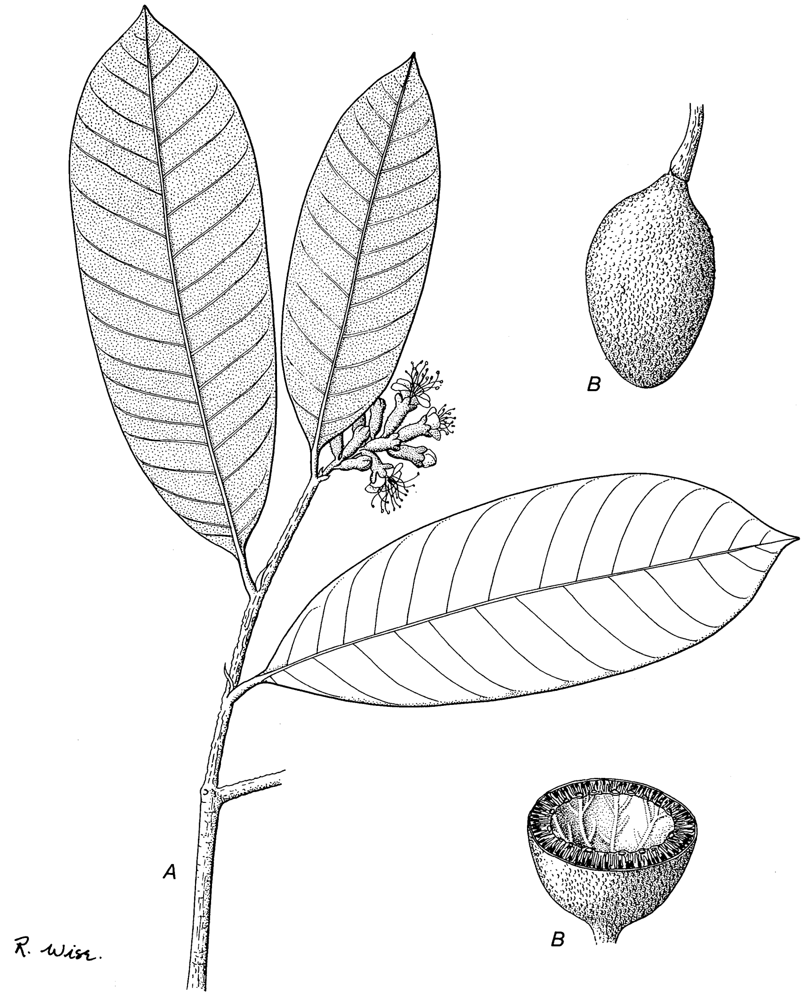


FIGURE 30. *Couepia magnoliifolia*: A, habit ($\times\frac{1}{2}$, Prance *et al.* 20729). *C. longipendula*: B, drupe and TS drupe ($\times\frac{1}{2}$, Prance *et al.* 4638).

The fertile stamens are inserted posteriorly in a few species, e.g. *C. guianensis*; in the bat-pollinated *C. longipendula* the stamens are inserted posteriorly and anteriorly in two fascicles with a few small staminodes in the lateral gaps between them. Sometimes in this species the lower fascicle is lacking. Two to three carpels are found occasionally in a few species, chiefly *C. grandiflora.* The latter sometimes has a rudimentary false dissepiment.

The receptacle is hairy inside in *C. caryophylloides*, *C. cidiana*, *C. excelsa*, *C. paraensis*, subsp. *paraensis* and in *C. recurva.*

Germination: cryptocotylar; cataphylls 8–20; eophylls alternate (*Fanshawe* no. 2232, *C. guianensis*).

Type species: *C. guianensis* Aubl.

Distribution and ecology: all 67 species are confined to America, where they range from Mexico to southern Brazil, but only one species, *C. polyandra*, occurs outside South America and the genus is unrepresented in the West Indies.

Two species, *C. ovalifolia*, which has conspicuous bud-scales, and *C. schottii*, occur in the coastal restingas of Brazil. *C. cognata* and *C. multiflora* are savanna species of Venezuela, Surinam and Guyana; the former is particularly abundant. *C. grandiflora* is a common small tree of the cerrado of the planalto of central Brazil. *C. uiti* occurs in the same general area on sandy and rocky riverbanks.

The genus has not been recorded from the Pacific coastal forests, but seven species (*C. belemii*, *C. bondarii*, *C. insignis*, *C. longipetiolata*, *C. meridionalis*, *C. parvifolia* and *C. venosa*) occur in the Atlantic coastal forests from Bahia southwards to São Paulo, and three others (*C. impressa*, *C. longipetiolata* and *C. pernambucensis*) are found further north in the forests of Pernambuco.

Four species are montane. *C. canescens* and *C. steyermarkii* occur at about 1000 m in the Guyana Highlands, *C. platycalyx* at 1700–1800 m in the northern Andes, and *C. recurva* at 1300 m in the Ecuadorian Andes.

The remaining 40 or so species occur in lowland rainforests of the Hylaean region. Eleven are confined to various types of groundwater forest. Two of them, *C. cataractae* and *C. maguirei*, are rheophytes. The latter is confined to the rocky banks of the Rio Negro and other rivers and is partly submerged for six months each year. Most of the flowers are borne during the dry season at low water on the main trunk 20–100 cm above ground level. The rising water washes off and distributes the fruits (Prance 1972). Another species of groundwater forest, *C. paraensis*, is codominant with *Licania apetala* on river beaches, especially those of black-water rivers. This species is an ecological and chorological transgressor (in the sense of White (1979*b*)) in that it also has a subsp. (*cerradoana* Prance) with thick corky bark, which grows in cerrado on the planalto of central Brazil.

A terra firme forest species, *C. racemosa*, which grows on white sand, also occurs in more stunted and open campina vegetation. Some terra firme species also occur in ground water forest. Three species, *C. canomensis*, *C. parillo* and *C. racemosa*, are frequent in secondary forest. Most forest Couepias are neither rare nor abundant.

Reproductive biology: all species, except the red-flowered, bat-pollinated *C. longipendula* and its close relative, *C. dolichopoda*, have white flowers.

In several white-flowered species, e.g. *C. paraensis*, *C. uiti* (G.T.P., personal observations), and *C. grandiflora* (Silberbauer-Gottsberger & Gottsberger 1975), the flowers, which open at night and are heavily scented, are visited by hawkmoths (Sphingidae). Their flowers may also occasionally be visited by hummingbirds during the day, and, in *C. paraensis*, by bees and other small nocturnal moths. Whether hummingbirds or bees effect pollination of these species, and, if so, their relative importance as pollinators, is completely unknown. In most species of *Couepia* the shape and size of the flowers, and the manner in which they are borne, are similar to those of the three species mentioned above, so that it is likely that hawkmoths are the principal pollinators in the genus. In a few species, e.g. *C. parillo* and *C. williamsii*, the receptacle-tube is so long and narrow that it is unlikely that hummingbirds are even occasional pollinators. Sphingophily is also reported for a Colombian species of *Couepia* by Vogel (1968).

C. longipendula is chiropterophilous (Vogel 1968; G.T.P., personal observations) and shows the 'brush mechanism'. Unlike other species of *Couepia*, the petals and filaments are wine-red, and the flowers have an 'umbelliferous' fragrance reminiscent of coriander (*Coriandrum sativum*).

In *C. longipendula* the congested, subcapitate inflorescence, which is probably best referred to as a compound corymb, is carried away from the foliage by a long, pendulous peduncle about 60 cm in length. Although each inflorescence produces about 200 flower-buds, only 1–3 flowers are open simultaneously, and the flowering period of the inflorescence is prolonged over several

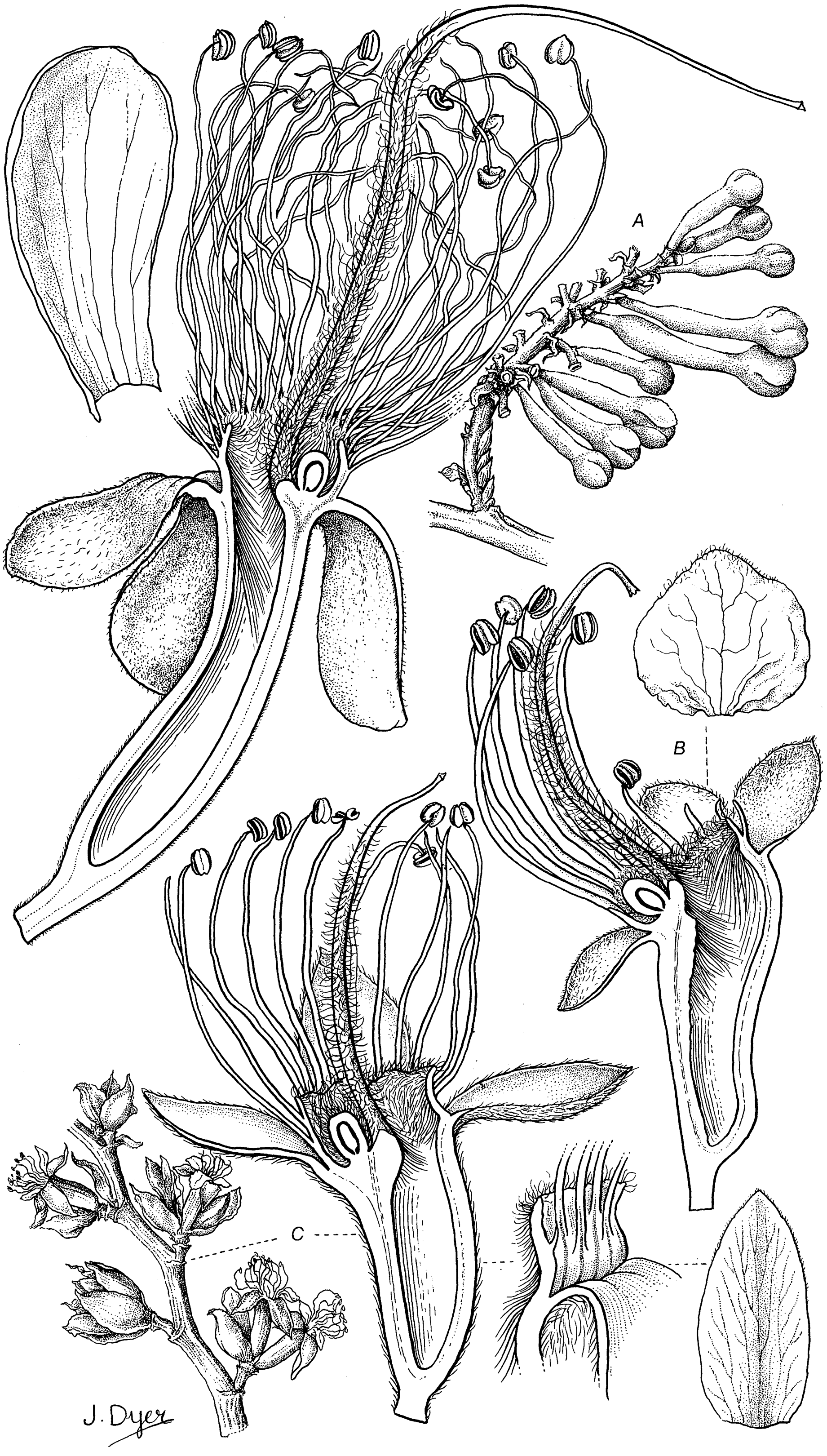


FIGURE 31. *Couepia chrysocalyx*: A, half flower and petal (× 4) and flower buds (× 1), all from Cazalet & Pennington 7690. *C. guianensis* subsp. *glandulosa*: B, half flower and petal (× 5, Irwin *et al.* 48443). *C. bracteosa*: C, half flower and petal (× 5), inflorescence (× 1) and base of stamens (× 10), all from Silva 59733.

months. Anthesis occurs at about 18h00 and the individual flowers last only for a single night. The pendulous flowers hang obliquely; they are almost unique in *Couepia* in having relatively long pedicels which carry them away from the mass of unopened flower-buds. At anthesis the numerous stamens, which were tightly folded in the bud, rapidly straighten and elongate to form a stiff conical crown about 6 cm long. The filaments are inserted in two fascicles, anterior and posterior, on the fleshy, glistening faucal annulus. In the gap between the fascicles, where entrance to the receptacle-tube can be effected, there are about a dozen small staminodes. Sometimes the lower fascicle is lacking. Abundant nectar is secreted by the nectary-lining in the receptacle-tube. Nectar is also produced by a pair of sessile glands on the abaxial face of each sepal. No other species of *Couepia*, except *C. dolichopoda*, has this feature. The petals, which are reflexed at anthesis, fall in the morning, when the filaments also lose their turgor. The latter, which are marcescent, become entangled, and are responsible for the untidy appearance of the inflorescence. Vogel observed and photographed visits by the bat *Glossophaga soricina* and a phyllostominid, probably *Phyllostomus discolor.* They take nectar and insects (H. C. Hopkins, personal communication). Pollen is transported on the wings and thorax.

Vogel was told by the local people that the plum-shaped fruit of *C. longipendula* is also dispersed by bats, although probably by species other than the pollinators. According to Huber (1910) the fruits of other species of *Couepia* are also bat-dispersed. Vogel also mentions that when the fruits of *C. longipendula* fall to the ground they are eaten by agoutis (*Dasyprocta agouti*) and 'Waldhühnern'. One of us (G.T.P.) has observed agoutis carrying the fruit of both *C. longipendula* and *C. racemosa.* In both cases chewed fruits were found up to 200 m from the parent tree. The agouti, by 'scatter-hoarding', is probably the most important dispersal agent. The pericarp of these and some other species of *Couepia* consists almost entirely of sclerenchyma and is unlikely to provide much nourishment to other potential distributors.

Taxonomic history and relationships: *Couepia* was described in 1775 by Aublet, who based it on a single species, *C. guianensis.* It appears in the classifications of R. Brown (1818) and de Candolle (1825). Otherwise, until the publication of Fritsch's synopsis of the genera of Chrysobalanaceae in 1888, it was confused with other genera by nearly all workers. Much of this confusion was nomenclatural and is discussed elsewhere (see §6*e*, where the differences between *Couepia* and *Hirtella* are discussed in some detail).

Since the time of Fritsch, *Couepia* has been a remarkably stable taxon, and its circumscription, apart from the inclusion of new species, has remained virtually unaltered. A few species of *Couepia*, however, have been described in other genera, namely *Parinari krukovii* Gleason (= *Couepia guianensis* Aubl.), *P. canescens* Gleason (= *C. canescens* (Gleason) Prance, 1974), *P. pilosa* Standl. (= *C. canomensis* (Mart.) Benth. ex Hook.f.), *P. hostmannii* Fritsch (= *C. cognata* (Steud.) Fritsch), *Licania exiguifolia* Standl. (= *C. cognata* (Steud.) Fritsch). Only two species in other genera have synonyms in *Couepia*: *Maranthes panamensis* (Standley) Prance & White (syn. *Couepia panamensis* Standley) and *Acioa edulis* Prance (*Couepia edulis* (Prance) Prance). *Acioa*, *Couepia* and *Maranthes* are closely related. *Couepia* and *Licania* and *Couepia* and *Parinari*, however, cannot be confused. One imperfectly known *Couepia*, *C. platycalyx* Cuatr., simulates *Licania* in having a very short, broadly turbinate (almost solid) receptacle, but is typical of *Couepia* in most other respects.

12. *Maranthes* (*figures* 32 *and* 33)

(Greek: withering flowers)

Maranthes Blume, *Bijdr. Fl. Nederl. Ind.*: 89 (1825). – Kosterm., *Candollea* **20**: 106 (1965). – Prance, *Bol. Soc. Brot.* sér. 2 **40**: 183 (1966); *Brittonia* **20**: 203 (1968); *Fl. Neotrop.* **9**: 201, t. 33 (1972). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 294 (1976); *Distr. Pl. Afr.* **10**: 313–325 (1976); *Fl. Zamb.* **4**: 41, t. 11 (1978). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 97, t. 29–33 (1978).

Exitelia Blume, *Fl. Jav. Praef.*: vii (1828) nom.illegit. (superfl.).

Grymania Presl, *Epim. Bot.*: 193 (1851) pro parte quoad *G. salicifolia* tantum.

Parinari sectio *Sarcostegia* Benth., in Hook., *Niger Fl.*: 335 (1849) excl. *P. jackiana* (*Petrocarya excelsa*).

Parinari subgenus *Sarcostegia* (Benth.) Miq., *Fl. Ind. Bat.* **1**: 335 (1855) excl. *P. jackiana*. – Hauman, *Bull. Jard. Bot. État Brux.* **21**: 185 (1951).

Parinari sectio *Exitelia* (Blume) C. Muell., in Walp., *Ann. Bot. Syst.* **4**: 645 (1857).

Parinari subgenus *Exitelia* Blume, *Mélanges Bot.* **2**: 10 (1885). – Hasskl., *Flora* 16: 255 (1858).

Trees. *Leaves* with a pair of glands at the junction of the lamina and eglandular petiole, rarely with marginal glands as well; lower surface glabrous or with an arachnoid indumentum; stipules intrapetiolar, deltate, free or variously united, mostly caducous. *Inflorescence* usually a many-flowered corymbose panicle, rarely a lax, few-flowered thyrse or a raceme of few-flowered monochasial cymes. Bracts and bracteoles eglandular, nearly always caducous, but bracteoles persisting up to anthesis in 2 species, not enclosing flower-buds in small groups. *Flowers* bisexual, slightly zygomorphic; receptacle-tube obconoidal, often slightly to strongly curved, always gradually narrowed into the pedicel, nearly always solid and almost completely filled with nectariferous tissue, only rarely hollow and then elongate and curved, glabrous inside on one side and hairy on the other or completely glabrous; faucal annulus well developed. Sepals 5, suborbicular, deeply concave. Petals 5, suborbicular to broadly lingulate. Stamens 20–60; filaments white, tightly undulate in bud with 2 or more undulations, inserted in two rows on the margin of the faucal annulus, forming a more or less complete circle, much longer than the sepals, usually occurring in a tangled mass; staminodes few and vestigial or absent. Ovary 1 (2–3)- carpellary, 2-locular, inserted laterally at mouth of receptacle-tube; style curved upwards, much longer than the sepals, glabrous except at base. *Drupe* fleshy; endocarp very hard, fibrous, with a rough exterior; densely tomentose inside, with 2 lateral plates which break away on germination and allow the seedlings to escape.

Germination: phanerocotylar; cotyledons fleshy, pale green, soon shrivelling; cataphylls absent; first 2 eophylls opposite, the others opposite or alternate, with narrowly lanceolate, persistent stipules (Mensbruge 1966, pp. 124–131, cum ic.).

Chromosome number: $2n = 20$ (*M. glabra* ('*Parinari glabra*'), Mangenot & Mangenot 1957, 1962).

Type species: *M. corymbosa* Blume.

Distribution and ecology: 12 species, of which 10 occur in tropical Africa and one each in tropical America and Asia. Of the African species, seven occur in the forests of the Guineo-Congolian region, one occurs in riparian forest slightly further north, one occurs in rainforest on the East African mountains, one occurs in the woodlands of the Sudanian region and another in the woodlands of the Zambezian region.

J. Dyer & R. Wise.

FIGURE 32. *Maranthes floribunda*: A, habit (×½, Astle 753); B, half flower (×5, Whellan 1553); C, developing fruits (×½, White 3484); D, endocarp (×1, White 3484). *M. glabra*: E, stipules (Chapman 5244).

Reproductive biology: pollination has been studied only for one species. *Maranthes polyandra* has been shown by Lack (1978), on whose study the following account is based, to be almost certainly pollinated by small fruit bats, including *Nanonycteris veldkampi*. Although various other visitors such as honeybees, hawkmoths, genets and several bird species feed on the nectar or pollen, they are unlikely to be important pollinators.

M. polyandra is a small tree of open woodland in West Africa. On the outside of the tree, well clear of the foliage, flattened corymbs, each producing about 200 flowers, are borne at the ends of stout branches.

Flowering extends over about two weeks, with up to 40 flowers open on a single night on each inflorescence. Each flower lasts only one night. They start to open and nectar secretion begins at 17h30. Anthesis occurs at about 19h30. At this stage the anthers are near the centre of the flower and the style is 14–15 mm long, and the stigma probably not receptive. During the night the anthers gradually move away from the centre of the flower, and the style grows to its full length of 16–19 mm; this process is completed by 01h00. By 10h00 only withered and unopened flowers can be seen. Some flowers, which have short styles, drop off very soon after the night of opening and may be functionally male. Nectar secretion, which is copious, is constant from 19h30 to 23h00, after which it declines. The smell and taste of the nectar is strong and sweet but unpleasant, a common feature of bat-pollinated flowers.

Small insects, including honeybees, visit the flowers when they open, to feed on nectar, but leave as darkness falls.

Visits by bats begin shortly after dark but are brief and sporadic. They become increasingly frequent until 21h30 and thereafter remain very frequent until just before the dawn at 05h30.

In addition to bats, hawkmoths (Sphingidae) and a few other moths visit the flowers in small numbers. Genets (*Genetta tigrina*) also regularly visit the flowers for nectar.

At the first trace of dawn, honeybees appear in large numbers and collect the remaining pollen, most of which has gone by 06h30. For the first few hours of the day, various birds, including the bulbul, *Pycnonotus barbatus*, and the sunbird, *Chalcomitra senegalensis*, visit the flowers for nectar.

The insects that visit the flowers at dusk are not involved in pollination, because anthesis occurs after dark when the style is still immature. The honeybees in the morning feed only on pollen and in general do not contact the stigma; hence they also are irrelevant to pollination. The birds foraging very early may occasionally effect pollination, but little pollen is available and shortly after dawn all has been taken by the bees.

All the nocturnal visitors are potential pollinators. The moths may be effective in pollination, because they contact both anthers and stigma, but their visits are infrequent and their importance is probably minor. The genets do not apparently damage the flowers and may act as occasional pollinators, although their importance must be negligible. By far the most abundant nocturnal visitors are bats, which presumably are the main pollinators. In Lack's study all the bats examined carried *Maranthes* pollen in their fur. No evidence was obtained for their feeding on anything except nectar. They probably travel several kilometres during the night.

Herbarium specimens of the other species of *Maranthes* show only withered and unopened flowers, indicating nocturnal flowers. Some species, e.g. *M. gabunensis*, have a long hollow receptacle tube and far-exserted anthers and are probably pollinated by moths, whereas others, e.g. *M. floribunda* and *M. chrysophylla*, have a very similar inflorescence-structure to *M. polyandra*, and it is likely that they are bat-pollinated. Baker (1961, 1973) has emphasized that hawkmoths and bat pollination involve some similar features. Both types of pollination also seem to go hand in hand in *Couepia*.

The flowers of the Asiatic species *M. corymbosa* are much smaller than those of the other species. A wide variety of insects, including three species of sweat bee (*Trigona*), moths belonging to the families Saturnidae and Sphingidae, the blue-bottle butterfly, *Graphium sarpedon*, a vespid and a hoverfly (Syrphidae), have been observed visiting the flowers of *M. corymbosa* (F. S. P. Ng, personal communication, 4 June 1973). The sweat bees were numerous and active, but it is not known whether they effect pollination. It seems, however, that *M. corymbosa* may also be pollinated by bats. In Kalimantan the flowers are eaten by three species of predatory squirrel, gibbons and the long-tailed macaque, *Macaca fascicularis.* In general, these mammals rarely eat flowers and when they do the latter are invariably found to be bat-pollinated, as in some species of *Dillenia* (M. Leighton, personal communication).

In Kalimantan the fruit of *M. corymbosa* is eaten by many species of bird, the most important of which are hornbills and fruit pigeons (M. Leighton, personal communication). Of the three hornbill species, *Rhyticeros corrugatus*, *R. undulatus* and *Anthracoceros malayanus*, the first two are nomadic and the third is territorial. The two *Rhyticeros* species are gregarious strong fliers, which forage probably 50–100 km from their roosting places. They are believed to be important dispersers. Hornbills regurgitate the endocarps. Mean regurgitation time is about 65 minutes, but some endocarps can be retained for up to two and one half hours. Two strong-flying nomadic pigeons, *Ducula aenea* and *D. badia*, are also important dispersers, especially the former. The endocarp is passed through the gut and is not regurgitated. The mynah, *Gracula religiosa*, and some other smaller birds occasionally take the fruit of *M. corymbosa.* The fruit is scatter-hoarded and presumably locally dispersed by the squirrel *Sundasciurus hippurus*. Primates ignore the fruit of *Maranthes corymbosa*. In Leighton's study area, *M. corymbosa* was fruiting when ripe fruit of other species was scarce. *Maranthes*, it seems, is of critical importance to immigrant *Ducula* pigeons and *Rhyticeros* hornbills at such times (M. & D. R. Leighton 1983).

Little is known about the African species, but the only animals so far recorded as eating the fruit are primates. Whether they effect dispersal is uncertain. The observation of de Souza (1979*a*) in Bénin suggest that their action is largely destructive. Monkeys there eat the seeds of *M. robusta* and *M. polyandra*, and when they have been feeding it is difficult to find any viable seed beneath the trees. In Zimbabwe the fruits of *M. goetzeniana* are said to be eaten by blue monkeys, *Cercopithecus mitis* (H. Wild, personal communication, 12 March 1951).

Taxonomic history and relationships: before the present study, the name *Maranthes* had been applied only to the Asiatic species. As an accepted genus it enjoyed only a very brief existence. Three years after describing it, its author (Blume 1825, 1828) transferred the type species, *M. corymbosa*, to his new and illegitimate genus *Exitelia*. The only other species that had been described in *Maranthes*, *M. multiflora* Korth. (1844), a synonym of *M. corymbosa*, was transferred to *Exitelia* by Walpers the very next year. The first African species to be discovered, *M. polyandra*, was placed in *Parinari* by its author (Bentham 1849) although with some hesitation (see §6*c*). Bentham used the spurious dissepiment, which separates the ovules, to define *Parinari* and in so doing created a highly artificial genus.

Bentham partly acknowledged the heterogeneity of his concept of *Parinari* by creating a section, *Sarcostegia*, to accommodate *Parinari polyandra* and his new Asiatic species, *P. griffithiana*, a synonym of *M. corymbosa*, which he described in the same work.

Presl's genus *Grymania* (1851) can only be regarded as an aberration in the history of the family. It was based on a new species, *G. salicifolia*, and on *Couepia polyandra* (Kunth) Rose, which at that time was mostly regarded as a species of *Hirtella*, although Martius and Zuccarini had excluded it as long ago as 1832.

Blume (1855) adopted Bentham's concept of *Parinari* and placed *Maranthes* in his subgenus *Exitelia* (with *Sarcostegia*, cited in synonymy, which included *P. polyandra*, *P. maranthes* (his illegitimate name for *P. corymbosa*) and *P. griffithiana*). In 1856, Miquel, in a revision of Asiatic Chrysobalanaceae, also adopted Bentham's concept of *Parinari*, to which he transferred *Maranthes corymbosa*, *M. multiflora*, *P. griffithiana* and *Grymania salicifolia*. He adopted Bentham's *Sarcostegia* as a subgenus, citing *Exitelia* as a synonym. In our opinion the four species mentioned above represent a single widespread species, *M. corymbosa*, which until recently has gone under various names in *Parinari*.

All the African species of *Maranthes* were first described in *Parinari*. Such was the authority of Bentham that his judgement was never questioned. In fact, *Maranthes* and *Parinari* sensu stricto are as distinct as any pair of genera in the family. Apart from the spurious dissepiment they have few features in common (see §6*d*). *Maranthes* appears to be more closely related to *Couepia* than to any other genus.

The 12 species of *Maranthes* are very similar in general appearance. They differ chiefly in the size and proportion of the flower (figure 33) and in leaf-shape and indumentum. The specific characters, although slight, are remarkably constant and little difficulty is experienced in identification. Each species is also ecogeographically distinct.

Conspectus of the species

1. Receptable-tube elongate–turbinate, much longer than wide, usually longer than the sepals, gradually narrowed into the pedicel:
  2. Flowers 3.5–5.5 cm long†:
    3. Leaves caudate–acuminate, cuneate or rounded at base; flowers 5.0–5.5 cm long, glabrous outside; filaments *ca.* 4.0 cm long; fruit angular in transverse section . . . . 5. *M. gabunensis*
    3. Leaves shortly cuspidate, subcordate at base; flowers *ca.* 3.5 cm long, grey–velutinous–tomentellous outside; filaments *ca.* 6.0 cm long; fruit terete . . . . 10. *M. sanagensis*
  2. Flowers up to 2.0 cm long:
    4. Pedicel distinctly shorter than the receptacle-tube:
      5. Lower leaf-surface persistently tomentose: indumentum fulvous, at least at first . 2. *M. chrysophylla*
      5. Lower leaf-surface glabrous:
        6. Receptable-tube glabrous outside . . . . 8. *M. kerstingii*
        6. Receptable-tube tomentellous outside . . . . 7. *M. goetzeniana*
    4. Pedicel at least as long as the receptable-tube:
      7. Receptable-tube+sepals *ca.* 1.0 cm long:
        8. Leaf-apex rounded or subacute . . . . 4. *M. floribunda*
        8. Leaf-apex acuminate . . . . 8. *M. kerstingii*
      7. Receptacle-tube+sepals *ca.* 0.7 cm long:
        9. Venation prominent on both surfaces; inflorescence few-flowered (*ca.* 20), a raceme of cymes; drupe narrowly obovoid, *ca.* 5 cm × 2 cm . . . . 9. *M. panamensis*
        9. Venation obscure; inflorescence many-flowered (> 50), a much branched panicle of cymes; drupe ellipsoid, *ca.* 4 cm × 3 cm . . . . 6. *M. glabra*
1. Receptacle-tube shortly turbinate, no longer than wide, more or less equalling or shorter than the sepals, sharply differentiated from the pedicel:
  10. Leaves cordate at base, denticulate towards apex; tertiary nerves subscalariform and conspicuous; bracteoles persistent up to or after anthesis . . . . 1. *M. aubrevillei*
  10. Leaves not cordate, entire; tertiary nerves not subscalariform, inconspicuous; bracteoles caducous:
    11. Leaves obtuse or apiculate at apex; receptacle-tube+calyx *ca.* 0.8 cm long; flowers grey-tomentellous outside . . . . 11. *M. polyandra*
    11. Leaves acuminate or subacuminate: receptacle-tube+calyx up to 0.7 cm long:
      12. Leaves subacuminate, lower surface arachnoid–tomentellous; receptacle-tube cinnamoneous–tomentellous . . . . 12. *M. robusta*
      12. Leaves acuminate, glabrous; receptacle-tube grey–tomentellous . . . . 3. *M. corymbosa*

1. ***Maranthes aubrevillei*** (Pellegr.) Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 295 (1976). – F. White, *Distr. Pl. Afr.* **10**: 314 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 99, t. 29 (1978). Type: Ivory Coast, fl., *Aubréville* 185 (P, holotype).

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† Measured from articulation of pedicel to tip of anterior sepal.

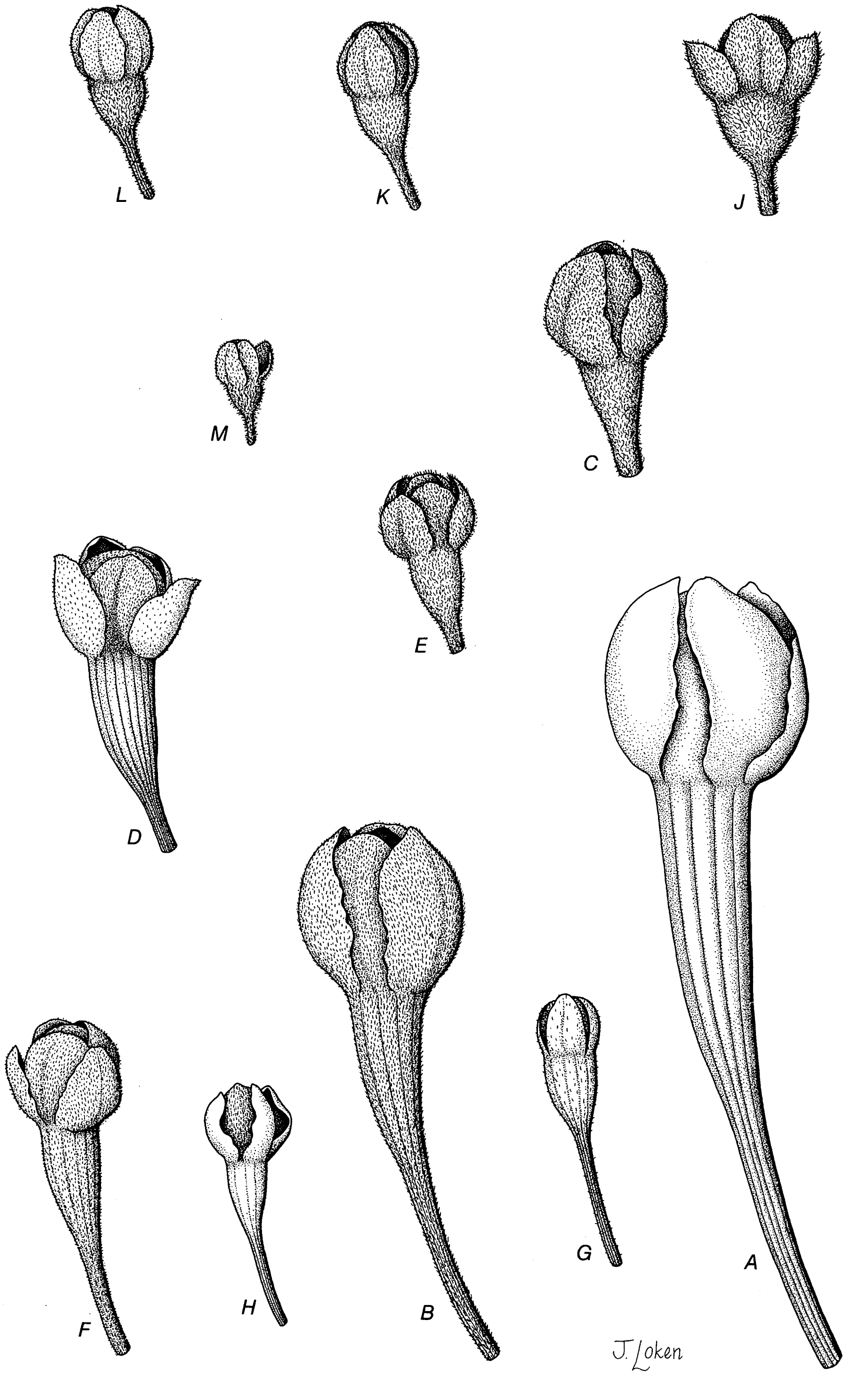


FIGURE 33. Flower buds in *Maranthes* ($\times 2\frac{2}{3}$): A, *M. gabunensis* (Maudoux 248); B, *M. sanagensis* (de Wilde 2652a); C, *M. chrysophylla* (Chevalier 26545); D, *M. kerstingii* (Leeuwenberg 7686); E, *M. goetzeniana* (Chase 8041); F, *M. floribunda* (Greenway & Hoyle 1056); G, *M. panamensis* (Hayes 900); H, *M. glabra* (Vigne 216); J, *M. aubrevillei* (Enti & Hall GC 39137); K, *M. polyandra* (Hoyle 683); L, *M. robusta* (FHO 21119); M, *M. corymbosa* (b.b. 32453).

Tall tree, up to 30 m. Leaf-lamina up to 12 cm × 5.5 cm, margin denticulate towards apex; apex shortly cuspidate, base cordate; tertiary nerves subscalariform; lower surface persistently grey–arachnoid–tomentellous. Bracteoles *ca.* 0.4 cm × 0.25 cm, persistent up to or after anthesis. Upper pedicel *ca.* 0.25 cm long. Receptacle-tube *ca.* 0.5 cm × 0.5 cm. Sepals *ca.* 0.5–0.6 cm long. Outside of flower cinnamoneous–tomentose.

In evergreen rainforest from Sierra Leone to Cameroun.

M. aubrevillei is one of the very few Chrysobalanaceae to have toothed leaves. In juvenile plants there are 8–12 conspicuous glandular teeth on each margin; in mature leaves the teeth are much less conspicuous. In *Licania michauxii* the toothed leaves are shallowly and irregularly crenate.

2. ***Maranthes chrysophylla*** (Oliv.) Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 295 (1976). – F. White, *Distr. Pl. Afr.* **10**: 315–317 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 100, t. 102 (1978). Type: Gabon, *Mann* 978 (K, holotype; P).

Tall tree up to 30 m. Leaf-lamina up to 25 cm × 13.5 cm, apex shortly acuminate or shortly cuspidate, base cuneate to subcordate; lower surface tomentellous, at first fulvous, ultimately fulvous or cinereous. Upper pedicel 0.2–0.3 cm long. Receptacle-tube 0.4–0.6 cm long, fulvous–tomentellous outside. Sepals 0.4–0.6 cm long, fulvous–tomentellous outside.

Subsp. *chrysophylla* occurs in evergreen rainforest in an interrupted band from Liberia to Gabon. The parapatric subsp. *coriacea* F. White occurs further inland from Cameroun to SW Zaire.

3. ***Maranthes corymbosa*** Blume, *Bijdr. Fl. Nederl. Ind*: 89 (1825). – Kosterm., *Candollea* **20**: 107, t. 1–3 (1965). – Prance & Whitmore, in Whitmore, *Tree Fl. Mal.* **2**: 330, t. 5 (1972) excl. syn. *Couepia panamensis*. Type: Java, fl., *Blume* 1516 (BO, L).

Tall tree up to 40 m tall, but sometimes flowering when only a few metres high. Leaf-lamina up to 14 cm × 6.5 cm, apex acuminate, base cuneate; lower surface glabrous. Upper pedicel 0.1–0.3 cm long. Receptacle-tube 0.25 cm × 0.25 cm to 0.4 cm × 0.4 cm. Sepals 0.25–0.4 cm long. Outside of flower grey–tomentellous with denser and paler indumentum on 'protected' part of sepals.

Extending from southern Thailand through the Malay Peninsula and the Indonesian Archipelago to the Caroline Islands, tropical Australia and the Solomon Islands. Throughout its range it is rarely found very far from the coast. In Malaysia it is common in coastal areas, especially on rocky and sandy hills by the sea; exceptionally it can occur inland up to 600 m. In Australia, besides occurring as a 30 m tall tree in fringing forest, it also is found as a shrub on sand dunes and immediately behind mangrove swamp.

Despite its very wide distribution, *M. corymbosa* is not very variable, other than in habit.

Kostermans (1965) gives full synonymy and an extensive bibliography.

4. ***Maranthes floribunda*** (Bak.) F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 297 (1976); *Distrib. Pl. Afr.* **10**: 318 (1976); *Fl. Zamb.* **4**: 41, t. 11 (1978). Type: Malawi, fl., *Whyte* s.n. (K, holotype).

Small tree up to 10 m tall. Leaf-lamina up to 15 × 8 cm, apex usually rounded, sometimes subacute, base rounded or subcordate, rarely cuneate; lower surface densely arachnoid–tomentose at first, glabrescent but with some hairs always persisting. Upper pedicel 0.7–1.2 cm long. Receptacle-tube 0.7–1 cm × 0.4 cm. Sepals 0.7–0.8 cm long. Outside of flower usually grey–velutinous–tomentellous, less often coarsely fulvous–tomentose with spreading hairs or completely glabrous.

Angola, Zambia, Malawi, Zaire (Shaba) and Tanzania. In wetter types of *Brachystegia*, *Julbernardia*, *Isoberlinia* woodland (*miombo*).

5. ***Maranthes gabunensis*** (Engl.) Prance, *Bol. Soc. Brot.* sér. 2 **40**: 184 (1966). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 299 (1976); *Distr. Pl. Afr.* **10**: 319 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 105, t. 31 (1978). Type: Gabon, fl., *Soyaux* 45 (B, destroyed, holotype; P, lectotype here designated; K).

Medium-sized tree up to 20 m tall. Leaf-lamina up to 26 × 12 cm, apex caudate–acuminate, base rounded or cuneate, lower surface glabrous. Inflorescence a relatively few-flowered (*ca.* 20) raceme of few-flowered cymes. Upper pedicel *ca.* 1.5 cm long. Receptacle-tube *ca.* 2.5 cm × 0.6 cm, often curved, glabrous outside. Sepals about 1.2 cm long, glabrous outside except for sparsely and minutely puberulous 'protected' parts. Filaments about 4 cm long.

In evergreen rain forest in West Africa in a narrow coastal belt from SE Nigeria to the extreme southwest corner of Zaire, just north of the River Zaire.

M. gabunensis is the only species with a truly hollow receptacle.

6. ***Maranthes glabra*** (Oliv.) Prance, *Bol. Soc. Brot.*, sér 2 **40**: 184 (1966). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 300 (1976); *Distr. Pl. Afr.* **10**: 320 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 108, t. 32 (1978). Type: Equatorial Guinea, fl., *Mann* 1832 (K, holotype; P).

Tall tree up to 30 (40) m tall, but sometimes flowering when only 5 m tall. Leaf lamina up to 14 cm × 5.5 cm, apex caudate–acuminate, base cuneate, lower surface usually glabrous, rarely with a sparse, whitish, caducous, arachnoid indumentum. Upper pedicel *ca.* 0.5 cm long. Receptacle-tube *ca.* 0.4 cm × 0.25 cm. Sepals *ca.* 0.3 cm long. Outside of flower usually glabrous except for the whitish-tomentellous 'protected' parts of the sepals. Drupe ellipsoid, *ca.* 4 cm × 3 cm.

Widely distributed throughout the greater part of the Guineo-Congolian region from Sierra Leone to Ituri in eastern Zaire. In evergreen and semi-evergreen rainforest; absent only from the drier types.

7. ***Maranthes goetzeniana*** (Engl.) Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 303 (1976). – F. White, *Distr. Pl. Afr.* **10**: 321 (1976); *Fl. Zamb.* **4**: 43 (1978). Type: Tanzania, fl., *Engler* 496a (B, destroyed, holotype).

Medium-sized to large tree 20–35 m tall. Leaf-lamina up to 15 × 8 cm, apex suddenly and acutely acuminate, base rounded or cuneate; lower surface glabrous. Upper pedicel *ca.* 0.2 cm long. Receptacle-tube 0.4 cm × 0.25 cm to 0.6 cm × 0.3 cm, tomentellous outside. Sepals 0.3–0.5 cm long, tomentellous outside.

In lowland and transitional rainforest on the mountains of East Africa from North Tanzania to Zimbabwe and Mozambique.

8. ***Maranthes kerstingii*** (Engl.) Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 303 (1976). – F. White, *Distr. Pl. Afr.* **10**: 322 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 112, t. 33 (1978). Type: Togo, fl., *Kersting* 547 (B, syntype, destroyed; K, lectotype, here designated).

Medium-sized tree up to 20 m tall. Leaf-lamina up to 14 cm × 6 cm, apex caudate–acuminate, base cuneate or rounded; lower surface glabrous. Upper pedicel *ca.* 0.3 cm long. Receptacle-tube *ca.* 1.0 cm × 0.4 cm, glabrous outside. Sepals *ca.* 0.5 cm long, sparsely and minutely puberulous outside on exposed parts, whitish-tomentellous on 'protected' parts.

In fringing forest in the wetter parts of the Sudanian Region from Togo to the Central African Republic. In West Africa it occurs mainly in upland areas.

9. ***Maranthes panamensis*** (Standl.) Prance & F. White, *Brittonia* **37**: 76 (1985). Type: Panama, fl., *Cooper* 279 (F, holotype; GH, NY, US).

Couepia panamensis Standl., *Trop. Woods* **44**: 22 (1935).

Maranthes corymbosa sensu Prance, *Brittonia* **20**: 203 (1968); *Fl. Neotrop.* **9**: 202 (1972). – van Steenis, *Fl. Males. Bull.* **23**: 1756 (1969).

Tall tree, up to 25 m. Leaf-lamina up to 13 cm × 4.5 cm, apex caudate–acuminate, base cuneate; venation prominent on both surfaces; lower surface glabrous. Inflorescence a few-flowered (*ca.* 20) raceme of cymes. Upper pedicel *ca.* 0.7 cm long. Receptacle-tube *ca* 0.5 cm × 0.3 cm. Sepals *ca.* 0.3 cm long. Outside of flower sparsely and minutely puberulous except for the whitish-tomentellous 'protected' parts of the sepals. Drupe narrowly obovoid, *ca.* 5 cm × 2 cm.

Previously known from a few localities in the Isthmus of Panama, and recently collected in Nicaragua and Costa Rica. Occurs in dense rainforest.

10. ***Maranthes polyandra*** (Benth.) Prance, *Bol. Soc. Brot.*, sér. 2 **40**: 184 (1966) pro parte excl. subsp. *floribunda*. – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 304 (1976); *Distr. Pl. Afr.* **10**: 323 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 116, t. 34 (1978). Type: Nigeria, fl., *Vogel* 3 (K, holotype).

Small tree, rarely more than 7 m tall. Leaf-lamina up to 15 cm × 8.5 cm, apex obtuse or apiculate, base rounded or obtuse; lower surface persistently grey–arachnoid–tomentellous or almost glabrous. Upper pedicel 0.3–0.4 cm long. Receptacle-tube *ca.* 0.4 cm × 0.4 cm. Sepals *ca.* 0.4 cm long. Outside of flower grey–tomentellous.

Widespread in woodland and wooded grassland of the Sudanian region from the Ivory Coast and eastern Mali to the Sudan Republic.

11. ***Maranthes robusta*** (Oliv.) Prance, in F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 306 (1976). – F. White, *Distrib. Pl. Afr.* **10**: 324 (1976). Type: Nigeria, fl., fr. *Mann* 481 (K, holotype).

Small tree, up to 12 m tall. Leaf-lamina up to 12.5 × 6 cm, apex subacuminate, base cuneate; lower surface persistently pale–fulvous–arachnoid–tomentellous. Upper pedicel 0.3–0.4 cm long. Receptacle-tube *ca.* 0.3 cm × 0.3 cm, tomentellous with cinnamoneous hairs. Sepals *ca.* 0.4 cm long, densely puberulous with greyish hairs.

In swamp forest and semi-evergreen rainforest in West Africa from the Ivory Coast to Nigeria.

12. ***Maranthes sanagensis*** F. White, *Adansonia* sér. 2 **16**: 232, t. 2 (1976); *Bull. Jard. Bot. Nat. Belg.* **46**: 307 (1976); *Distr. Pl. Afr.* **10**: 325 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 119, t. 36 (1978). Type: Cameroun, fl., *Leeuwenberg* 5476 (P, holotype; BR, K, WAG).

Small tree, 6–8 m tall. Bole short, but up to 1 m in diameter, often twisted and prostrate. Leaf-lamina up to 15 cm × 9.5 cm, apex abruptly cuspidate, base subcordate, lower surface glabrous. Inflorescence a relatively few-flowered (*ca.* 20) simple or branched raceme of few-flowered cymes. Upper pedicel *ca.* 1.2 cm long. Receptacle-tube *ca.* 1.5 cm × 0.5 cm., grey–velutinous–tomentellous outside. Sepals *ca.* 1 cm long, grey–velutinous–tomentellous outside. Filaments *ca.* 6 cm long.

Only known from the banks of the Sanaga River in Cameroun and the lower courses of its tributaries.

13. *Atuna* (*figure* 34)

(from a Moluccan vernacular name)

Atuna Rafin., *Sylva Tellur.*: 153 (1838); Kosterm., *Reinwardtia* **7**: 421 (1969).

[*Atunus* Rumph., *Herb. Amboin.* **1**: 171, t. 66 (1741). – Lam., *Encycl. Méth.* **1**: 329 (1783), non *Atunus* Rumph. (1743)].

Cyclandrophora Hasskl., *Flora* **25** (2), Beibl. 2 (3): 47 (1842). – Kosterm., *Candollea* **20**: 118 (1965).

Moquilea sectio *Cyclandrophora* (Hasskl.) Endl., *Gen. Pl.* suppl. **3**: 103 (1843).

Parinari subgenus *Macrocarya* Miq., *Fl. Ind. Bat.* **1**: 354 (1855).

Parinari sectio *Cyclandrophora* (Hasskl.) C. Muell., in Walp., *Ann. Bot. Syst.* **4**: 644 (1857).

Parinari subgenus *Cyclandrophora* (Hasskl.) Blume, *Mélanges Bot.* **2**: 10 (1855). – Hasskl., *Flora* **16**: 255 (1858).

Entosiphon R. H. Beddome, *Madras J. Lit. Sci.* ser. 3 **1**: 44 (1864).

Petrocarya auct. non Schreb. quoad *P. excelsa* Jack, *P. glaberrima* (Hasskl.) Miers et *P. scabra* (Hasskl.) Miers tantum.

Trees up to 45 m tall, ultimate shoots with a complicated system of divaricate branching. *Leaves* with a pair of glands on the midrib at or near its base on lower surface; petiole eglandular; lower surface or lamina almost glabrous, with minute papillae on veins giving a beaded appearance; stipules large, prominently keeled, lateral, persistent or subpersistent. *Inflorescence* a raceme or sparsely branched, contracted panicle. Bracts and bracteoles conspicuous, persistent, eglandular, not enclosing the flower-buds in groups. *Flowers* bisexual, zygomorphic. Receptacle-tube obconic, as long as to much longer than the sepals, hollow, hairy inside throughout, throat blocked by long retrorse hairs. Sepals 5, broadly ovate to lanceolate, apiculate, keeled, tomentellous on both surfaces. Petals 5, glabrous on both surfaces. Stamens 10–25, posterior; filaments inserted on margin of faucal annulus, free to base, exserted, up to twice as long as sepals; staminodes forming a barely visible denticulate margin to the faucal annulus. Ovary monocarpellary, 2-locular, becoming unilocular in fruit owing to development of a single ovule, inserted at mouth of receptacle-tube. *Drupe* large, epicarp glabrous, densely verrucose; mesocarp transversely fibrous; endocarp hard, thick, shortly and sparsely hairy inside; breaking up irregularly at germination. Cotyledons large and strongly ruminate.

Germination: cryptocotylar, eophylls alternate.

Type species: *A. racemosa* Rafin.

Distribution and ecology: From southern India eastwards to Samoa. Kostermans recognized 11 species but the differences between some of them are slight and further work may lead to a reduction in their number.

Reproductive biology: the fruit of *A. excelsa* (‘*Parinari laurina*’) is dispersed by ocean currents and retains its buoyancy for months (Ridley 1930). In Kalimantan (M. Leighton, personal communication) it is scatter-hoarded by the squirrel *Sundasciurus hippurus*. Three other squirrels eat the seed but are mainly destructive. The pig *Sus barbatus*, which also eats the seeds, is a predator, although it may occasionally effect dispersal.

Taxonomic history and relationships: All the species now included in *Atuna* had previously been placed in *Parinari*, despite the fact that virtually the only character the two genera have in common is the bilocular ovary. One species, however, which is a synonym of *A. excelsa* (Jack)

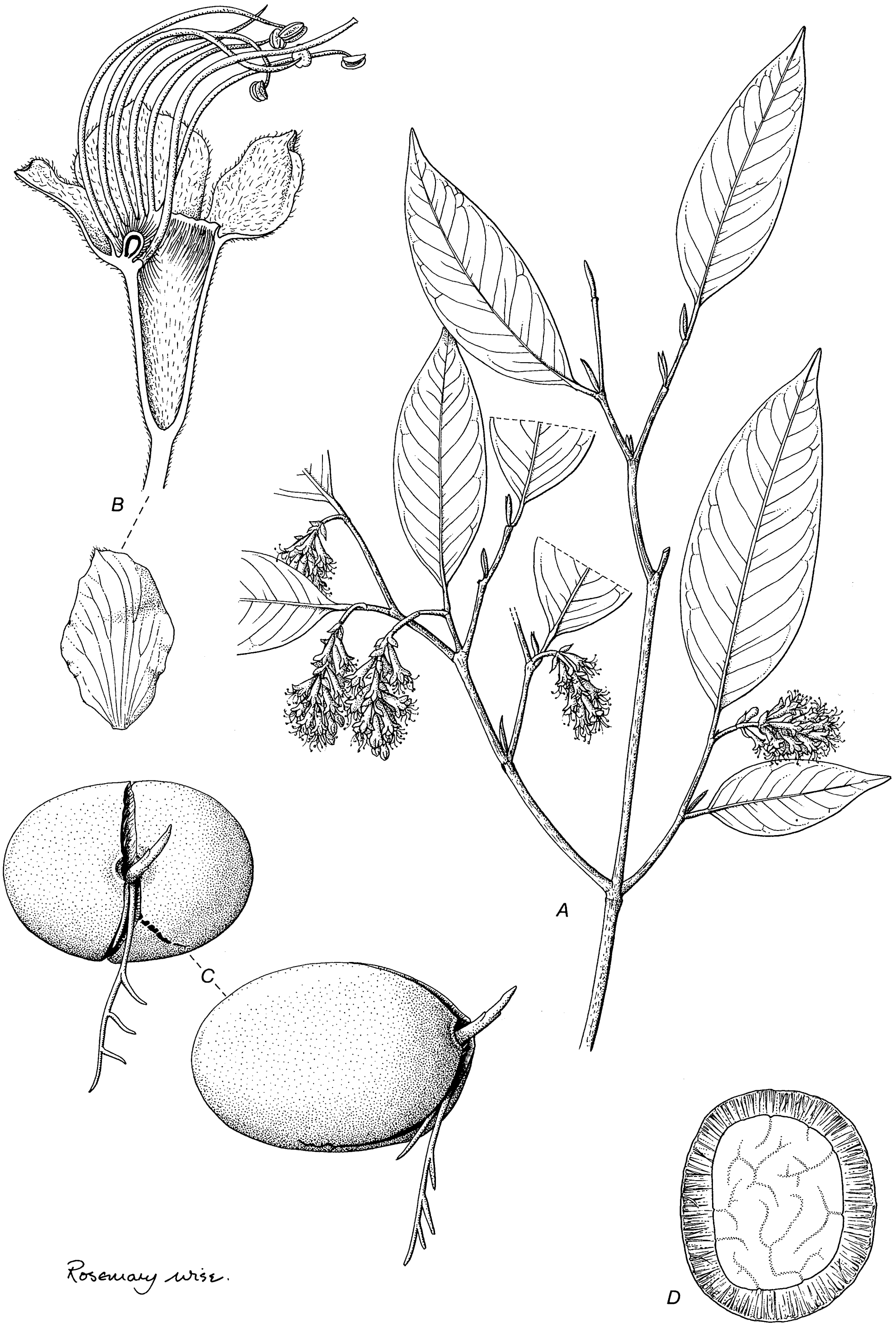


FIGURE 34. *Atuna excelsa*: A, habit ($\times\frac{1}{2}$, Shing FRI (Kep) 6960); B, half flower and petal ($\times 5$, Hamid 11594); C, fruit and emerging seedling ($\times\frac{1}{2}$, Starzecha s.n.); D, TS fruit showing ruminate cotyledons ($\times\frac{1}{2}$, Starzecha s.n.).

Kosterm., was originally described as the type species of *Cyclandrophora* (*C. glaberrima*), but Hasskarl, its author, transferred it to *Parinari* the following year. Blume (1855, p. 10) treated *Cyclandrophora* as a subgenus of *Parinari*.

During an earlier phase of this work it appeared that *Cyclandrophora* was the correct name for this group of species (Prance 1963; Kostermans 1965*d*; Prance *et al.* 1969), but Kostermans subsequently (1969) discovered the overlooked name *Atuna* of Rafinesque and this seems to be the legitimate name.

This genus was first described by Rumphius in 1741, who latinized the vernacular name 'atun' as *Atunus*. It is not the same as the *Atunus* of the third volume of his *Herbarium Amboinense* (1743, p. 95) which is a *Heritiera* (Sterculiaceae). The chrysobalanaceous *Atunus* of Rumphius is included by Lamarck in his *Encyclopedia* (1783) under the heading of its vernacular name. It is quite clear that Lamarck did not intend to describe *Atunus* as a new genus, and was merely communicating some information he had gleaned from the publication of Rumphius about a species he was not personally acquainted with. The genus apparently was first legitimately published by Rafinesque (1838) as *Atuna* and the type species designated as *A. racemosa* Rafin. These names, however, were not taken up by later workers, partly because the species now placed in *Atuna* were regarded as belonging to *Parinari*, but possibly also because the *Index Kewensis* cited *Atuna* Rafinesque as synonym of *Heritiera*. Kostermans (1969), who united *Cyclandrophora* with *Atuna*, also failed to completely clarify the situation; he states that *Atunus* [Rumph.] Lamarck is a *Heritiera*, whereas, because Lamarck specifically refers to the first volume of the *Herbarium Amboinense*, his *Atunus* is unmistakably the genus under discussion. Panigrahi & Purohit (1983) have recently independently reached a similar conclusion.

The differences between *Atuna* and *Parinari* are given elsewhere (§6*d*).

As revised by Kostermans, *Atuna* consists of two closely related, widespread, parapatric species, *A. excelsa* (Jack) Kosterm. and *A. racemosa* Raf., and nine species of much more local distribution. Kostermans admits that *A. excelsa* and *A. racemosa* are difficult to separate and that hybrids may occur. The differences mentioned by Kostermans do not hold, and on present evidence we see no justification for keeping them apart. For that reason, in the general chapters we provisionally adopt the name *A. excelsa* for a single entity which extends from the Malay Peninsula to Samoa. Further work may show that more than one species can be recognized in this complex, based on characters other than those that Kostermans used, but that would not alter the fact that *A. excelsa* sensu lato is a useful taxonomic and ecogeographic entity. There is some doubt, however, about the epithet '*excelsa*', the oldest one available. It is based on *Petrocarya excelsa* Jack of which, apparently, no type material is known (Merrill 1952). According to Merrill, Jack's descriptions often allow his species to be unequivocally identified in the absence of original material. The description of *Petrocarya excelsa*, however, is ambiguous and futher work may result in its rejection.

New combination

Atuna latifrons (Kosterm.) Prance & F. White comb.nov.

Parinari latifrons Kosterm., *Reinwardtia* **7**: 54 (1965). Type: Malay Peninsula, fl., *Haniff* SFN 21119 (K, holotype).

Parinari latifolia M. R. Henderson, *Gard. Bull. Straits Settl.* **7**: 102 (1933) non *P. latifolia* (Oliv.) Exell (1928). Type: as above.

Cyclandrophora latifolia (R. M. Henderson) Kosterm., *Candollea* **20**: 121 (1965). Type as above.

Atuna latifolia (R. M. Henderson) Kosterm., *Reinwardtia* **7**: 421 (1969). Type as above.

14. *Dactyladenia* (*figures* 35–38)

By R. Letouzey

(Greek, 'glandular fingers', referring to the stalked glands in some species)

Dactyladenia Welw., Apont., *Ann. Cons. Ultram.* **1**: 572 (1859 ['1858']). – Prance & F. White, *Brittonia* **31**: 483 (1979) non × *Dactyladenia* Garay & H. R. Sweet (1966, Orchidaceae).

Griffonia Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 608 (*ca.* 19 Oct. 1865). – Oliver, *F.T.A.* **2**: 371 (1871) non *Griffonia* Baill., *Adansonia* **6**: 188 (7 Oct. 1865, Leguminosae: Caesalpinioideae).

Acioa auct. non Aubl. quoad spec. et syn. Afr. tantum; Baill., *Adansonia* **7**: 221 (1867). – Focke, in Engl. & Prantl, *Nat. Pflanzenf.* **3** (3): 60 (1891). – Hutch., *Gen. Fl. Pl.* **1**: 192 (1964).

Acioa subgen. *Afracioa* R. Letouzey, in Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 7 (1978).

Shrubs or small trees, sometimes scandent. *Leaves* usually with two glands on lower surface near base of lamina, often also with smaller glands near apex or scattered over surface; petiole eglandular; lower surface of lamina glabrous or with stiff ferruginous hairs, more rarely with whitish arachnoid or lanate indumentum; stipules lateral, often persistent. *Inflorescence* a simple raceme of zig-zag, usually lax, false racemes, more rarely a subcapitate spike (*D. whytei*). Bracts and bracteoles not enclosing the flower-buds in small groups, often with stalked or sessile glands. *Flowers* bisexual, strongly zygomorphic. Receptacle-tube usually elongate and narrowly obconic-tubular, usually longer than the upper pedicel, often slightly gibbous at the base, glabrous inside except near the throat. Sepals 5, rounded or acute, usually spreading or reflexed, often with stalked or sessile, marginal glands; adaxial surface whitish-tomentellous. Petals 5, caducous. Stamens 10–75, coiled in bud; filaments ligulately connate for most of length, inserted on posterior rim of faucal annulus, far-exserted, much longer than combined length of calyx and receptacle-tube. Staminodes short, filiform or denticulate. Ovary monocarpellary, 1-locular, inserted at mouth of receptacle-tube; style filiform, slightly longer than the stamens, slightly 3-lobed at apex. *Drupe* usually more than 3 cm long, more or less ovoid, but usually markedly tapered towards the pointed apex; epicarp often ferruginous-tomentose and with longer hispid hairs, less often glabrous; mesocarp thin; endocarp thin but hard, with a roughish surface, hairy inside, with no special mechanism allowing seedlings to escape.

Germination: cryptocotylar; eophylls opposite.

Chromosome number: $2n = 22$ (*D. barteri*, as '*Acioa barteri*' (Mangenot & Mangenot 1958, 1962)).

Type species: *D. floribunda* Welw.

Distribution and ecology: 27 species in tropical Africa, virtually confined to the Guineo-Congolian region. Most species occur in riparian or secondary forest, more rarely in coastal thicket. To judge from the paucity of herbarium material, it seems that several species are very rare. An important exception is *D. barteri*, which plays a significant role in agricultural practice in southeast Nigeria. Here it has been found that even on soils inherently low in mineral

URE 35. *Dactyladenia barteri*: A, habit ($\times\frac{1}{2}$, Daramola FHI 45684); B, half flower and petals ($\times 7\frac{1}{2}$) and anthers ($\times 15$) from Daramola FHI 45684; C, fruit ($\times\frac{1}{2}$, MacGregor 373).

reserves, under a rainfall as high as 2250 mm per year, it is possible to follow one and a half years of cropping with only two and a half years of fallow of *Acioa barteri* (Nye & Greenland 1960). In the same region this species is also planted with *Anacardium occidentale* and *Erythrophleum suaveolens* on badly eroded sites to restore forest conditions.

Reproductive biology: Vogel (1954) suggests pollination by butterflies and hawkmoths. Confirmation is needed.

Taxonomic history and relationships: when Baillon (1867) restored Aublet's American genus *Acioa* to generic rank, he united J. D. Hooker's African genus *Griffonia* with it, pointing out that the latter was antedated by his own genus of that name in Leguminosae: Caesalpinioideae by a few days. Oliver, however (*F.T.A.* 2, p. 371 (1871)), continued to use *Griffonia*, though all other authors have followed Baillon.

The first African '*Acioa*' to be described, however, was placed by Welwitsch in 1859 in his new genus *Dactyladenia* as *D. floribunda*. The latter was universally overlooked until Exell transferred it to *Acioa* in 1928. A recent detailed comparison of the American and African species of *Acioa* has shown that they share few characters other than the staminal ligule. Accordingly, the African species have been moved to *Dactyladenia* (Prance & White 1979), a view forshadowed by Letouzey (in Letouzey & White 1978*a*, *b*) who emphasized the isolation of the African species by proposing a subgenus, *Afracioa*, to accommodate them.

Conspectus of the species

1\. Inflorescence a simple raceme:
  2\. Receptacle and exterior of sepals glabrous (but see also 27 and 10):
    3\. Receptacle-tube ± equalling upper pedicel:
      4\. Branchlets and lower leaf-surface glabrous:
        5\. Bracteoles ovate-lanceolate, denticulate-glandular; leaves with 5–8 pairs of lateral nerves . . . 24. *D. scabrifolia*
        5\. Bracteoles lanceolate, 5–7-dentate, with substipitate to stipitate glands near the base; leaves with 3–5 pairs of lateral nerves . . . . 17. *D. letestui*
      4\. Branchlets and lower leaf-surface ± hispid; bracteoles 5–7-palmatisect; bracts with glandular margin and 1–2 pairs of basal stipitate glands . . . . 25. *D. smeathmannii*
    3\. Receptacle-tube longer than upper pedicel:
      6\. Bracteoles ovate, eglandular; receptacle-tube sometimes hispidulose . . . . . . 27. *D. whytei*
      6\. Bracteoles palmatilobed to palmatisect:
        7\. Branchlets not densely covered with persistent golden tomentum; but variously pubescent, hispidulose or glabrescent:
          8\. Branchlets with hairs less than 0.1 cm long:
            9\. Stipules linear, 0.5–0.6 cm long; leaves with 6–8 pairs of lateral nerves; bracteoles 3-(5)-palmatisect; receptacle-tube 1.2–2 cm long; sepals 0.6–0.8 cm long; stamens *ca.* 25 . . . 11. *D. gilletii*
            9\. Stipules lanceolate, 0.3–0.4 cm long; leaves with 4–5 pairs of lateral nerves; bracteoles 5-palmatilobed to palmatipartite; receptacle-tube 0.7–1 cm long; sepals 0.4–0.5 cm long; stamens *ca.* 15 . . . . 18. *D. librevillensis*
          8\. Branchlets with hairs more than 0.1 cm long:
            10\. Stipules linear, 0.6–0.8 cm long; lower leaf-surface hispid; lateral nerves in 6–10 pairs:
              11\. Bracteoles 3–5-palmatipartite; receptacle-tube 0.8–1.2 cm long; sepals 0.6 cm long; androecium 2.5–3 cm long; stamens *ca.* 30 . . . . 2. *D. bellayana*
              11\. Bracteoles transversely ovate but furnished with (3)-5 triangular teeth bearing a stipitate gland; receptacle-tube 1.6–2.2 cm long; sepals 0.6–1 cm long; androecium 3.5–4.5 cm long; stamens *ca.* 20 . . . . 12. *D. hirsuta*
            10\. Stipules lanceolate, 1–1.6 cm × 0.3–0.8 cm; lower leaf-surface glabrous; lateral nerves in 8–16 pairs . . . . 3. *D. campestris*
        7\. Branchlets densely covered with persistent golden tomentum:
          12\. Raceme 12–30 cm long; leaf-lamina cordate at base; lateral nerves in 10–16 pairs; bracteoles 5-palmatipartite to palmatisect . . . . 13. *D. icondere*

12. Raceme 2-6 cm long; leaf-lamina rounded at base; lateral nerves in 7–10 pairs; bracteoles 5-palmatilobed to palmatipartite; receptacle-tube sometimes very sparsely pubescent . . . 10. *D. floribunda*
2. Receptacle-tube and exterior of sepals hairy:
13. Receptacle-tube more or less as long as upper pedicel; leaf-lamina glabrous; base acute, lateral nerves in 4–6 pairs; bracteoles lanceolate, sometimes glandular . . . 1. *D. barteri*
13. Receptacle-tube longer than upper pedicel:
14. Bracteoles subreniform; leaf-lamina cordate at base, undersurface hairy; lateral nerves in *ca.* 12 pairs . . . 23. *D. sapinii*
14. Bracteoles not subreniform:
15. Receptacle-tube and exterior of sepals densely silvery–tomentose; bracteoles ovate, entire or denticulate–glandular:
16. Receptacle-tube *ca.* 1.8 cm long; stamens 60–75; midrib densely puberulous to glabrescent below; lateral nerves in 8–12 pairs . . . 21. *D. pallescens*
16. Receptacle-tube *ca.* 1.5 cm long; stamens 35 or fewer; midrib glabrous or glabrescent; lateral nerves in 5–8 pairs . . . 19. *D. lujae*
15. Receptacle-tube and exterior of sepals sparsely pubescent to densely villous, not densely silvery–tomentose:
17. Branchlets and flowers densely fulvous–villous; bracteoles deltate with glandular appendages near base; racemes 3–4.5 cm long, few-flowered; lower pedicel *ca.* 0.5 cm long; receptacle-tube 1.2–2 cm long; sepals 0.6–0.8 cm long; stamens 3–5 cm long . . . 26. *D. staudtii*
17. Branchlets and flowers sparsely pubescent, sometimes hispidulose; bracteoles 5(-10)-palmatisect; racemes 10–15 cm long; lower pedicels 1 cm long; receptacle-tube 0.6–1 cm long, distinctly gibbous at base; sepals 0.4–0.5 cm long, often with marginal glands; stamens 2–2.5 cm long . . . 6. *D. dewevrei*
1. Inflorescence compound (but sometimes subsimple in no. 16):
18. Receptacle-tube and exterior of sepals glabrous:
19. Bracteoles subreniform, 5-denticulate, inserted at middle of pedicel below the articulation . . . 15. *D. laevis*
19. Bracteoles 5–7-palmatifid to palmatipartite; inflorescence sometimes a subsimple raceme . . . 16. *D. lehmbachii*
18. Receptacle-tube and exterior of sepals not glabrous:
20. Bracteoles ovate, without conspicuous glandular denticulation (but see no. 20, *D. mannii*):
21. Inflorescence puberulous; bracteoles inserted near the middle of lower pedicel, sometimes denticulate . . . 20. *D. mannii*
21. Inflorescence tomentellous to tomentose; bracteoles inserted near apex of lower pedicel:
22. Stipules ovate, 0.4–0.8 cm long . . . 22. *D. pierrei*
22. Stipules linear to lanceolate:
23. Receptacle-tube up to 1.2 cm long:
24. Branchlets very sparsely puberulous or glabrescent; lamina subcordate or cordate at base . . . 9. *D. eketensis*
24. Branchlets tomentose at first, glabrescent; lamina rounded to subcordate . . 7. *D. dichotoma*
23. Receptacle-tube *ca.* 1.8 cm long; branchlets and inflorescence golden–tomentose . . . 8. *D. dinklagei*
20. Bracteoles with stipitate glands:
25. Stipules subdeltate with flabellate nerves; bracts and bracteoles with a clavate apical gland . . . 5. *D. cinerea*
25. Stipules linear or lanceolate:
26. Branchlets and lower leaf-surface hispid; stipules linear, with long-stipitate glands; bracts and bracteoles deltate, with long-stipitate glands . . . 14. *D. johnstonei*
26. Branchlets and lower leaf-surface arachnoid–tomentose; stipules falcate–lanceolate; bracts and bracteoles ovate, with stipitate glands . . . 4. *D. chevalieri*

1. ***Dactyladenia barteri*** (Hook.f. ex Oliv.) Prance & F. White, *Brittonia* **31**: 484 (1979). Type: Nigeria, fl. fr., *Barter* 2183 (K, lectotype of Prance & White, 1979; P).

Griffonia barteri Hook.f. ex Oliv., *F.T.A.* **2**: 373 (1871).

Acioa barteri (Hook.f., ex Oliv.) Engl., *Bot. Jahrb.* **26**: 382 (1899). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 10, t. 1 (1978).

Branchlets hispidulose, rapidly glabrescent. Racemes 3–4 (12) cm long, puberulous. Bracteoles 0.1–0.15 cm long, lanceolate, sometimes with stipitate glands. Upper pedicel

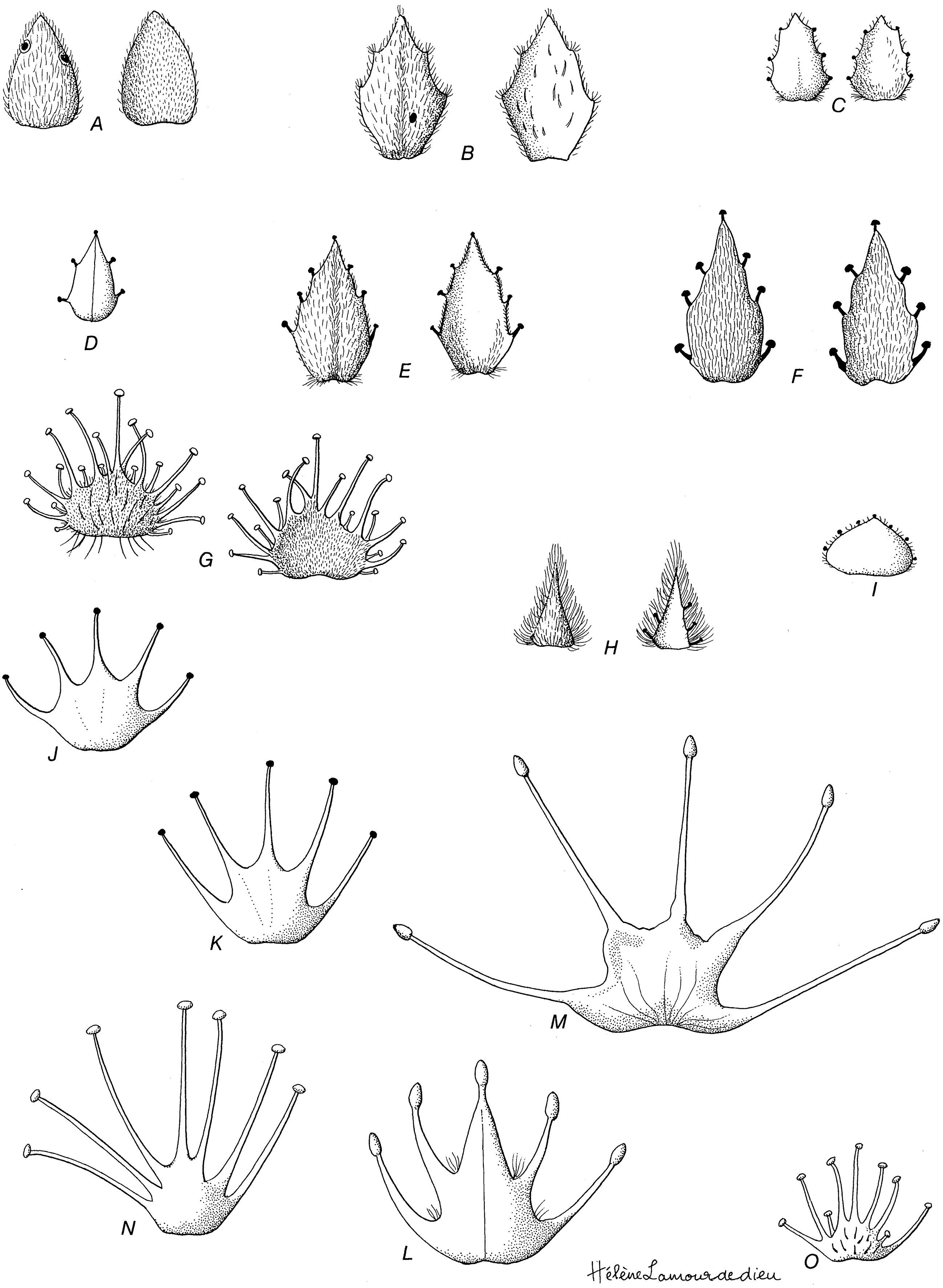


FIGURE 36. Bracteoles in *Dactyladenia* ($\times 10\frac{2}{3}$): A, *D. pierrei* (Klaine 176); B, *D. pallescens* (Staudt 618 and Zenker 855); C, *D. scabrifolia* (Pobéguin K14); D, *D. letestui* (Le Testu 9352); E, *D. chevalieri* (Pobéguin 28); F, *D. cinerea* (Zenker 2903); G, *D. johnstonei* (Hepper 1927); H, *D. staudtii* (Le Testu 8425); I, *D. laevis* (Klaine 3538); J, *D. hirsuta* (Chevalier 19738); K, *D. librevillensis* (Klein 55); L. *D. campestris* (Zenker 4200); M, *D. icondere* (Hallé & Villiers 5510); N, *D. smeathmannii* (Thomas 5503), O, *D. dewevrei* (Louis 11162).

(0.5) 0.8–1.2 (1.5) cm long. Receptacle-tube 0.4–0.6 cm long, more or less gibbous at base. Sepals 0.4–0.5 cm long. Stamens 15–20, (1.5) 2.5 (3) cm long. Drupe 4 cm × 2 cm, glabrous.

Climbing shrub or small tree up to 12 m tall. Extending from Sierra Leone to Gabon and perhaps Zaire. Usually on river banks. Closely related to *D. scabrifolia.*

2. ***Dactyladenia bellayana*** (Baill.) Prance & F. White, *Brittonia* **31**: 484 (1979). Type: Gabon, fl., *Griffon de Bellay* 602 (P, holotype).

Acioa bellayana Baill., *Adansonia* **7**: 224 (1867) – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 13, t. 2 (1978).

Branchlets hispid. Racemes 5–10 cm long; axis sparsely hispidulous, glabrescent. Bracteoles 0.1–0.2 cm long, terminal or subterminal, glandular, 3–5-palmipartite. Upper pedicel 0.2–0.4 cm long. Receptacle-tube 0.8–1.2 cm long, glabrous, gibbous at base. Sepals 0.6 cm long, glabrous. Stamens *ca.* 30, (2.5) 3 cm long. Drupe 5 cm × 2.5 cm × 2.5 cm.

Climbing shrub. Only known from Cameroun, Gabon and Bas Zaire. Closely related to *D. campestris*, *D. floribunda* and *D. icondere.*

3. ***Dactyladenia campestris*** (Engl.) Prance & F. White, *Brittonia* **31**: 484 (1979). Type: Gabon, fl., *Soyaux* 362 (B, holotype, destroyed; P, lectotype of Prance & White 1979).

Acioa campestris Engl., *Bot. Jahrb.* **17**: 87 (1893). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 16, t. 3 (1978).

Branchlets hispid, rapidly glabrous. Racemes 6–12(20) cm long, axis sparsely hispidulous, glabrescent. Bracteoles 5-palmatipartite, with 0.5 cm long stipitate glands. Upper pedicel 0.3–0.5 cm long. Receptacle-tube 1.5–2.2 cm long, glabrous; base gibbous. Sepals 0.6–0.9 cm long, glabrous. Stamens *ca.* 30, 4–6 cm long. Drupe 7 cm × 3 cm × 2.5 cm.

Sprawling shrub 5 m high. Extending from SE Nigeria to Cabinda. In forest regrowth and disturbed forest. Rarely in seasonally flooded forest. Closely related to, and frequently confused with, *A. bellayana* and *A. icondere.*

4. ***Dactyladenia chevalieri*** (De Wild.) Prance & F. White, *Brittonia* **31**: 484 (1979). Type: Gabon, fl. fr., *Fleury in Chevalier* 26665 (P, lectotype of Prance & White 1979).

Acioa chevalieri De Wild., *Bull. Jard. Bot. État. Brux.* **7**: 213 (1920) – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 19, t. 4 (1978).

Branchlets and lower leaf-surface with pink to grey, slowly caducous, arachnoid indumentum. Inflorescence 8–12 cm long, tomentose. Bracteoles 0.3 cm long, broadly ovate, with 7–9 stipitate glands 0.05 cm long. Upper pedicel (0.2) 0.4–0.6 cm long. Receptacle-tube 0.6–1.2 cm long. Sepals 0.4–0.5 cm long with 7–9 stipitate glands 0.05 cm long. Stamens 20–25, 3 cm long. Drupe 4 cm × 2 cm × 2.5 cm.

Shrubs or trees said to attain a height of 30–35 m. Only known from the margins of lakes on the Lower Ogooué R. in Gabon.

5. ***Dactyladenia cinerea*** (Engl. ex De Wild.) Prance & F. White, *Brittonia* **31**: 484 (1979). Type: Cameroun, fl., *Zenker* 2903 (B, holotype, not destroyed; BR, K, Z).

Acioa cinerea Engl. ex De Wild., *Bull. Jard. Bot. État Brux.* **7**: 211 (1920). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 22, t. 5 (1978).

Branchlets and inflorescence with whitish, slowly caducous, arachnoid tomentum. Inflorescence 8–10 cm long, slender, few-flowered. Bracteoles 0.05 cm long, ovate–deltate, with a clavate apical and *ca.* 6 marginal stipitate glands. Upper pedicel 0.2–0.3 cm long. Receptacle-tube 1–1.5 cm long. Sepals 0.4–0.5 cm long. Stamens *ca.* 20, 2–3 cm long. Fruit unknown.

Shrub. Only known from the type locality. Appears to be closely related to *D. chevalieri*.

6. ***Dactyladenia dewevrei*** (De Wild. & Th. Dur.) Prance & F. White, *Brittonia* 31: 484 (1979). Type: Zaire, fl., *Dewèvre* 743 (BR, holotype).

Acioa dewevrei De Wild & Th. Dur., *Ann. Mus. Congo, Bot.* sér. 2, *Contrib. Fl. Congo* **1** (2): 19 (1900). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 24, t. 6 (1978).

Branchlets yellowish–villous–pubescent, glabrescent. Racemes 10–15 cm long, with numerous flowers crowded near apex. Bracteoles palmatisect with *ca.* 5 (10) stipitate glands each 0.05–0.15 cm long. Upper pedicel 0.3–0.5 cm long. Receptacle-tube 0.6–1 cm long, narrowly obconic, gibbous at the base, slightly pubescent. Sepals 0.4–0.5 cm long, often with marginal, substipitate glands. Stamens *ca.* 15, 2–2.5 cm long. Drupe 5 cm × 3 cm × 2 cm.

Shrub or small tree, sometimes scandent. From Nigeria, East Cameroun and the Central African Republic southwards to Zaire and the Congo Republic. Always in groundwater forest.

7. ***Dactyladenia dichotoma*** (De Wild.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Nigeria, fl., *Talbot* 3048 (BM, holotype).

Acioa dichotoma De Wild., *Bull. Jard. Bot. État Brux.* **7**: 216 (1920).

Branchlets tomentose, glabrescent. Inflorescence 7–12 cm long, entirely covered with greyish tomentum. Bracteoles 0.2–0.3 cm long, terminal, ovate. Upper pedicel 0.2–0.4 cm long. Receptacle-tube 0.7–1.1 cm long, narrowly obconic. Sepals 0.4–0.5 cm long. Stamens 15–20, 2–3 cm long. Fruit unknown.

Only known from the type locality in SE Nigeria.

8. ***Dactyladenia dinklagei*** (Engl.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Liberia, fl., *Dinklage* 1748 (B, holotype, not destroyed; BM, E, W).

Acioa dinklagei Engl., *Bot. Jahrb.* **26**: 381 (1899).

Branchlets tomentose. Inflorescence 5–10 cm long, golden-tomentose. Bracteoles 0.2 cm long, terminal, ovate. Upper pedicel 0.2–0.3 cm long. Receptacle-tube 1.8–2.8 cm long. Sepals 0.6–0.8 cm long, with lateral glands. Stamens 30–35, 3–3.5(5) cm long. Drupe 4.5 cm × 4 cm × 2 cm.

Small spreading tree 9 m high. From Liberia to Ghana. On river banks. Some small-flowered specimens from Ghana resemble *D. dichotoma* and *D. pierrei*.

9. ***Dactyladenia eketensis*** (De Wild.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Nigeria, fl., *Talbot* s.n. (BM, holotype).

Acioa eketensis De Wild., *Bull. Jard. Bot. État Brux.* **7**: 214 (1920) – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 28, t. 7 (1978).

Branchlets sparsely puberulous. Inflorescence 10 cm long. Bracteoles more or less 0.2 cm long, ovate. Receptacle-tube 0.6–0.7 cm long, narrowly obconic. Sepals 0.5–0.6 cm long (sometimes with lateral glands, but only in Gabon). Stamens *ca.* 20, (3.5) 4–4.5 cm long. Fruit unknown.

An imperfectly known species only recorded from SE Nigeria and Gabon.

10. ***Dactyladenia floribunda*** Welw., *Apont. Ann. Conselho Ultram.* **1**: 572 (1859) [1858]. Type: Angola, fl., *Welwitsch* 1289 (LISU, lectotype of Mendes, 1970; BM, COI, K, P).

Acioa floribunda (Welw.) Exell, *J. Bot.* **66**, *Suppl. Polypet.*: 161 (1928). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 30, t. 8 (1978).

Branchlets with dense, persistent, golden tomentum. Racemes 2–6 cm long, congested. Bracteoles 0.2 cm long, subterminal, 5-palmatilobed to palmatipartite with elongate

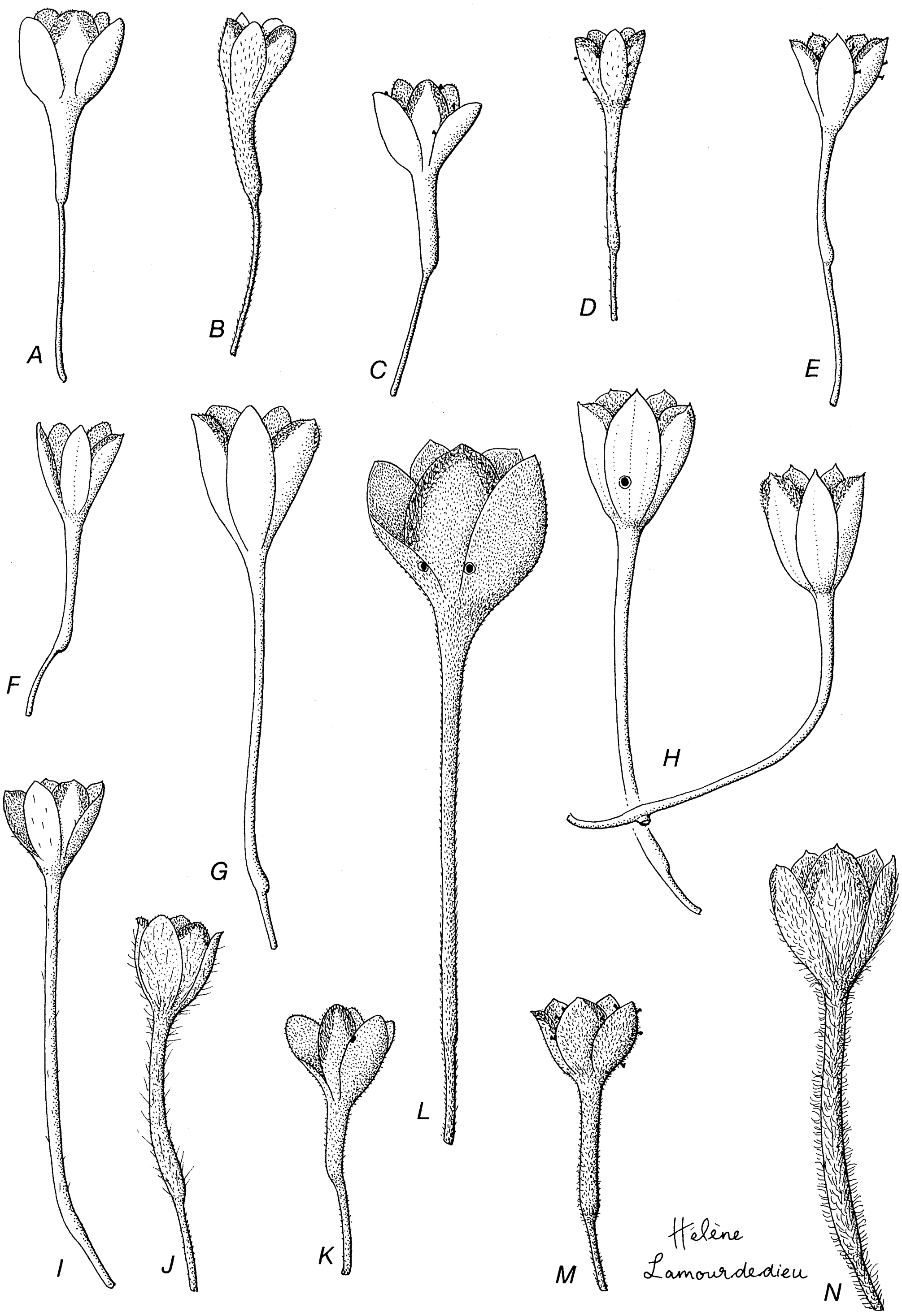


FIGURE 37. Upper pedicel, receptacle tube and sepals in *Dactyladenia* ($\times 2\frac{2}{3}$): A, *D. scabrifolia* (Maclaud s.n.); B, *D. barteri* (De Wilde 2698); C, *D. letestui* (Le Testu 9352); D, *D. dewevrei* (Louis 11162); E, *D. smeathmannii* (Thomas 5502); F, *D. librevillensis* (Klein 550); G, *D. hirsuta* (Chevalier 19738); H, *D. icondere* (Letouzey 9267); I, *D. whytei* (Chillou 1086); J, *D. johnstonei* (Hepper 1927); K, *D. eketensis* (Chevalier 27127); L, *D. pallescens* (Hallé 3827); M, *D. chevalieri* (Fleury-Chevalier 26665); N, *D. staudtii* (Staudt 263).

triangular, glandular lobes. Upper pedicel 0.3 cm long. Receptacle-tube 1.2–1.8 cm long, sometimes sparsely pubescent, distinctly gibbous. Sepals 0.6–0.8 cm long. Stamens (15) 20–25 (30), (3) 3.5–4.5 (6) cm long. Drupe 4 cm × 2.5 cm × 2 cm.

Shrub or tree up to 20 m high. In inland forest. From Cameroun to Zaire (Mayumbe) with outlying populations in Angola (Cuanza Norte). Closely related to *D. icondere*, which, however, is a species of coastal thicket.

11. ***Dactyladenia gilletii*** (De Wild.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Zaire, fl., *Gillet* s.n. (BR, holotype).

Acioa gilletii De Wild., *Ann. Mus. Congo.*, 5, *Ét. Fl. Bas Moyen – Congo*, **1**: 47 (1903).

Branchlets hispid, glabrescent. Racemes 3–5 (10) cm long, glabrous. Bracteoles *ca.* 0.15 cm long, inserted near middle of lower pedicel, palmatisect with 3(5)stipitate glands. Upper pedicel 0.4–0.7 cm long. Receptacle-tube 1.2–2 cm long, glabrous, with slightly gibbous base. Sepals 0.6–0.8 cm long, glabrous. Stamens *ca.* 25, 2.5–3.5 cm long. Drupe 5 cm × 3 cm × 2 cm.

Tree up to 15 m high. In Lower Congo, Zaire (Bas Zaire, Kasai, Forestier central) and Angola (Lunda). In swamp and fringing forest. Differs from *D. dewevrei* in its glabrous inflorescence, longer receptacle-tube and (usually) 3-lobed bracteoles.

12. ***Dactyladenia hirsuta*** (A. Chev. ex De Wild.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Ivory Coast, fl., *Chevalier* 19738 (P, holotype).

Acioa hirsuta A. Chev. ex De Wild., *Bull. Jard. Bot. État. Brux.* **7**: 200 (1920).

Branchlets hirsute. Racemes 2–4 cm long with hispidulous axis. Bracteoles 0.15 cm long, with (3) 5 triangular teeth bearing stipitate glands 0.15 cm long. Upper pedicel 0.1–0.5 cm. Receptacle-tube 1.6–2.2 cm long, glabrous, base gibbous. Sepals 0.6–1 cm long, glabrous. Stamens *ca.* 20, 3.5–4.5 cm long. Fruit unknown.

Only known from the Ivory Coast.

13. ***Dactyladenia icondere*** (Baill.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Gabon, fl., *Griffon de Bellay* 313 (P, lectotype of Prance & F. White, 1979).

Acioa icondere Baill., *Adansonia* **7**: 223 (1867). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 33, t. 9 (1978).

Branchlets with dense golden tomentum. Racemes 12–24 (30) cm long. Bracteoles 0.2–0.5 cm long, palmatipartite to palmatisect with 5 more or less stipitate glands. Upper pedicel 0.2–0.6 cm long. Receptacle-tube 1.6–2.2 cm long, glabrous, gibbous, often glandular. Sepals 0.6–0.8 cm long, glabrous outside, sometimes with a basal gland. Stamens 30–40, 4–4.5 cm long. Drupe 5 cm × 3 cm × 2.5 cm.

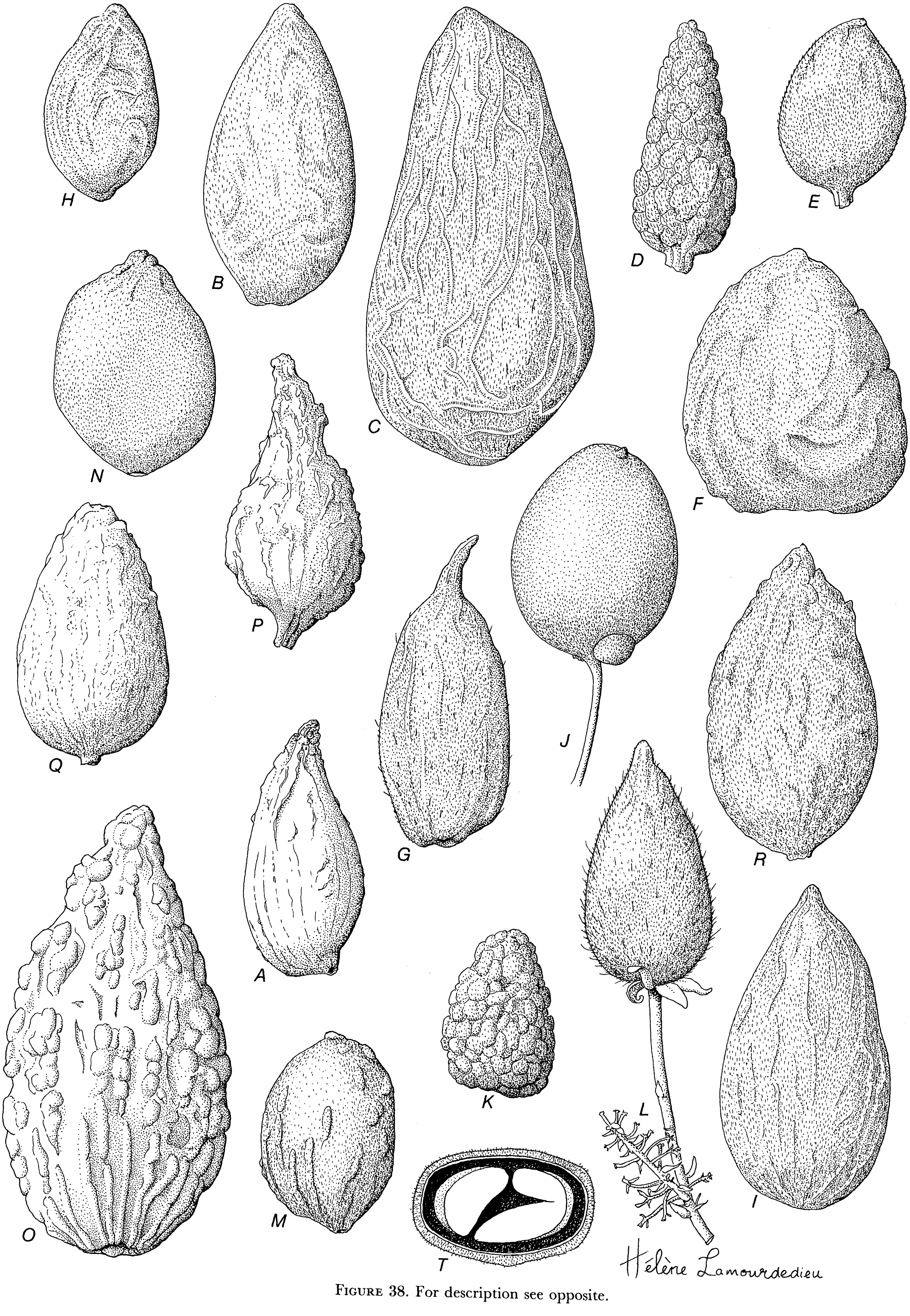
Climbing shrub 5–8 m tall. From Cameroun to Zaire (Mayumbe). Mostly in coastal thicket. Closely related to *D. floribunda*.

14. ***Dactyladenia johnstonei*** (Hoyle) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Cameroun, fl., *Johnstone* 74/31 (K, holotype; FHO).

Acioa johnstonei Hoyle, *Kew Bull.* **1932**: 258 ((1932).

Branchlets hispid with 0.2–0.3 cm long hairs. Inflorescence 10 cm long, hispid and puberulent. Bracts deltate, with *ca.* 3–5, 0.2 cm long, stipitate, proximal glands and shorter glands distally. Bracteoles *ca.* 0.1 cm long, subterminal, broadly deltate, with *ca.* 5–7 marginal, 0.15 cm long, stipitate glands alternating with shorter ones. Upper pedicel 0.4–0.6 cm long. Receptacle-tube 1–1.2 cm long, gibbous. Sepals *ca.* 0.5 cm long. Stamens *ca.* 20, 2.5 cm long. Drupe 3.5–4 cm × 3 cm × 2–2.5 cm.

Shrub or small tree. At edges of upland forest and in riparian forest in grassland between 1000 and 1600 m in Cameroun.



Hélène Lamourdedieu

FIGURE 38. For description see opposite.

15. ***Dactyladenia laevis*** (Pierre ex De Wild.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Gabon, fl. fr., *Klaine* 1890 (P, holotype).

Acioa laevis Pierre ex De Wild., *Bull. Jard. Bot. État Brux.* **7**: 205 (1920). – Letouzey & F.White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 39, t. 11 (1978).

Branchlets with whitish, arachnoid, caducous indumentum. Inflorescence 4–8 cm long, entirely glabrous. Bracteoles 0.05–0.1 cm × 0.15 cm, subreniform, with *ca.* 5 marginal denticulations. Upper pedicel (0.4) 0.5–0.8 cm long. Receptacle-tube (1.2) 1.8–2.6 cm long. Sepals (0.6) 0.8–0.9 cm long. Stamens 20–25, 3–4 cm long. Drupe 2.5 cm × 2 cm × 1.8 cm.

Shrub or small tree up to 20 m high. Only known from the Libreville region in Gabon.

This species differs from all others in its subreniform bracteoles.

16. ***Dactyladenia lehmbachii*** (Engl.) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Cameroun, fl. fr., *Lehmbach* 115 (B, holotype, not destroyed).

Acioa lehmbachii Engl., *Bot. Jahrb.* **26**: 379 (1899) – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 40, t. 12 (1978).

Branchlets with golden-brown pubescence. Inflorescence 3–5 cm long. Bracteoles 0.1–0.15 cm long, ovate-deltate, palmatifid to palmatipartite, with 5–7 substipitate to stipitate glands, each 0.1–0.25 cm long. Upper pedicel 0.3–0.6 cm long. Receptacle-tube 1.2–1.8 cm long, glabrous, gibbous. Sepals 0.6–0.8 cm long, glabrous. Stamens 15–20, 2.5–3 (6) cm long. Drupe up to 6 cm × 4.5 cm × 4 cm.

Tree up to 20 m tall. In SE Nigeria and Cameroun. Closely related to *D. gilletii.*

17. ***Dactyladenia letestui*** (Letouzey) Prance & F. White, *Brittonia* **31**: 485 (1979). Type: Gabon, fl. fr., *Le Testu* 9352 (P, holotype).

Acioa letestui Letouzey, *Adansonia* sér. 2 **16**: 240, t. 5 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 44, t. 13 (1978).

Branchlets glabrous. Inflorescence 3–8 cm long, many-flowered, entirely glabrous. Bracteoles 0.1–0.15 cm long, lanceolate, 5–7-dentate with substipitate glands. Upper pedicel 0.6–1 cm long. Receptacle-tube 0.5–0.6 cm long, more or less gibbous. Sepals 0.4–0.5 cm long, sometimes with glandular margins. Stamens *ca.* 15, 2–2.5 cm long. Drupe up to 3 cm × 2.5 cm × 1.7 cm.

Tree up to 25 m tall. In swamp forest in Cameroun and Equatorial Guinea. Closely related to *D. barteri* and *D. scabrifolia*, differing in its globose fruit.

18. ***Dactyladenia librevillensis*** (Letouzey) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Gabon, fl., *Klein* 55 (P, holotype; B).

Acioa librevillensis Letouzey, *Adansonia* sér. 2 **16**: 238, t. 4 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 48, t. 14 (1978).

Branchlets sparsely hispidulous, glabrescent. Inflorescence 3–5 cm long. Bracteoles 0.1–0.2 cm long, palmatilobed to palmatipartite, with 5 stipitate glands. Upper pedicel 0.2–0.6 cm long. Receptacle-tube 0.7–1 cm long, glabrous, gibbous. Sepals 0.4–0.5 cm long, glabrous outside. Stamens *ca.* 15, 2–2.5 cm long. Fruit unknown.

FIGURE 38. Drupes in *Dactyladenia* (× 1): A, *D. barteri* (Aubréville 375); B, *D. bellayana* (Klaine 29); C, *D. campestris* (Klaine 12); D, *D. chevalieri* (Chevalier 188); E, *D. dewevrei* (immature, Letouzey 4917); F, *D. dinklagei* (Aubréville 19); G, *D. floribunda* (Gossweiler 719); H, *D. gilletii* (immature, Louis 10674); I, *D. icondere* (Zenker 1949); J, *D. johnstonei* (Letouzey 14044); K, *D. laevis* (Klaine 1890); L, *D. lehmbachii* (Letouzey 14101); M, *D. letestui* (Le Testu 9352); N, *D. pallescens* (Letouzey 13689); O, *D. pierrei* (Klaine 2033); P. *D. scabrifolia* (Chevalier 12712); Q, *D. smeathmannii* (Smeathmann in Herb. Juss. 15895); R, *D. whytei* (Jacques-Félix 2197); S, *D. lehmbachii* (Letouzey 14101).

Tree. Only known from Gabon. Closely related to *D. gilletii*, and differing chiefly in its less deeply divided bracteoles and smaller flowers with few stamens.

19. ***Dactyladenia lujae*** (De Wild.) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Zaire, fl., *Luja* 38 (BR, lectotype of Prance & White 1979).

Acioa lujae De Wild., *Bull. Jard. Bot. État. Brux.* **7**: 209 (1920).

Branchlets pubescent. Inflorescence 5–10 cm long, pale grey–tomentose. Bracteoles 0.2–0.3 cm long, entire or denticulate–glandular, sometimes tricuspidate. Upper pedicel 0.1–0.3 cm long. Receptacle-tube 0.8–1.5 cm long. Sepals 0.5–0.8 cm long. Stamens 25–35, 2–3 cm long. Drupe 4.5 cm × 3 cm × 2.5 cm.

Tree up to 8 m high. Central African Republic, Congo, Zaire and Angola. Closely related to and perhaps only subspecifically distinct from *D. pallescens*.

20. ***Dactyladenia mannii*** (Oliv.) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Bioko (Fernando Po), fl., *Mann* 1427 (K, holotype; P).

Griffonia mannii Oliv., *F.T.A.* **2**: 382 (1871).

Acioa mannii (Oliv.) Engl., *Bot. Jahrb.* **26**: 381 (1899). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 50, t. 15 (1978).

Branchlets with caducous, whitish, arachnoid indumentum. Inflorescence 8–12 cm long, puberulous. Bracteoles 0.1 cm long, ovate, acute, sometimes denticulate. Upper pedicel 0.2–0.8 cm long. Receptacle-tube 1.4–2 cm long, gibbous. Sepals 0.6–0.7 cm long, sometimes with a lateral basal gland. Stamens *ca.* 30, 3–4 (5) cm long. Fruit unknown.

Climbing shrub 4–6 m high. Only known from Bioko and the vicinity of Mount Cameroun.

21. ***Dactyladenia pallescens*** (Baill.) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Gabon, fl., *Griffon du Bellay* 261 (P, holotype).

Acioa pallescens Baill. *Adansonia* **7**: 224 (1867). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 52, t. 16 (1978).

Branchlets pubescent, glabrescent. Inflorescence 8–15 (40) cm long, robust, pale grey–tomentose. Bracteoles 0.2–0.3 cm long, ovate, denticulate–glandular or tricuspidate. Upper pedicel 0.2–0.4 cm long. Receptacle-tube 1.8–3.6 cm long. Sepals 0.8–1.0 cm, often with a lateral basal gland. Stamens 60–75, 4–6 cm long. Drupe 4 cm × 3 cm × 2.5 cm.

Shrub, sometimes multiple-stemmed, 5–8 m high. Nigeria to Zaire (Mayumbe). Riparian and secondary forest. Closely related to *D. lujae* and *D. sapinii*.

22. ***Dactyladenia pierrei*** (De Wild.) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Gabon, fl., *Klaine* 196 in *Pierre* 6395 (P, lectotype of Prance & White, 1979; E, K).

Acioa pierrei De Wild., *Bull. Jard. Bot. État Brux.* **7**: 212 (1920). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 55, t. 17 (1978).

Branchlets with dense, silvery, long-persistent, arachnoid tomentum. Inflorescence 5–20 cm long, lax, greyish–tomentellous. Bracteoles 0.2 cm long, ovate, acute, sometimes with lateral glands. Receptacle-tube 1.2–1.8 cm long. Sepals 0.6–0.8 cm, with lateral glands. Stamens 20–30, 2–4 cm long. Drupe 6.5 (7.5) cm × 4 cm × 3 cm.

Shrub up to 8 m high. Only known from Gabon.

23. ***Dactyladenia sapinii*** (De Wild.) Prance & F. White *Brittonia* **31**: 486 (1979). Type: Zaire, fl., *Sapin* s.n. (BR, holotype).

Acioa sapinii De Wild., *Bull. Jard. Bot. État Brux.* **4**: 80 (1914).

In riparian forest in Zaire (Kasai). Closely related to *D. pallescens*, and differing chiefly in its hairy leaf-undersurface, longer pedicels, smaller flowers and subreniform bracteoles.

24. ***Dactyladenia scabrifolia*** (Hua) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Guinea, fl., *Miquel* 24 (P, holotype).

Acioa scabrifolia Hua, *Bull. Mus. Nat. Hist. Nat. Paris* **3**: 328 (1897).

Branchlets glabrous. Inflorescence 6–10 cm long, axis hispidulous. Bracteoles 0.15 cm long, ovate–lanceolate, glandular–denticulate. Upper pedicel 0.6–1.4 cm long. Receptacle-tube 0.4–0.8 cm long, narrowly obconic, gibbous, glabrous. Sepals 0.4–0.6 cm long, glabrous. Stamens *ca.* 20, 1.5–2.5 cm long. Drupe 4 cm × 3 cm × 2 cm, glabrous.

In riparian forest and forest regrowth. From Guinea to Ghana. Closely related to *A. barteri* but differing in its stouter peduncle and pedicels, glabrous receptacle-tube and scabrid leaves.

25. ***Dactyladenia smeathmannii*** (Baill.) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Sierra Leone, fr., *Smeathmann* s.n. (P, in Herb. Juss. no. 15895, holotype).

Acioa smeathmannii Baill., *Adansonia* **10**: 244 (1872).

Branchlets hispid. Inflorescence 10–12 cm long; axis hispidulous. Bracteoles 0.3 cm long, palmatisect, with 5–7 stipitate glands. Upper pedicel 0.8 cm long. Receptacle-tube 0.8 cm long, glabrous, gibbous. Sepals 0.4–0.6 cm long, glabrous, with marginal stipitate glands. Stamens *ca.* 15, (1.5) 2.5–3 cm long. Drupe 4 cm × 2.5 cm × 2 cm.

Shrub. Only known from Sierra Leone. Differs from *D. johnstonei* in its simple inflorescence and glabrous receptacle and sepals.

26. ***Dactyladenia staudtii*** (Engl.) Prance & F. White, *Brittonia* **31**: 486 (1979). Type: Cameroun, fr. *Staudt* 263 (B, holotype, destroyed; P, lectotype of Prance & White, 1979, K).

Acioa staudtii Engl., *Bot. Jahrb.* **26**: 379 (1899). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 58, t. 18 (1978).

Branchlets with dense, long-persistent, yellowish-grey, villous tomentum. Inflorescence 3–4.5 cm long, few-flowered, villous–tomentose. Bracteoles 0.1–0.15 cm long, deltate–acuminate, with 2–4 stipitate glands. Upper pedicel 0.2–0.4 cm long, not very distinct. Receptacle-tube 1.2–2 cm long. Sepals 0.6–0.8 cm long. Stamens 15–20, (3) 4–5 cm long. Fruit unknown.

Shrub or small tree up to 15 m high. From SE Nigeria to Gabon.

27. ***Dactyladenia whytei*** (Stapf) Prance & F. White, Brittonia, **31**: 486 (1979). Type: Liberia, fl., *Whyte* s.n. (K, holotype).

Branchlets hispid to glabrescent. Inflorescence 1–3 cm long, dense; axis hispidulous. Bracteoles 0.15 cm long, ovate, acute. Upper pedicel 0.2–0.8 cm long. Receptacle-tube 1.6–2.2 cm long, gibbous, glabrous or hispidulous. Sepals 0.4–0.6 cm long, glabrous or sparsely hispidulous. Stamens *ca.* 30, 3–5 cm long. Drupe 5 cm × 3 cm × 2.5 cm.

Shrub or small tree up to 5 m high. Guinea, Sierra Leone and Liberia. In riparian forest and forest regrowth. This species is distinct in its short, congested, subcapitate racemes with the pedicels concealed by foliaceous bracts.

15. *Hirtella* (*figure* 39)

(from the Latin, *hirtus* = hairy)

Hirtella L. [*Hort. Cliff.*: 17 (1738)], *Sp. Pl.*: 34 (1753); *Gen. Pl.* ed. 5: 20 (1754). – DC., *Prodr.* **2**: 528 (1825). – Mart. & Zucc., *Abh. Akad. München* **1**: 372 (1832). – Zuccarini, *Flora*, **15** (Beibl. 2): 78 (1832). – Hook. f., in Benth. & Hook. f., *Gen. Pl.* **1**: 608 (1865). – Focke, in Engl. & Prantl, *Nat. Pflanzenf.* **3** (3): 59, t. 31–32 (1891). – Hutch., *Gen. Fl. Pl.* **1**: 193

(1964). – Prance, *Fl. Neotr.* **9**: 259, t. 43–57 (1972). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 276 (1976); *Distr. Pl. Afr.* **10**: 287–292 (1976); *Fl. Zamb.* **4**: 44, t. 9 fig. b (1978).

Tachibota Aubl., *Hist. Pl. Guiane Fr.* **1**: 287 t. 112 (1775).

Causea Scop., *Introd.*, n. 928, 210 (1777).

Salmasia Schreb., *Linn. Gen. Pl.* ed. 8. **1**: 201 (1798), nom.illegit.

Cosmibuena Ruiz & Pav., *Prodr. Fl. Peruv.*: 10 t. 2 (1794); non *Cosmibuena* Ruiz & Pav., *Fl. Peruv. Chil.* **3**: 2 (1802), t. 198 (1789).

Thelira Thou., *Gen. Nov. Madag.*: 21 (1806). – DC., *Prodr.* **2**: 527 (1825) as '*Thelyra*'.

Brya Vell., *Fl. Flum.*: 146 (1825) and **4**, t. 1 (1835) non *Brya* P. Br. (1756, Leguminosae).

Sphenista Rafin., *Sylva Tellur.*: 90 (1838).

Zamzela Rafin., *Sylva Tellur.*: 90 (1838).

Trees and shrubs. *Leaves* sometimes with 2 large, bulbous, myrmecophilous inflations at base of lamina, otherwise lacking large basal glands but often with many small, submarginal or scattered, discoid glands; petiole eglandular; lower surface of lamina glabrous or with a few strigose or strigulose hairs; stipules lateral, often subulate or filiform, subpersistent. *Inflorescence* usually a lax raceme with patent flowers, or an elongate, narrow, lax thyrse with patent lateral branches, the latter often bearing several sterile bracts and ending in a single flower or a few cymosely arranged flowers, more rarely a corymb, or a very short raceme, or a dense thyrse, or a complex cyme. Pedicels usually longer than and often much longer than the receptacle-tube. Bracts and bracteoles not enclosing the flower-buds in small groups, often with stalked or sessile glands. *Flowers* bisexual, slightly zygomorphic. Receptacle-tube subcampanulate to narrowly cylindric, slightly gibbous, usually shorter than the sepals, usually glabrous inside except near the throat. Sepals 5, subequal, usually spreading or reflexed, acute, often with sessile or shortly stalked glands on the margin. Petals 5, shorter than the sepals. Stamens 3–9; filaments usually coiled in bud, rarely laxly undulate with a single undulation, inserted on posterior rim of faucal annulus, far-exserted, usually much longer than the combined length of calyx and receptacle-tube. Staminodes short, filiform. Ovary monocarpellary, 1-locular, usually inserted at mouth of receptacle-tube; style filiform, far-exserted, very shortly 3-lobed at apex. *Drupe* usually less than 2.2 cm long, with exiguous mesocarp and smooth, thin, hard, non-granular endocarp with 4–7 longitudinal shallow channels which represent the lines of weakness that permit the seedling to escape.

Germination: cryptocotylar; cataphylls *ca.* 5, minute; eophylls alternate, with small, subulate, persistent stipules (Duke 1965, p. 320, t. 4 fig. 36; *Prance* Blastogeny colln. no. 9. *H. duckei*).

Type species: *H. americana* L.

Distribution and ecology: 103 species, of which 102 are confined to tropical and subtropical America. The remaining species, *H. zanzibarica* (see below) occurs in East Africa and Madagascar.

Most American species of *Hirtella* are small trees or treelets and only a few species, such as *H. obidensis* and *H. guyanensis*, contribute to the forest canopy, in contrast to *Couepia*, *Licania* and *Parinari*.

Hirtella occurs in a wider range of vegetation types than the other American genera of Chrysobalanaceae, and extends further south, to 30° S, where *H. hebeclada* is a constituent of the forests of Rio Grande do Sul. It is also the only genus other than *Chrysobalanus* to occur in the Greater Antilles, where it is represented by two widespread species, *H. americana* and *H. triandra*, and in Puerto Rico by the endemic *H. rugosa*.

FIGURE 39. *Hirtella glandulosa* (Irwin *et al.* 16435, 16745): A, habit (×½); B, part of inflorescence (×2); C, half flower (×10). *H. martiana*: D, flower bud (×2, Irwin *et al.* 18039). *H. ciliata*: E, fruit (×1, Prance & Silva 58456).

As in other genera of Chrysobalanaceae, there are few species in Mexico and Central America. Three South American species, *H. americana*, *H. racemosa* and *H. triandra*, extend as far north as Mexico, and *H. tubiflora* is found on the Pacific coast of Colombia and Costa Rica. There are also three endemic species in Central America, including Panama.

In South America the majority of species occur in the rainforests of the Hylaea, but the genus is well represented elsewhere. Thus, two species, *H. enneandra* and *H. pauciflora*, occur in the Pacific coastal forests of Colombia and Ecuador. In the same region *H. carbonaria* occupies the inner margin of mangrove swamps. On the other side of the continent about half-a-dozen species, including *H. bahiensis* and *H. glaziovii*, occur in the coastal forests that extend from Bahia to Rio de Janeiro. *H. mutisii* is found in the forests of central and southern Colombia, and *H. lightioides* in Bolivia. Four species, including *H. cowanii* and *H. orbicularis*, which occur above 1500 m in the Guayana Highlands, are montane.

A few species, including *H. araneosa*, occur in scrubby formations on sterile white fluviatile sands. *H. angustissima* is a rheophyte.

Eleven species are found in savanna and in scrub forest at savanna margins. They include *H. dorvalii*, the only non-forest myrmecophilous species, and *H. paniculata*, which is abundant in Guyana and also occurs in Trinidad and St. Vincent. Two species, *H. ciliata* and *H. gracilipes*, occur in the cerrados of the planalto of Central Brazil. Three other species, *H. hoehnei*, *H. glandulosa* and *H. martiana*, are characteristic of gallery forest in the same region.

Reproductive biology: the structure and colour of the flower in *Hirtella* is remarkably uniform. The filaments, in the great majority of species, are red, at least distally, and are often white towards their base. Only very rarely are they white throughout. Nectar is produced in the narrow receptacle-tube, which has a very narrow entrance. If pollination is effected by a visitor that only takes nectar, the latter must have a proboscis at least 10–30 mm long; that is the distance, in different species, between the nectar supply and the anthers and stigma. The predominantly reddish coloration of the flowers and their structure suggest that butterflies are the legitimate pollinators, and butterflies have been observed visiting the flowers of *Hirtella elongata* in Peru and of *H. racemosa* var. *hexandra* in Amazonian Brazil (G.T.P., personal observations).

In *H. elongata* the young inflorescences are soft and green, and the lateral branches are short with few bracts. The older inflorescences are hard and woody with longer laterals and many bracts. It is clear that growth and flowering continues over an extended period. Few flowers, however, set fruit. In this and other species such as *H. glandulosa* it is unusual to find more than one fruit developing on an inflorescence. Flowers that fail to set are shed after active meristematic activity that leads to a well-defined articulation.

The flowers of *H. racemosa* (G.T.P., personal observations) are also visited by small bees, which use the stamens as a landing platform before probing into the hollow receptacle after nectar. Because the bees examined were carrying pollen on their legs, it is possible that they also collect pollen of this species and in so doing may effect pollination. But if this is so, pollination in *Hirtella* by small bees is likely to be a secondary phenomenon. It may be significant that, whereas the petals in all other species of *Hirtella* for which information is available are white or pink, in *H. racemosa* they are said to be blue and the filaments are purple. This might suggest that *H. racemosa* has become secondarily pollinated by small bees, or is pollinated by both bees and butterflies.

The small size and the structure of the fruit suggest dispersal by birds. This has been confirmed by direct observation for *H. racemosa* (Macedo 1977; Macedo & Prance 1978).

Taxonomic history and relationships: although *Hirtella* does not appear to be very closely related to other genera of Chrysobalanaceae, it has been confused with some. Thus, early in the nineteenth century it was often united with *Couepia*, which was erroneously thought to be synonymous with *Moquilea* (see §6*b*). Most species of the African and Malagasy genus *Magnistipula* have been placed in *Hirtella* at one time or another. This is discussed under *Magnistipula*.

The single old-world species of *Hirtella* was originally described as *Thelira* by Du Petit-Thouars in 1806, but no species was assigned to it. *Thelira* was maintained as a genus by several authors during the first half of the nineteenth century. In the *Genera plantarum* (1865) J. D. Hooker, who had seen no material, treated it as an uncertain genus related to *Parinari*, and in the eighth edition of Willis (1973) it is stated to be a synonym of *Parinari*, although Baillon as long ago as 1868 had shown that it is a *Hirtella*. Baillon's manuscript name, *H. thouarsiana*, based on the type of *Thelira*, was published in 1886 by Lanessan. In the meantime, however, the same species had been described from Mafia Island off the coast of East Africa as *H. zanzibarica* Oliv. (1876). *H. zanzibarica* appears to occupy an isolated position in the genus, but in some respects is very similar to the recently described South American species, *H. bahiensis* Prance.

The non-American species of Hirtella

1. ***Hirtella zanzibarica*** Oliv., in Hook. *Ic. Pl.* 12: 81, t. 1193 (1876). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 276 (1976); *Distr. Pl. Afr.* **10**: 287–292 (1976); *Fl. Zamb.* **4**: 44, t. 9 fig. b (1978). Type: Tanzania, Mafia Isl., fl., *Kirk* (K, holotype).

Evergreen tree up to 25 m tall, but sometimes flowering as a shrub 1–5 m tall. Subsp. *zanzibarica* is widespread in various types of forest in East Africa from Kenya to Mozambique. Four other subspecies occur in Madagascar.

16. *Kostermanthus* (*figures* 40 *and* 41)

(after Dr A. J. G. H. Kostermans, student of Indo-Pacific botany)

Kostermanthus Prance, *Brittonia* **31**: 91 (1979).

Parinari auct. non Aubl. quoad *P. heteropetala* Scortech. ex King et *P. myriandra* Merr. tantum.

Acioa auct. non Aubl., sensu Kostermans, *Reinwardtia* **7**: 9 (1965).

Large trees; ultimate shoots not divaricate. *Leaves* with a few, submarginal, discoid glands; petiole eglandular; lower surface of lamina glabrous, with minute papillae on veins giving a beaded appearance; stipules small, caducous. *Inflorescence* an unbranched or little-branched terminal or axillary raceme which bears shortly stalked, congested cymules proximally and singly inserted flowers distally. Bracts and bracteoles small, suborbicular, persistent, eglandular, not enclosing the young flowers in groups. *Flowers* bisexual, strongly zygomorphic, subsessile. Receptacle-tube much shorter than the sepals, broadly obconic, asymmetric, hollow inside, hairy throughout, but throat not blocked by long retrorse hairs. Sepals 5, markedly unequal, suborbicular to lingulate, deeply concave, strongly imbricate. Petals 5, minutely puberulous outside, glabrous inside, very unequal in shape and size, the 2 posterior larger than the others, markedly unguiculate and enclosing the stamens in the bud. Stamens 30–75, posterior; filaments united for half to three quarters of their length; staminodes 5–8, inserted opposite the stamens on the free margin of the faucal annulus. Ovary of 1 (2–3) carpels, inserted laterally at the mouth of the receptacle-tube; carpels unilocular. *Drupe* hard; epicarp glabrous,

FIGURE 40. *Kostermanthus heteropetalus*: A, habit ($\times\frac{2}{3}$, b.b. 13841); B, fruit ($\times\frac{2}{3}$, Elmer 21848).

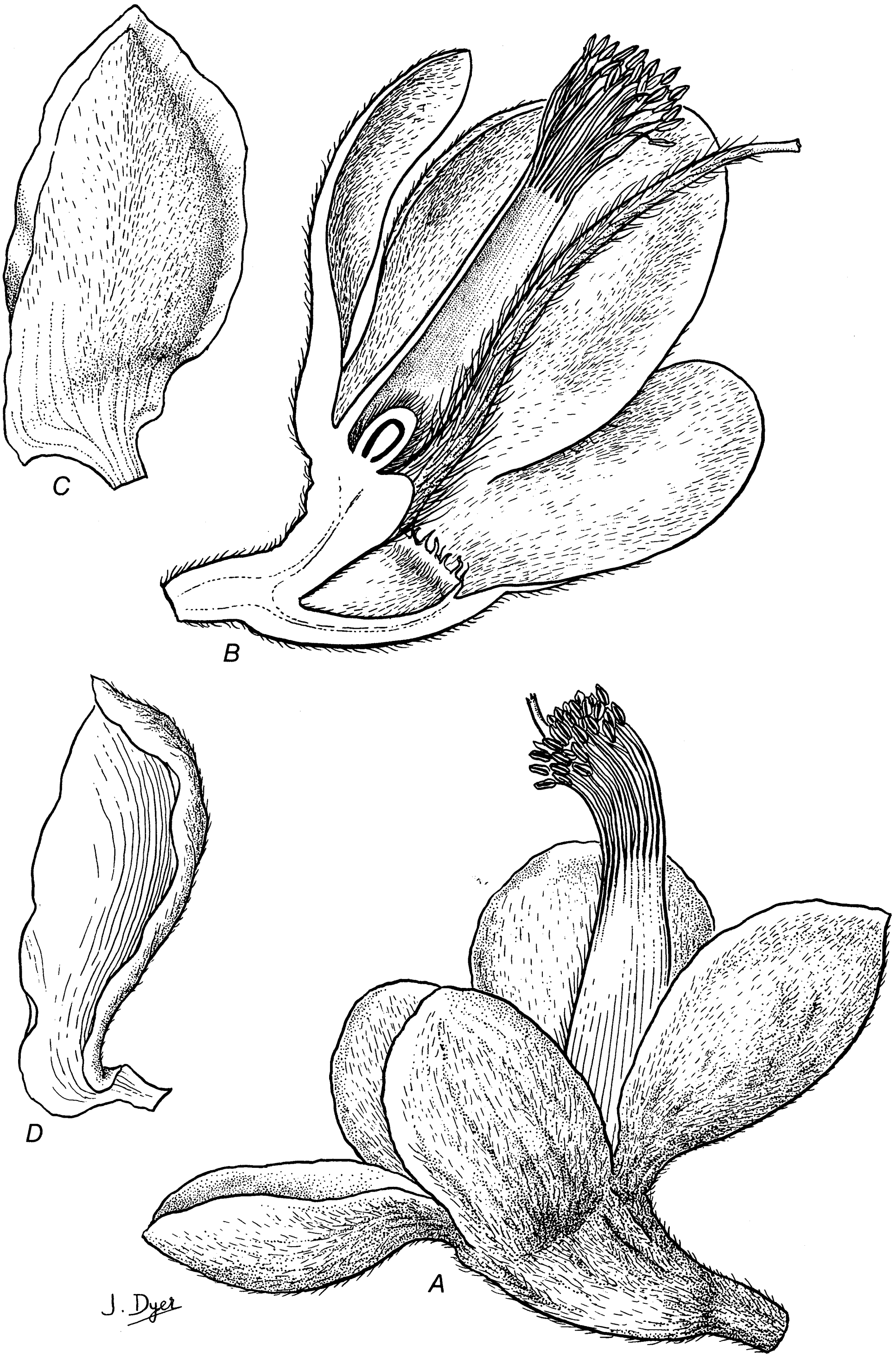


FIGURE 41. *Kostermanthus heteropetalus*: flower, half flower and petal (× 6⅔, Puasa & Enggoh 1087).

verrucose; endocarp hard, thick, glabrous inside, breaking irregularly on germination. Cotyledons slightly ruminate.

Type species: *K. heteropetalus* (Scortech. ex King) Prance.

Distribution and ecology: one, or possibly two or more, species in tropical Asia.

Reproductive biology: nothing appears to have been published.

Taxonomic history and relationships: the type species was originally placed in *Parinari*, although the two genera share no important character, not even the bilocular ovary of the latter (see §6*d*). Kostermans (1965*a*) transferred it to *Acioa*, a genus otherwise only known from tropical America, but at that time thought also to occur in Africa (see *Dactyladenia*), and described two new species, *A. malayana* and *A. percoriacea*, the latter based on a single sterile gathering. The former is based on a single very incomplete gathering and may not be congeneric with *K. heteropetalus*.

Apart from the possession of a staminal ligule, *Acioa* and *Kostermanthus* have few characters in common. The flowers of *Kostermanthus* are unique in the family in possessing a very short receptacle-tube combined with a ligulate androecium enclosed by a pair of long-unguiculate petals.

Conspectus of the species

1. ***Kostermanthus heteropetalus*** (Scortech. ex King) Prance, *Brittonia* **31**: 91, t. 6 (1979). Type: Malay Peninsula, fl., *Scortechini* 2040 (SING, holotype; BO, CGE).

Tree up to 35 m high. Malay Peninsula, Sumatra, Philippines, Borneo and Celebes. From sea level to 500 m altitude.

2. ***Kostermanthus malayanus*** (Kostermans) Prance, *Brittonia* **31**: 94 (1979). Type: Malay Peninsula, *Haniff* SFN 21059 (SING, holotype; K).

Tree 8–10 m high. Only known from the type specimen.

Until more material is available the relationships of this species will remain uncertain. Although it has a staminal ligule, the inflorescence, bracts and receptacle-tube resemble those of *Atuna*. The Kew isotype lacks petals, and the fruit, which would also provide crucial evidence, is unknown.

17. *Magnistipula* (*figures* 42–44)
(Latin: 'large stipule')

Magnistipula Engl., *Bot. Jahrb.* **36**: 226 (1905). – Hauman, *Bull. Jard. Bot. État Brux.* **21**: 173 (1951). – R. Graham, *Kew Bull.* **1957**: 230 (1957); *F.T.E.A.*, Rosaceae: 55 (1960). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 281 (1976); *Distr. Pl. Afr.* **10**: 294–314 (1976); *Fl. Zamb.* **4**: 45, t. 12 (1978). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 71, t. 21–28 (1978).

Hirtella subgenus *Afrohirtella* Hauman, *Bull. Jard. Bot. État Brux.* **21**: 178 (1951).

Hirtella auct. non L.; A. Chev., *Bull. Mus Nat. Hist. Nat. Paris* sér. 2 **3**: 192 (1931). – Hauman, *F.C.B.* **3**: 37 (1952). – Keay, *F.W.T.A.* ed. 2 **1**: 430 (1958).

Trees, shrubs or geoxylic suffrutices. *Leaves* usually with several small glands towards base of lamina and fewer towards the apex, rarely with 2 large glands near the base, or (*M. bimarsupiata*) with a pair of swollen pouches at base of lamina, or (*M. tessmanii*) 2–4 small glands on the decurrent base of lamina; petiole eglandular; lower surface of lamina glabrous or with a few strigose or setulose hairs; stipules free and lateral, and then subulate or narrowly deltate to foliaceous, or (subgenus *Tolmiella*) fused and intrapetiolar. *Inflorescence* a simple or branched raceme of cymules or of sessile glomerules, sometimes extremely contracted and racemoid, rarely a short simple raceme. Bracts and bracteoles not enclosing flower-buds, sometimes eglandular, in some species with 1 or 2 pairs of sessile glands, and in *M. glaberrima* with *ca.* 10 shortly stipitate, marginal glands. *Flowers* bisexual, distinctly zygomorphic, usually sigmoid in bud. Receptacle-tube very variable in shape and size, nearly always curved, or gibbous at the base, or both, very rarely turbinate or subcampanulate and neither curved nor gibbous (only in subgenus *Tolmiella*); distinctly oblique at the throat, sometimes markedly so; throat blocked by long retrorse hairs (except in *Tolmiella*). Sepals 5, unequal, acute (except in *M. tamenaka*). Petals 5, longer than the sepals, persistent or caducous. Stamens 5–9, usually 7; filaments white, bent or curved through at least 90° at anthesis, scarcely longer than the sepals, inserted opposite the posterior sepal, flattened and expanded towards the base and united for at least one third of length; staminodes very variable in development and configuration, more or less completely united to form an elongate tongue-shape ligule, or more or less completely united to form a short denticulate ligule, or partly united to form a comb-shaped ligule or partly united in two groups of 3 with 2 others completely free. Ovary monocarpellary, 1-locular (2-locular in subgenus *Pellegriniella*); inserted at or just below mouth of receptacle-tube. Style arcuate; scarcely longer than the sepals, glabrous or hairy in lower half. *Drupe* fleshy; endocarp densely hairy inside, thick, hard and woody in subgenus *Pelegriniella* and *Tolmiella*, otherwise thin and crustaceous or fibrous.

Germination: cryptocotylar; cataphylls absent; eophylls opposite or in fours; stipules subulate, persistent.

Type species: *M. conrauana* Engl.

Distribution and ecology: 9 species in tropical Africa and 2 in Madagascar. The latter occur in rainforest on the wetter eastern half of the island. Eight of the African species occur in the Guineo-Congolian region, and 7 of them are confined to the relatively narrow band of wetter coastal forests in the Upper and Lower Guinea subcentres of endemism (White 1978*b*, 1979*b*, 1983*a*, *b*), whereas one, *M. butayei*, also extends throughout Congolia and far beyond. The remaining species, *M. sapinii*, is a rhizomatous geoxylic suffrutex confined to Kalahari Sand in the heart of the Zambezian region (White 1976*c*).

Reproductive biology: nothing, it appears, has been published. The filaments are inserted on one side of the flower opposite to the odd sepal and are flexed or curved through *ca.* 90°, as is the style, so that the anthers and the stigma are situated immediately above the entrance to the receptacle-tube. In *M. zenkeri*, *M. conrauana* and *M. cuneatifolia* they lie just above the tongue-shaped staminodial ligule, which probably guides the visiting insect's proboscis into the receptacle-tube, the entrance to which is rather narrow. The length of the receptacle-tube in these species suggests pollination by Lepidoptera.

In all other species the receptacle-tube is shorter and the entrance is much wider; the staminodes do not seem to form a 'proboscis guide'. In all species (except *M. tamenaka*) the throat is blocked by a dense mat of hairs. According to one collector (*Semsei* no. 120) the flowers of *M. butayei* subsp. *bangweolensis* are much visited by bees and fireflies.

In *M. zenkeri* (syn. *Hirtella fleuryana*) many flowers fall precociously, and leave in their place a small, pedicellate, orbicular gland (Chevalier 1931). The bracts also have two pairs of sessile glands. The inflorescences swarm with small black ants, which obtain nectar from these extrafloral nectaries. Access to the floral nectar is prevented by the hairs which block the throat to the receptacle-tube.

Taxonomic history and relationships: widely divergent views have been expressed on the

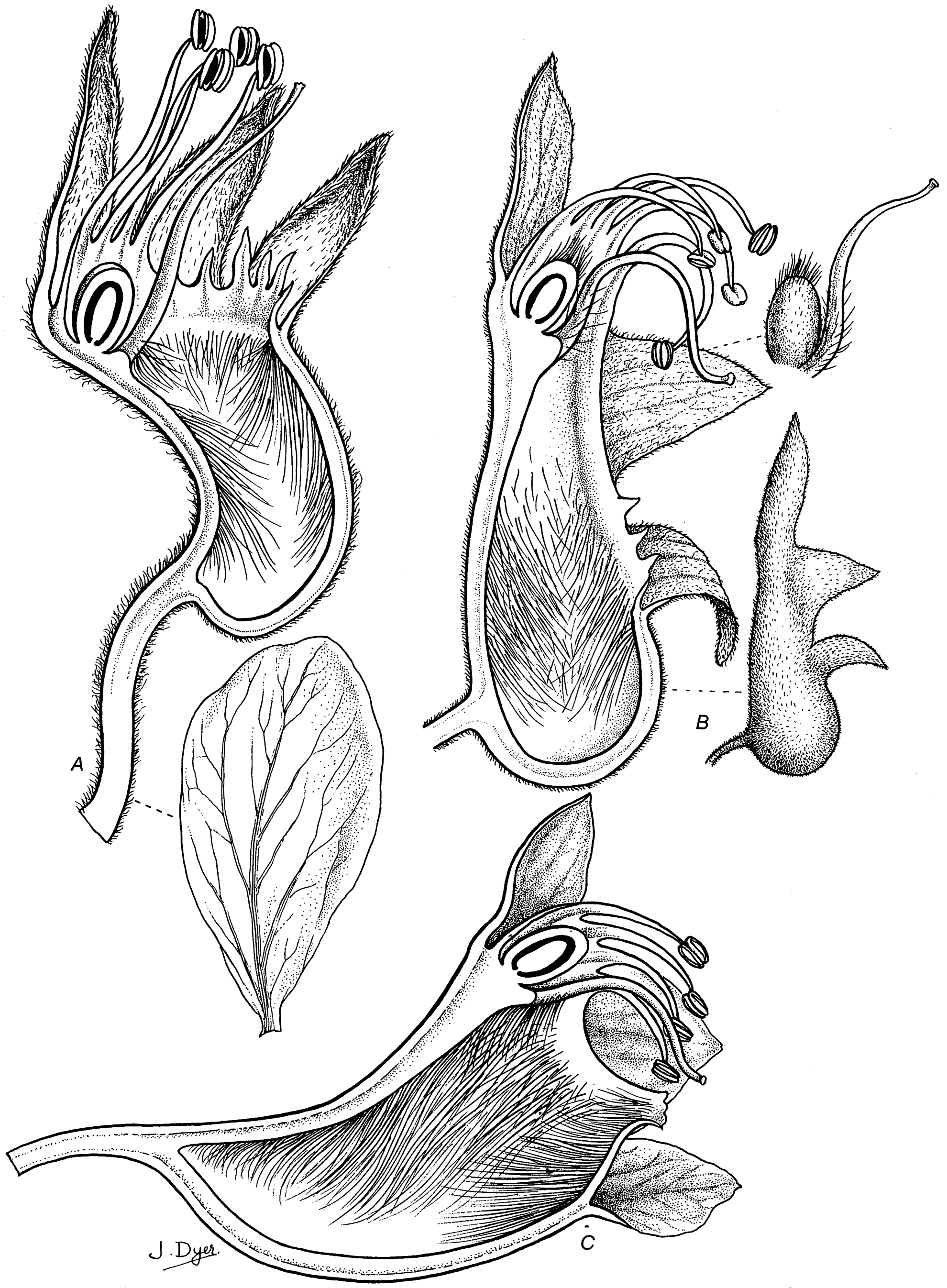


FIGURE 42. *Magnistipula butayei* subsp. *bangweolensis*: A, half flower and petal (×10, Hoyle 1274); *M. cupheiflora*: B, half flower (×10) and calyx (×5), both from Thomas 118; *M. conrauana*: C, half flower (×7½, Conrau 65).

relationships between *Magnistipula* and *Hirtella*, and on the circumscription of the former when it is kept apart. *Magnistipula* has also been confused with *Parinari* (see §6*c*).

Magnistipula, based on *M. conrauana* and *M. zenkeri*, was described by Engler in 1905, who thought it was unique in Chrysobalanaceae in having large, foliaceous, intrapetiolar stipules, a deep, obliquely campanulate receptacle-tube, which is ventricose on the posterior side, a crenulate appendage arising from the rim of the receptacle-tube, and in having only 6–7 stamens, united in their lower half. In fact the stipules are laterally inserted.

In specimens of *M. zenkeri* from the type locality the stipules vary considerably in development from 0.6 cm × 0.2 cm to 4 cm × 4 cm; sometimes they are bladdery and surround the internode. Hauman (1951, p. 173) suggests that the large stipules are abnormal. They are possibly ant-shelters, but this requires confirmation. *Hirtella fleuryana* (a synonym of *M. zenkeri*) is said to be inhabited by ants (see above). According to Chevalier (1931, p. 192) the stipules of *H. fleuryana* are small and caducous, but just beneath some of the inflorescences normal leaves are replaced by large stipules up to 5 cm long and 3 cm wide.

Additional species of *Magnistipula* were described by De Wildeman (*M. butayei*, 1908; *M. sapinii*, 1911), Engler (*M. glaberrima*, 1913), and Mildbraed (*M. cupheiflora*, 1921). Of these, only *M. glaberrima* has foliaceous stipules, and they are rather small. All four species differ from the original members of *Magnistipula* in having smaller flowers with a gibbous base to the receptacle-tube, and a comb-like staminodial appendage. Mildbraed pointed out that *M. cupheiflora* differs somewhat in floral structure from Engler's three species but did not consider the differences sufficient to justify generic rank.

When Chevalier described *Hirtella fleuryana* in 1931 he stated that *Magnistipula* is not distinct, and transferred all its previously described species to *Hirtella*, except for *M. butayei*, which he apparently overlooked. Chevalier does not appear to have made a critical comparison of the flowers and fruits of *Hirtella* and *Magnistipula*; he seems to have attached more importance to the fact that both genera are myrmecophilous. At the time when Chevalier wrote, only two species occurring on the African mainland had previously been placed in *Hirtella*: *H. zanzibarica* Oliv. and *H. eglandulosa* Greenway. In our opinion the former is a true *Hirtella* and the latter is a synonym of *Magnistipula sapinii*.

In 1946 Brenan transferred *Magnistipula butayei* to *Hirtella*, within which he recognized two 'groups', based on several differences. Group I corresponds to our concept of *Magnistipula*, and Group II to *Hirtella* sensu stricto.

A different opinion was expressed by Hauman, who reviewed all African species of *Hirtella* and *Magnistipula* in 1951. Hauman restricted *Magnistipula* to four closely related species: the two original species, *M. cupheiflora* and *M. zenkeri*, *M. fleuryana* (in our view synonymous with *M. zenkeri*), and his new species, *M. cuneatifolia*. He divided *Hirtella* into two subgenera as follows: *Hirtella* ('*Euhirtella*'), which corresponds to our concept of the genus *Hirtella*, and *Afrohirtella*, which includes *Magnistipula butayei*, *M. sapinii* and *M. cupheiflora* plus other species regarded by us as synonymous with them. He included *M. glaberrima* in this subgenus as an 'aberrant' species.

Although Graham, in his work for the Flora of Tropical East Africa, was only concerned with four species, two of *Magnistipula* and two of *Hirtella*, his study was widely based. Graham returned to the concept of *Magnistipula* of Engler, De Wildeman and Mildbraed. We have found no evidence, however, to support his view that *Magnistipula* is closely related to *Parinari* subgenus *Sarcostegia* (now *Maranthes*).

The different views of Engler, Brenan, Hauman and Graham on the relationships of *Hirtella* and *Magnistipula*, and the characters they used to separate them, are summarized in table 7.

Magnistipula is represented in Madagascar by two species, *M. tamenaka* (R. Cap.) F. White and *M. cerebriformis* (R. Cap.) F. White. Both were originally described in *Hirtella* by Capuron

Table 7. The diagnostic characters of *Magnistipula* according to Engler, Brenan, Hauman and Graham

	Engler	Brenan	Hauman	Graham
circumscription	*M. conrauana*, *M. zenkeri*, *M. glaberrima*	as circumscribed here but as a 'group' in *Hirtella*	*M. conraui*, *M. zenkeri*, *M. fleuryana*, *M. cuneatifolia.*	as circumscribed here
1. stipules	large, foliaceous, 'intrapetiolar'	not used	discounted	not used
2. shape of bracts and bracteoles	not used	narrow	not used	not used
3. glands on inflorescence	not used	inflorescence eglandular	sessile glands present on bracteoles or sepals	bracteoles and sepals without stipitate glands
4. flower size	not used	not used	flowers 1.2–2.5 cm long from apex of petals to base of receptacle	not used
5. receptacle shape	obliquely campanulate ventricose on posterior side	mouth of receptacle markedly oblique	not used	mouth of receptacle asymmetric
6. sepals	not used	porrect	not used	erect or reflexed
7. stamens and style	not used	shortly or scarcely exserted	'exserted'	included
8. staminodes	united to form an appendage	not used	united to form a narrow tongue 0.5–0.7 cm long	connate at least at base and forming a comb- or tongue-like structure

(1972) who nevertheless pointed out that they should be placed in *Magnistipula* if that genus is maintained. Although they share several important features with *Magnistipula* they are also so different from the mainland species that a subgenus is needed to accommodate them.

Some species of *Magnistipula* were originally described in *Parinari*. Among them *P. sargosii* Pellegr., *P. tisserantii* Aubr. & Pellegr. and *P. bangweolensis* R.E. Fr., in our opinion, represent three subspecies of *M. butayei*, and *P. versicolor* Engl. is a synonym of *M. zenkeri*. They all lack the bilocular ovary of *Parinari*. *Parinari tessmannii* Engl., however, comes into a different category. It does share a spurious dissepiment with *Parinari*, but it differs in most other features. Its flowers are virtually indistinguishable from those of some species of *Magnistipula*, except for the dissepiment. The fruit, however, has a hard, thick and woody, not thin, soft and fibrous, endocarp. The best solution seems to be to place it in its own subgenus of *Magnistipula*. Hauman (1951: 188) had already created a subgenus, *Pelegriniella*, for it in *Parinari*. This species was transferred to *Magnistipula* by one of us (G.T.P.) in 1966.

It will be apparent from the foregoing that *Magnistipula* is somewhat variable in floral and fruit characters, much more variable in this respect than any other genus we accept. Variation in floral characters, however, although the extremes are so different, forms a continuous series as shown in figure 44. Variation in fruit characters is independent of variation in other features. Some taxonomists doubtless would wish to split *Magnistipula*, but this would entail the recognition of 6 or 7 genera for as few as 11 species. Such splitting could then be used to justify further 'Balkanization' elsewhere in the family, leading to a situation as unsatisfactory as that in Sapotaceae and some other families.

A more acceptable solution seems to be to divide the genus into three subgenera, one of which is further divided into three sections (White 1979*a*).

Conspectus of the species

I. *Ovary and endocarp unilocular*; *endocarp soft and fibrous*; *stipules free, lateral*; *receptacle-tube either distinctly curved or gibbous, throat lined with long retrorse hairs*; *receptacle-tube plus posterior sepal more than 0.7 cm long*: Subgenus *MAGNISTIPULA*

1. Receptacle-tube horn-shaped, gradually narrowed to the non-gibbous base, only slightly oblique at the throat; staminodes fused to form a narrow ligule which is longer than wide; stipules, at least those just beneath the inflorescence, usually foliaceous and *ca.* 1 cm × 1 cm–3 cm × 3 cm; receptacle-tube plus posterior sepal 1–2 cm long: . . . . Section ***Magnistipula***

2. Inflorescence-axes and outside of receptacle and sepals tomentellous; staminodial ligule about half as long as filaments:

3. Leaves broadly rounded at the base; receptacle-tube plus posterior sepals 1.5–2 cm long; receptacle-tube *ca.* 1.5 times as long as sepals, twice as long as wide; sepals acute . . . . . 1. *M. zenkeri*

3. Leaves broadest in upper half, acuminate at apex, cuneate at base; receptable-tube plus posterior sepal *ca.* 1 cm long; receptacle-tube ± as long as sepals; ± as long as wide; sepals rounded or obtuse . . . . 2. *M. cuneatifolia*

2. Inflorescence-axes etc. glabrous; staminodial ligule about one quarter as long as filaments; leaves broadest in lower half, cuspidate at apex, broadly rounded at the base, sometimes also with the lamina decurrent along the petiole; receptacle-tube plus posterior sepal *ca.* 1 cm long; receptacle-tube twice as long as sepals; at least twice as long as wide; sepals rounded or obtuse 3. *M. conrauana*

1. Receptacle-tube not horn-shaped, slightly to strongly gibbous at the base†, strongly oblique at the throat; staminodes partly fused to form a short comb-shaped ligule which is much wider than long; stipules rarely foliaceous:

4. Inflorescence lax; pedicels longer than receptacle-tube; flowers very asymmetric, anterior sepals inserted ± halfway along total length of receptacle-tube . . . . Section ***Animalculum***

5. Leaf-lamina with 2 swollen pouches at the base . . . . 4. *M. bimarsupiata*

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† In *M. butayei* subsp. *montana* the receptacle-tube is slightly curved and is non-gibbous. Its flowers, however, are much smaller than those of *M. zenkeri* and its relatives, and it keys out with the rest of *M. butayei* in all other respects.

5. Leaf-lamina without swollen pouches:
  6. Stipules foliaceous, 0.4 cm × 0.25 cm–0.7 cm × 0.5 cm, persistent; leaves coriaceous, venation inconspicuous; inflorescence a compound raceme; flowers glabrous outside . . 5. *M. glaberrima*
  6. Stipules *ca.* 0.4 cm × 0.1 cm, caducous; leaves chartaceous, venation laxly reticulate, prominent; inflorescence a simple raceme or a raceme of very shortly stalked cymules; flowers tomentellous outside . . . . 6. *M. cupheiflora*

4. Inflorescence congested; pedicels much shorter than the receptacle-tube; flowers less asymmetric, anterior sepals inserted in upper half of receptacle-tube . . . . Section ***Peregrinator***
  7. Rhizomatous, geoxylic suffrutex, usually less than 20 cm tall; inflorescence essentially a raceme bearing subsessile cymules, sometimes with 1 or more similar, markedly ascending branches from the base; receptacle-tube not gibbous, *ca.* 0.7 cm long . . . . 7. *M. sapinii*
  7. Trees or shrubs, more than 4 m tall; inflorescence richly branched for greater part of length, branches mostly wide-spreading; receptacle-tube mostly less than 0.5 cm long and distinctly gibbous, if non-gibbous (subsp. *montana*) then less than 0.5 cm long; if 0.7 cm long or more (subsp. *youngii*) then strongly gibbous . . . . 8. *M. butayei*

II. *Ovary bilocular; endocarp bilocular, thick, hard and woody; stipules fused, intrapetiolar; receptacle-tube curved, not gibbous, throat lined with long retrorse hairs; flowers small; receptacle-tube plus posterior sepal ca. 0.6 cm long* Subgenus *PELLEGRINIELLA*

III. *Ovary unilocular; endocarp unilocular, hard and woody; stipules fused, intrapetiolar; receptacle-tube not curved, not gibbous; throat not lined with long retrorse hairs; flowers small, receptacle-tube plus posterior sepal 0.4–0.45 cm long* . . . . Subgenus *TOLMIELLA*

1. Inflorescence-axes glabrous; receptacle-tube subcampanulate, much longer than the sepals, puberulous throughout inside; staminodes 8, subulate, up to 0.2 cm long; cotyledons shallowly ruminate 10. *M. tamenaka*
1. Inflorescence-axes tomentellous; receptacle-tube turbinate, shorter than the sepals, filled with cottony hairs; staminodes fused to form a short (0.05 cm) fleshy ligule with 8 minute teeth 11. *M. cerebriformis*

SUBGENUS 1. *MAGNISTIPULA*

Sectio 1. ***Magnistipula***

1. ***Magnistipula zenkeri*** Engl., *Bot. Jahrb.* **36**: 227 (1907). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 293 (1976); *Distr. Pl. Afr.* **10**: 312 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 93, t. 28 (1968). Type: Cameroun, fl., *Zenker* 2469 (B, holotype; BR, E, K, P).

Tree up to 30 m tall, but sometimes flowering as a shrub 5–6 m tall. In evergreen rainforest in West Africa, especially along watercourses and in swampy places. From Liberia to Gabon but with an interval of *ca.* 1600 km between Upper and Lower Guinea.

2. ***Magnistipula cuneatifolia*** Hauman, *Bull. Jard. Bot. État. Brux.* **21**: 175 (1951). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 289 (1976); *Distr. Pl. Afr.* **10**: 305 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 82, t. 24 (1978). Type: Gabon, fl., *Le Testu* 9376 (P, holotype).

Large tree, only known from lowland rainforest in Cameroun and Gabon.

3. ***Magnistipula conrauana*** Engl., *Bot. Jahrb.* **36**: 226 (1905). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 289 (1976); *Distr. Pl. Afr.* **10**: 304 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**; 79, t. 23 (1978). Type: Cameroun, fl., *Conrau* 65 (B, holotype, destroyed; E, lectotype, here designated).

Tree up to 12 m tall, or a shrub *ca.* 5 m tall. Only known from Cameroun, where it occurs in rainforest between 900 and 1000 m.

Sectio 2. ***Animalculum*** F. White, *Brittonia* **31**: 481 (1979).

4. ***Magnistipula bimarsupiata*** Letouzey, *Adansonia* sér. 2 **16**: 229, t. 1 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 73, t. 21 (1978). Type: Gabon, fl., *Bernard* 507 (P, holotype).

Tree. Only known from rainforest at the type locality.

M. bimarsupiata is closely related to *M. glaberrima* but differs in having hollow swollen internodes with a perforation towards the base, a pair of swollen pouches at the base of the

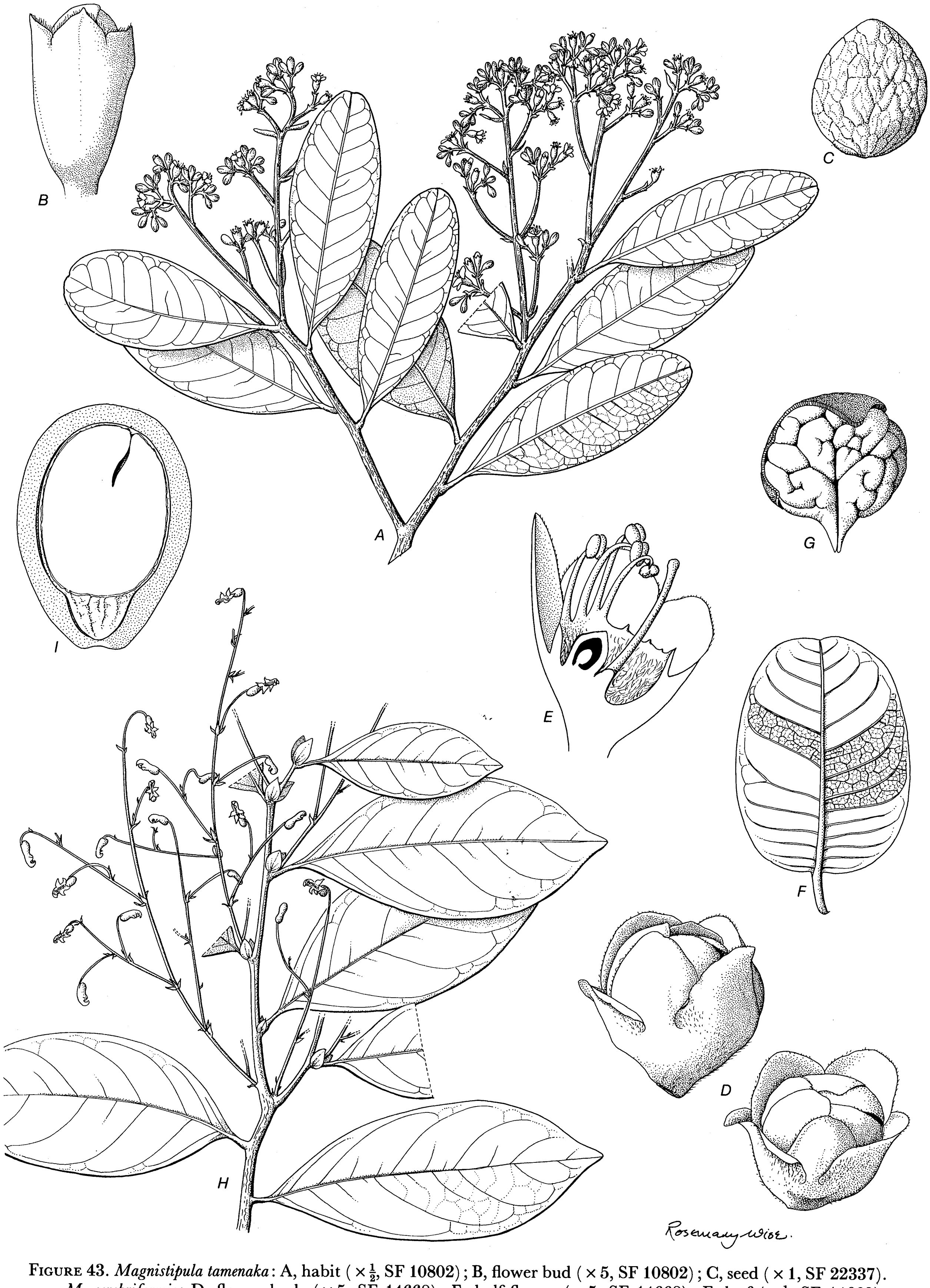

FIGURE 43. *Magnistipula tamenaka*: A, habit (× ½, SF 10802); B, flower bud (× 5, SF 10802); C, seed (× 1, SF 22337). *M. cerebriformis*: D, flower buds (× 5, SF 14668); E, half flower (× 5, SF 14668); F, leaf (× ½, SF 14668); G, fruit with part of pericarp removed showing ruminate cotyledons (× 1, Capuron SF 18165). *M. glaberrima*: H, habit (× ½, Le Testu 6026). *M. butayei* subsp. *bangweolensis*: I, fruit, LS (× 1, Hoyle 1358).

lamina, and sparse hispid hairs *ca.* 0.2 cm long on the young shoots. These features are probably associated with ants.

5. ***Magnistipula glaberrima*** Engl., *Notizbl. Bot. Gart. Berl.* **6**: 35 (1913). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 290 (1976); *Distr. Pl. Afr.* **10**: 309 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 87, t. 89 (1978). Type: Cameroun, fl., *Zenker* 4509 (B, holotype, destroyed; K, lectotype, here designated; BR, LE, P).

Tree 10–15 m tall. In evergreen rainforest in Cameroun and Gabon.

6. ***Magnistipula cupheiflora*** Mildbr., *Notizbl. Bot. Gart. Berl.* **8**: 57 (1921). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 84 (1976); *Distr. Pl. Afr.* **10**: 306–308 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 84, t. 25 (1978). Type: Cameroun, fl., *Mildbraed* 8307 (B, holotype, destroyed; K, lectotype, here designated).

Tree up to 10 m tall. In evergreen rainforest. Subsp. *leonensis* F. White occurs in Sierra Leone and subsp. *cupheiflora* in Cameroun and Gabon.

Sectio ***Peregrinator*** F. White, *Brittonia* **31**: 481 (1979).

7. ***Magnistipula sapinii*** De Wild., *Bull. Jard. Bot. État. Brux.* **3**: 262 (1911). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 291 (1976); *Distr. Pl. Afr.* **10**: 310 (1976); *Fl. Zamb.* **4**: 47, t. 12, fig. a (1978). Type: Zambia, fl., *Borle* 254 (K, holotype; FHO, PRE).

Rhizomatous geoxylic suffrutex, usually less than 20 cm tall. Confined to the Kalahari Sands of the upper Zambezi basin and adjacent parts of Angola and Zaire. In seasonally waterlogged grassland.

8. ***Magnistipula butayei*** De Wild., *Ann. Mus. Congo Belg. Bot.* sér. 5 **2**: 255 (1908). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 281 (1976); *Distr. Pl. Afr.* **10**: 295–303 (1976); *Fl. Zamb.* **4**: 45, t. 12 fig. b–c (1978). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 74 t. 22 (1978). Type: Zaire, fl., *Butaye* 1440 (BR, holotype).

Small or large tree. *M. butayei* is an ecological and chorological transgressor. It is one of the very few larger woody African species that occur both in the rainforests of the Guineo-Congolian region and in woodland and wooded grassland in the Sudanian and Zambezian regions. Of its 8 subspecies, 7 are parapatric or slightly allopatric and one is markedly allopatric.

SUBGENUS 2. *PELLEGRINIELLA* (Hauman) Prance, *Bol. Soc. Brot.* sér. 2 **40**: 185 (1966).

Parinari subgenus *Pellegriniella* Hauman, *Bull. Jard. Bot. État. Brux.* **21**: 188 (1951) pro parte quoad *P. tessmannii* tantum.

Hauman based *Parinari* subgenus *Pellegriniella* on *P. tessmanii*, but associated with it two South American species, *P. coriacea* Benth. and *P. gardneri* Hook. f. They differ from *P. tessmannii* in many important respects, and are now placed in *Exellodendron.*

9. ***Magnistipula tessmannii*** (Engl.) Prance, *Bol. Soc. Brot.* ser. 2 **40**: 185 (1966). – F. White, *Bull. Jard. Bot. Nat. Belg.* **46**: 292 (1976); *Distr. Pl. Afr.* **10**: 311 (1976). – Letouzey & F. White, *Fl. Cam.* **20**; *Fl. Gab.* **24**: 88, t. 27 (1978). Type: Equatorial Guinea, *Tessmann* 81 (B, holotype, destroyed; K, lectotype of F. White, 1976; HBG, P).

Tree up to 40 m tall. In evergreen rainforest from SE Nigeria to Cabinda.

SUBGENUS 3. *TOLMIELLA* F. White, *Brittonia* **31**: 482 (1979).

10. ***Magnistipula tamenaka*** (R. Cap.) F. White, *Brittonia* **31**: 482 (1979). Type: Madagascar, fl., *Capuron* SF 18247 (P, holotype).

Hirtella tamenaka R. Cap., *Adansonia* sér. 2 **12**: 379, t. 2 (1972).

Madagascar. Widespread in the Eastern Domain from the basin of the Fanambana River,

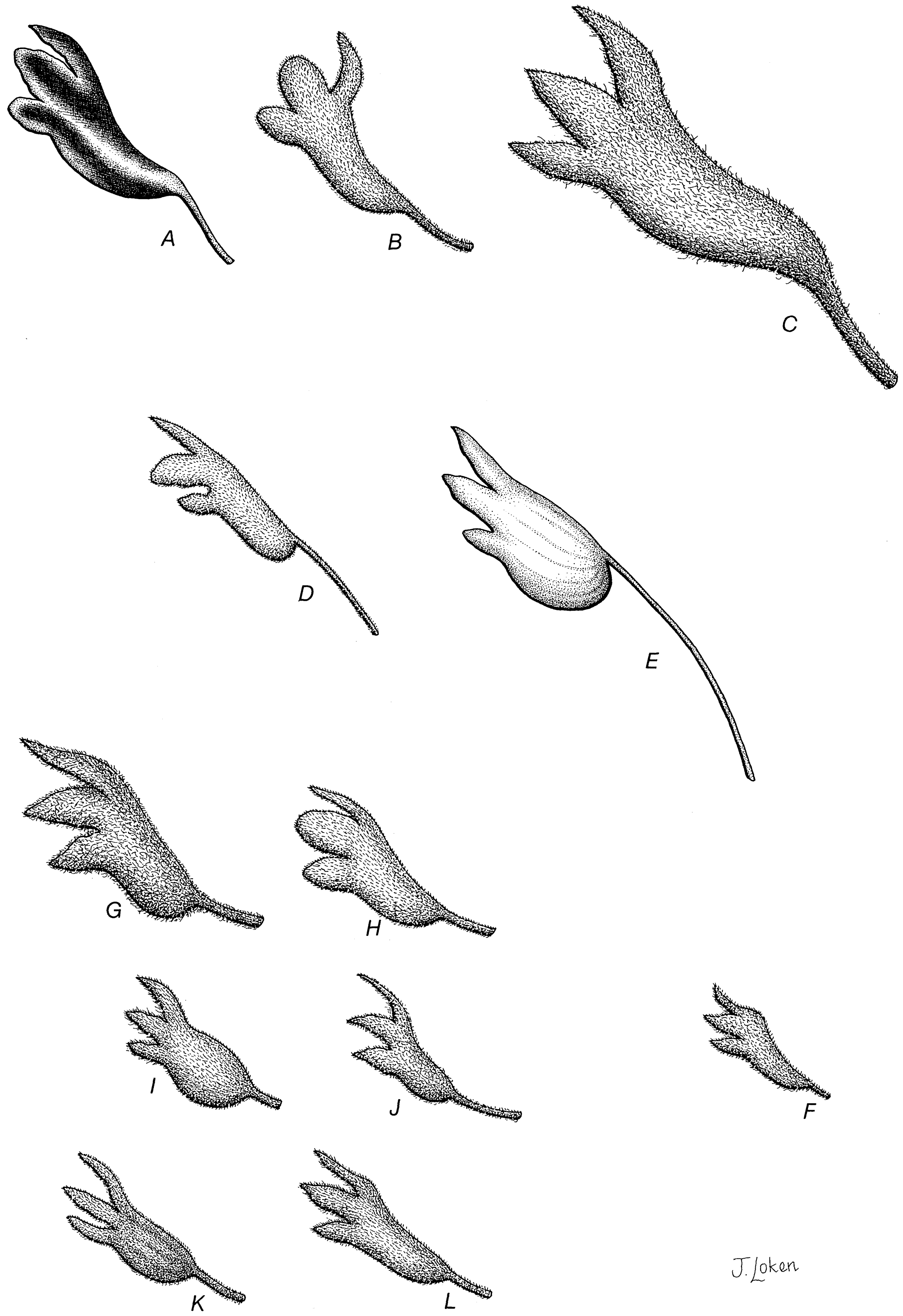

FIGURE 44. Receptacle tube and calyx in *Magnistipula* (×4): A, *M. conrauana* (Conrau 65); B, *M. cuneatifolia* (Le Testu 9376); C, *M. zenkeri* (Zenker 2469); D, *M. cupheiflora* (Le Testu 5472); E, *M. glaberrima* (Le Testu 6026); F, *M. tessmannii* (Le Testu 8014). G, *M. sapinii* (Strid 2394). H–L, *M. butayei*: H, subsp. *youngii* (Young 410); I, subsp. *bangweolensis* (Holmes 34); J, subsp. *butayei* (Goossens 6012); K, subsp. *tisserantii* (Le Testu 3814); L, subsp. *montana* (Michelson 762).

south of Vohémar in the north, to Fort Dauphin in the south. It is a large tree, up to 30 m tall, and occurs in rainforest up to altitudes of 500–600 m.

11. ***Magnistipula cerebriformis*** (R. Cap.) F. White, *Brittonia* **31**: 482 (1979). Type: Madagascar, fl., SF 12920 (P, holotype).

Hirtella cerebriformis R. Cap., *Adansonia* sér. 2 **12**: 382 (1972).

Widespread in rainforest on the eastern side of Madagascar. Tree 8–15 m tall.

M. cerebriformis is very similar in its leaves to *M. tamenaka* and they share the same vernacular name ('Tamenaka'). They are very different, however, in the structure of their flowers.

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† Until recently no copies of this publication were known to exist and it was thought to have been suppressed by the author before publication. See *Flora Malesiana* (ser. 1), 4: CLXXIII (1954). However, copies have now been found in two libraries in Paris, including the Bibliothèque Centrale of the Muséum d'Histoire Naturelle.

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APPENDIX 1. CHARACTERS USED IN THE EXPERIMENTS DESCRIBED IN §6*e*

(*a*) *Types of character*

There are two main types of taxonomic character, namely *absolutely diagnostic* and *imperfectly diagnostic* or *differential*.

An absolutely diagnostic character has one character state which occurs in all the members (species in the present study) of one of the groups under consideration (genera in the present study), and a contrasting, mutually exclusive, character state which occurs in all the members of a second group with which the first group is being compared. By definition, an absolutely diagnostic character has a diagnostic value of 100 %. In the present study only character 6 (see below) is absolutely diagnostic.

There are two types of differential character, *overlapping* and *non-overlapping*. In both cases the diagnostic value is less than 100 %. The taxonomic usefulness of overlapping differential characters partly depends on the precise way in which the character states are formulated, partly on the number of objects in the region of overlap and partly on the way in which the character states of different characters are correlated among themselves in the taxa being compared.

Non-overlapping characters can only be formulated in one way and their usefulness depends on their relative representation in the taxa under consideration.

The character states of *overlapping differential characters* may be formulated so as to exclude the region of overlap entirely, in which case all objects outside the area of overlap are correctly placed but those objects inside the area of overlap are not placed at all. When this is done the diagnostic value of the character will be relatively low. Or the character states may be demarcated at some point in the region of overlap, in which case all objects will be placed, and a higher proportion of the total will be correctly placed, but some objects inevitably will be placed incorrectly. The number of misplaced objects will depend on the precise place of demarcation. If the objective is to increase the chances of correct identification, then demarcation should be made at that point at which fewest objects are misplaced.

For example, table A1 below shows that if the character states of the character 'ratio of pedicel length to receptacle length' are demarcated so as to exclude the region of overlap then 60 out of 77 of the objects can be correctly placed and the character has a diagnostic value of 78 %. When the data are presented, as in the table, there are nine places where the character can be divided into two character states. Each point of partition involves the misplacement of some objects, but fewest are misplaced if the partition is made at the index value 1.29. If this is done, the diagnostic value is increased to 94 %. Imperfectly diagnostic characters are only useful if their diagnostic value is high and if the misplaced objects are correctly placed by a majority of the other characters used. Two or more imperfectly diagnostic characters in combination are often found to be absolutely diagnostic.

In the present study five of the eight characters scored in Appendix 2 are overlapping differential characters and their diagnostic value varies from 94 to 97 %. Only two characters come in the non-overlapping differential category. Filament colour has a diagnostic value of 95 %, whereas the presence or absence of glands scores only 32 %.

(*b*) *Formulation of character states in Couepia and Hirtella*

(i) *Inflorescence*

In both genera there is quite a wide range of variation, although there is very little overlap between them. Because of its variability this character cannot be formulated concisely. The range in the two genera is as follows.

Couepia. Inflorescence: a dense thyrse with non-racemoid lateral branches, without numerous vestigial or retarded flowers and sterile bracts, or a short, few-flowered (less than 15) raceme or spike, or flowers crowded in a very long-pedunculate (flagelliflorous) inflorescence.

Hirtella. Inflorescence: a lax, elongate, many-flowered (more than 30) raceme, or a lax elongate, racemoid thyrse, usually with many retarted or vestigial flowers or sterile bracts, or a short, many-flowered subcapitate raceme, or a lax raceme of lax cymules, or a corymb with many sterile bracts (rarely a dense thryse).

In the absence of development studies and observations on the pattern of flowering and the arrangements of the flowers in space on the living plant, it is difficult to characterize the inflorescence of the two genera more precisely. Figures 3 and 4, which cover the range of variation of *Couepia* and *Hirtella* respectively, except for the thyrsoid species of the latter, do, however, show that the inflorescences of the two genera are very different.

The commonest inflorescence type in *Hirtella* is a simple raceme. Comparative studies within the genus indicate that this has been derived by reduction from a thyrse, which is the prevalent type in the family. In *Hirtella* the thyrse, when present, is most commonly racemoid and this is the second most common type. A racemoid thyrse is similar in appearance to a raceme. The lateral branches are relatively short and usually end in a single flower. Their axes appear to be sympodial in origin and are sometimes slightly zigzag. They frequently bear sterile bracts, and often also a few small flower-buds. The latter rarely seem to open at the same time as the terminal flower. Whether they are vestigial or juvenile, only a study of the living plant will decide.

The dense thyrse is the prevalent inflorescence type of *Couepia* shared by 19 species in the present study. Only four species of *Hirtella* have a dense thyrse with non-racemoid lateral branches. Their resemblance to *Couepia* is superficial and a detailed study of the living plant would certainly enable their inflorescences to be distinguished verbally.

If the inflorescence character is formulated so as to exclude the region of overlap caused by the occurrence of dense thyrses in both genera it has a diagnostic value of 69 %, but 23 species cannot be placed. If it is formulated so that the dense thyrse is stated to be a *Couepia* feature then four species of *Hirtella* are misplaced and the diagnostic value rises to 95 %.

(ii) *Glands on bracts and bracteoles*

These are unknown in *Couepia* but are found in 25 of the 47 species of *Hirtella*. It is a *unilateral* non-overlapping differential character with a diagnostic value of 32 %. When present, such characters are valuable aids to identification, but if their diagnostic value is low, their uncritical inclusion in numerical comparisons could blur generic distinctness.

(iii) *Ratio of pedicel length to receptacle-tube length*

The apparent stalk of the flower was measured rather than the true pedicel. In those species of *Hirtella* where a single flower terminates a flowerless sympodial axis, the latter was measured. Twelve species of *Couepia* overlap with *Hirtella* and five species of *Hirtella* overlap with *Couepia*. As will be seen from Table A1, the following character formulation results in fewest species' being misplaced, in this case five species of *Hirtella*. Demarcated thus the diagnostic value is 94 %.

1. Pedicel:receptacle ratio up to 1.29 . . . . *Couepia*
1. Pedicel:receptacle ratio > 1.29 . . . . *Hirtella*

TABLE A1. PEDICEL: RECEPTACLE RATIO

(Distribution of species of *Couepia* and *Hirtella* in region of overlap. The bottom row of figures shows the number of species misplaced if the character states are demarcated at that value.)

	0–0.49	0.5–0.59	0.6–0.69	0.7–0.79	0.8–0.89	0.9–0.99	1.0–1.09	1.1–1.19	1.2–1.29	1.3–15.0
Couepia	18	5	—	2	2	—	1	1	1	—
Hirtella	—	2	—	1	—	—	1	1	—	42
misplaced	12	9	9	8	6	6	6	6	5	

(iv) *Flower size*

This was measured from the base of the receptacle-tube to the tip of the posterior sepal. Ten species of *Couepia* overlap with *Hirtella* and fourteen of *Hirtella* overlap with *Couepia*. Table A2 shows that the following two alternative character formulations result in the fewest species' being misplaced, namely, either one species of *Couepia* and three of *Hirtella* or two of *Couepia* and two of *Hirtella*. Demarcated thus the diagnostic value is 95 %.

1. Flowers up to 8.9 mm long . . . . *Hirtella*
1. Flowers more than 8.9 mm long . . . . *Couepia*
1 *a*. Flowers up to 9.9 mm long . . . . *Hirtella*
1 *a*. Flowers more than 9.9 mm long . . . . *Couepia*

TABLE A2. FLOWER LENGTH (IN MILLIMETRES)

(Distribution of species of *Couepia* and *Hirtella* in region of overlap. The bottom row of figures shows the number of species misplaced if the character states are demarcated at that value.)

	4–6.9	7–7.9	8–8.9	9–9.9	10–10.9	11–11.9	12–12.9	over 13
Couepia	—	1	—	1	4	1	3	20
Hirtella	33	9	2	1	—	1	1	—
misplaced	14	6	4	4	8	8	8	10

(v) *Ratio of calyx length to receptacle-tube length*

The range of *Couepia* is from 0.3 to 1.09 and in *Hirtella* from 0.5 to 3.0. Twenty-three species of *Couepia* overlap with *Hirtella* and three species of *Hirtella* overlap with *Couepia*. Table A3 shows that the following character formulation results in the fewest species' being misplaced, namely three species of *Hirtella*. Formulated in this way the diagnostic value is 96 %.

1. Calyx:receptacle ratio up to 1.09 . . . . *Couepia*
1. Calyx:receptacle ratio over 1.09 . . . . *Hirtella*

TABLE A3. CALYX: RECEPTACLE RATIO

(Distribution of species of *Couepia* and *Hirtella* in the region of overlap. The bottom row of figures shows the number of species misplaced if the character states are demarcated at that value.)

	0.3–0.49	0.5–0.59	0.6–0.69	0.7–0.79	0.8–0.89	0.9–0.99	1–1.09	1.1–3.0
Couepia	7	5	5	6	4	1	2	—
Hirtella	—	1	—	—	1	—	1	44
	23	19	14	8	5	4	3	

(vi) *Orientation of filaments in the bud*

In all species of *Couepia* examined the filaments were found to be undulate (U) in the bud, with three or more bends. In all species of *Hirtella* they were coiled like a watch spring (C). The diagnostic value is 100 %.

(vii) *Ratio of filament length to receptacle-tube length*

The range in *Couepia* is from 0.9 to 2.5 and in *Hirtella* from 1.5 to 11.3. Sixteen species of *Couepia* overlap with *Hirtella* and three species of *Hirtella* overlap with *Couepia*. Table A4 shows that the following character formulation results in the fewest species being misplaced. Formulated in this way the diagnostic value is 97 %.

1. Filament:receptacle ratio up to 2.59 . . . . *Couepia*
1. Filament:receptacle ratio over 2.59 . . . . *Hirtella*

TABLE A4. FILAMENT: RECEPTACLE RATIO

(Distribution of species of *Couepia* and *Hirtella* in the region of overlap. The bottom row of figures shows the number of species misplaced if the character states are demarcated at that value.)

	0.9– 1.49	1.5– 1.59	1.6– 1.69	1.7– 1.79	1.8– 1.89	1.9– 1.99	2.0– 2.09	2.1– 2.19	2.2– 2.29	2.3– 2.39	2.4– 2.49	2.5– 2.59	2.6– 11.3
Couepia	14	1	2	1	1	2	3	1	1	—	2	2	—
Hirtella	—	1	—	—	—	—	—	—	—	1	—	—	45
misplaced	16	16	14	13	12	10	7	6	5	6	4	2	

(viii) *Filament colour*

This is a *bilateral* non-overlapping differentiated character. In all species of *Couepia* for which information is available, except one, the filaments are white or cream. All species of *Hirtella*, except two, were found to have reddish filaments at least towards the apex. If white is regarded as a *Couepia* feature, and red a *Hirtella* feature, the diagnostic value of the character is 95%.

(*c*) *An index of generic conformity*

In Appendix 2 the character states are given for eight features of the flower and inflorescence for 30 species of *Couepia* and 47 of *Hirtella*, and for each species an *index of generic conformity* has been calculated, based on the seven characters for which information was complete. It will be seen that *Couepia* is much more uniform than *Hirtella*. In *Hirtella* two species have an index value as low as 43%, but there is no evidence for true intermediates between the two genera. *H. bahiensis*, for example, resembles *Couepia* in having relatively short pedicels and filaments and relatively short calyx lobes, and also in having white flowers. However, it shares with *Hirtella* several other features (e.g. filament number and type of fruit indumentum) not included in the table, and on overall resemblance it unequivocally belongs to that genus.

APPENDIX 2. TABLE GIVING, FOR 30 SPECIES OF *COUEPIA* AND 47 SPECIES OF *HIRTELLA*, THE CHARACTER STATES OF THE EIGHT CHARACTERS USED IN THE EXPERIMENTS DESCRIBED IN §6*e*, THE DIAGNOSTIC VALUE OF EACH CHARACTER, AND AN INDEX OF GENERIC CONFORMITY FOR EACH SPECIES

(Numbers at heads of columns indicate: 1, type of inflorescence; c = *Couepia* type other than a dense thyrse; h = *Hirtella* type; Th = dense thyrse. 2, Occurrence of glands on bracts and bracteoles; gl = absent; Gl = present. 3, Ratio of pedicel length to length of receptacle-tube; 4, length of 'flower'; 5, ratio of calyx length to receptacle-tube length; 6, filaments undulate (U) or coiled (C) in bud; 7, ratio of filament length to receptacle-tube length; 8, Filament colour; W = white or cream; R = red.

For further explanation of these characters, see Appendix 1.

Figures or letters in brackets indicate those species that occur in the area of overlap for that character. Figures or letters in bold type indicate those species that would be misplaced when the character states are formulated so as to produce minimum misplacement; X, information not available.

I_c is the index of generic conformity based on the seven characters for which information is complete.)

Couepia	1	2	3	4	5	6	7	8	I_c
belemii	(Th)	gl	0.06	16	(1.0)	U	(2.5)	W	100
bracteosa	(Th)	gl	0.1	14	(0.6)	U	0.9	W	100
canomensis	c	gl	0.14	(12)	(0.7)	U	(1.9)	W	100
chrysocalyx	c	gl	0.3	25	(0.7)	U	(1.6)	W	100
comosa	(Th)	gl	(0.8)	20	(0.67)	U	(2.0)	X	100
elata	c	gl	(0.5)	(10.5)	(0.75)	U	(2.5)	W	100

APPENDIX 2. (*cont.*)

Couepia	1	2	3	4	5	6	7	8	I_c
eriantha	(Th)	gl	0.3	26	(1.0)	U	1.3	W	100
excelsa	(Th)	gl	0.12	14	(0.75)	U	(2.0)	W	100
glandulosa	(Th)	gl	0.4	15	(0.5)	U	1.1	W	100
grandiflora	(Th)	gl	(1.1)	17	(0.88)	U	(2.0)	W	100
habrantha	(Th)	gl	0	(10)	(0.67)	U	(1.7)	W	100
impressa	(Th)	gl	(0.57)	(12)	(0.71)	U	1.4	W	100
krukovii	c	gl	0.02	40	(0.53)	U	1.2	W	100
latifolia	c	gl	0	30	(0.5)	U	0.8	W	100
leptostachya	(Th)	gl	0.37	(12)	(0.5)	U	1.1	W	100
longipendula	c	gl	(0.88)	24	0.41	U	(2.4)	**(R)**	100
magnoliifolia	c	gl	0.11	25	0.47	U	1.3	W	100
maguirei	(Th)	gl	(0.57)	13	(0.85)	U	(1.9)	W	100
multiflora	(Th)	gl	(0.5)	(11)	0.37	U	(1.8)	W	100
ovalifolia	(Th)	gl	(0.7)	(10)	0.42	U	1.3	W	100
paraensis	(Th)	gl	0.4	13	0.3	U	1.4	W	100
parillo	c	gl	0	21	(0.5)	U	1.0	W	100
racemosa	(Th)	gl	(1.0)	(9)	(0.8)	U	(2.4)	W	86
recurva	c	gl	0.26	21	0.4	U	1.0	X	100
robusta	(Th)	gl	0.18	18	(0.63)	U	(1.6)	W	100
steyermarkii	c	gl	0.16	(10)	(0.66)	U	(1.5)	W	100
suberosa	(Th)	gl	(0.50)	19	(0.90)	U	1.4	W	100
ulei	(Th)	gl	(0.75)	**(7)**	(0.75)	U	(2.25)	W	86
uiti	(Th)	gl	(1.2)	13	(0.85)	U	(2.1)	W	100
williamsii	c	gl	0.26	27	0.42	U	1.0	W	100
Hirtella									
americana	h	Gl	7.0	5.0	1.5	C	5.5	R	100
angustifolia	h	Gl	5.2	(7.5)	2.0	C	7.2	X	100
bahiensis	**(Th)**	Gl	**(0.5)**	6.0	**(0.5)**	C	**(1.5)**	(W)	43
bicornis	h	gl	2.5	6.0	2.0	C	7	R	86
brachystachya	h	gl	6.0	6.5	1.6	C	4	R	86
bullata	h	Gl	6.0	5.0	1.5	C	5	R	100
burchellii	h	gl	**(1.0)**	6.0	2.0	C	6.5	R	71
caduca	h	Gl	7.0	5.0	1.5	C	4.5	X	100
ciliata	h	Gl	15.0	5.0	1.5	C	4	X	100
davisii	h	Gl	2.0	6.0	1.4	C	6.8	R	100
duckei	h	gl	2.0	6.0	**(1.0)**	C	4.0	R	71
elongata	h	gl	2.0	5.0	1.5	C	7.5	R	86
eriandra	h	gl	2.0	5.0	1.5	C	7.0	R	86
excelsa	h	Gl	5.0	(7.0)	1.3	C	3.3	R	100
fasciculata	**(Th)**	gl	**(0.5)**	**(12.0)**	1.1	C	4.25	R	43
floribunda	h	gl	15.0	4.0	3.0	C	9.0	X	86
glandistipula	h	Gl	2.0	6.5	2.3	C	6.0	R	100
glandulosa	h	Gl	6.0	6.0	2.0	C	5.5	X	100
gracilipes	h	gl	4.0	(8.5)	1.4	C	3.4	R	86
guyanensis	h	gl	**(0.75)**	**(11.0)**	1.75	C	2.7	R	57
hebeclada	h	gl	6.5	6.0	2.0	C	6.5	X	86
hispidula	h	Gl	2.8	(7.5)	2.0	C	6.5	R	100
hoehnei	h	Gl	4.0	(7.0)	1.8	C	4.4	X	100
lightioides	h	gl	3.0	6.0	2.0	C	3.0	X	86
longifolia	h	gl	7.3	4.5	2.0	C	10.0	X	86
macrophylla	h	Gl	10.0	2.0	1.7	C	5.3	R	100
macrosepala	h	gl	4.0	(8.0)	1.7	C	5.3	R	86
martiana	h	Gl	2.0	(7.5)	1.5	C	4.3	**(W)**	100
mutisii	h	gl	4.3	(7.0)	1.3	C	5.7	R	86
myrmecophila	h	Gl	2.0	6.0	2.0	C	10.5	R	100
obidensis	**(Th)**	gl	1.3	6.0	2.0	C	6.0	R	71
paniculata	h	Gl	3.5	6.0	2.0	C	7.0	R	100
paraensis	h	Gl	3.0	5.0	1.5	C	6.0	R	100
physophora	h	Gl	**(1.1)**	(7.5)	1.1	C	7.1	X	86

Appendix 2. (*cont.*)

Hirtella	1	2	3	4	5	6	7	8	I_c
pilosissima	h	Gl	2.0	4.0	1.7	C	11.3	R	100
punctillata	h	gl	3.5	5.0	1.5	C	6.5	X	86
racemosa	h	Gl	3.0	6.0	2.0	C	5.0	R	100
rodriguesii	h	gl	2.0	5.0	1.5	C	8.0	R	86
scabra	h	gl	2.4	6.0	1.4	C	4.0	R	86
silicea	h	Gl	2.4	(7.0)	1.8	C	4.4	R	100
sprucei	h	gl	2.8	6.5	1.6	C	6.0	X	86
subscandens	h	Gl	4.0	5.0	1.5	C	6.5	R	100
tentaculata	h	Gl	4.0	4.0	1.7	C	10.4	R	100
tocantina	h	gl	4.0	6.0	2.0	C	7.0	R	86
triandra	h	gl	5.6	6.5	1.6	C	4.8	X	86
ulei	h	Gl	9.3	(7.0)	1.3	C	4.8	X	100
zanzibarica	h	Gl	1.6	**(9.0)**	**(0.8)**	C	**(2.4)**	X	57
diagnostic value of character	95%	32%	94%	95%	96%	100%	97%	95%	—

Appendix 3. Index of scientific names of plants mentioned in the text, with authorities, and, for plants other than Chrysobalanaceae, the names of their families

The names of tribes and genera in the Chrysobalanaceae accepted by the authors are printed in capital letters. Genera, infrageneric groups, and species in Chrysobalanaceae regarded as synonyms are in italic. Taxa in other families are listed without any indication of possible synonymy. Numbers in bold type refer to the pages in the taxonomic conspectus where tribes, genera and species are described. Numbers in italic refer to pages with illustrations. Specimens cited are those used in the experiments (see §6*e* and Appendixes 1 and 2).)

Appendix 3. (*cont.*)

Appendix 3. (*cont.*)

Appendix 3. (*cont.*)

APPENDIX 3. (*cont.*)

Appendix 3. (*cont.*)

APPENDIX 3. (*cont.*)

APPENDIX 3. (*cont.*)

APPENDIX 4. INDEX OF ANIMAL NAMES MENTIONED IN THE TEXT

Notes added in proof, 29 *March* 1988

(1) A supplement (Prance 1988) to the *Flora neotropica* monograph (Prance 1972) gives full details and descriptions of the 40 species listed in table 1 (p. 11) and includes an additional 18 new species: twelve in *Licania*, four in *Couepia* and one each in *Hirtella* and *Chrysobalanus*. The

last was discovered in the low mountains on the border between the state of Bolívar and Territorio Delta Amacura of Venezuela; it closely resembles the Antillean species *C. cuspidatus*. Revised keys incorporate all species that have been described since the publication of the monograph. Also included are distribution maps of all species based on their presence in degree squares of longitude and latitude.

(2) Two new species, *Hirtella margae* and *Licania granvillei*, are described in a paper (Prance 1986*a*), which preceded the publication of Chrysobalanaceae in a new Flora of the Guianas (Prance 1986*b*); the latter also includes an up-to-date treatment of the wood anatomy of the Guiana species (ter Welle & Détienne 1986).

(3) A treatment of the family for Flora Malesiana (Prance 1989) recognizes, for the region covered by the flora, five species of *Atuna*, three of *Hunga*, two of *Kostermanthus*, three of *Licania*, one of *Maranthes*, three of *Parastemon* and thirteen of *Parinari*. An additional three species of *Atuna*, eight of *Hunga* and two of *Parinari* occur elsewhere in the tropical Far East. Although the *Flora malesiana* account has resolved some of the outstanding taxonomic problems (see pp. 11–12 and 73), it was based largely on herbarium studies, and further fieldwork is important, especially for the Far Eastern species of *Atuna* and *Parinari*. In a precursory paper, Prance (1987) had already described *Atuna cordata* and *Parastemon grandifructus* as new species. *Hunga fusicarpa* Kostermans (see p. 102) has been transferred to *Licania*, the first record of that genus from New Guinea.

(4) The works referred to above mean that some of the figures in table 6 (p. 45) need to be altered, but the general pattern remains unchanged.

(5) To the three publications of Hopkins mentioned on p. 61, a fourth (Hopkins 1986) should be added.

(6) Since 1980, T. D. Pennington (personal communication) has been working on a worldwide generic monograph of Sapotaceae which is nearly finished. He recognizes fewer genera than some previous workers (see p. 157) especially in Africa, and has been able to define most of them on correlated suites of vegetative, floral and fruit characters, as we have done for Chrysobalanaceae.

(7) Two nomenclatural inconsistencies should be removed; on pp. 38 and 175 and in Appendix 3 replace *Couepia glandulosa* by *C. guianensis* subsp. *glandulosa*; on p. 175 and in Appendix 3 replace *C. suberosa* by *C. grandiflora*.

(8) Thanks are due to Alison Strugnell and Michael Wilkinson for their painstaking help in compiling the indexes.

Additional references

Hopkins, H. C. 1986 *Flora neotropica*, monograph no. 43 (*Parkia*, Leguminosae: Mimosoideae), pp. 1–124. New York Botanical Garden.

Prance, G. T. 1986*a* Studies in the flora of the Guianas, 19. New taxa of Chrysobalanaceae for the Flora of the Guianas. *Proc. K. Ned. Akad. Wet.* **89**, 111–116.

Prance, G. T. 1986*b* Chrysobalanaceae. Family 85 in *Flora of the Guianas* (ed. A. R. A. Görts-van Rijn). Koenigstein: Koeltz Scientific Books.

Prance, G. T. 1987 Notulae de Chrysobalanaceis malesianis praecursoriae. *Brittonia* **39**, 364–370.

Prance, G. T. 1988 *Flora neotropica*, monograph no. 9 (*Chrysobalanaceae*: supplement). New York Botanical Garden. (In the press.)

Prance, G. T. 1989 *Flora malesiana* (ser. I) *Spermatophyta* (*Chrysobalanaceae*). Dordrecht: Martinus Nijhoff Publishers. (In the press.)

ter Welle, J. H. & Détienne, P. 1986 Wood and timber. In Chrysobalanaceae, family 85 in *Flora of the Guianas* (ed. A. R. A. Görts-van Rijn), pp. 109–126. Koenigstein: Koeltz Scientific Books.

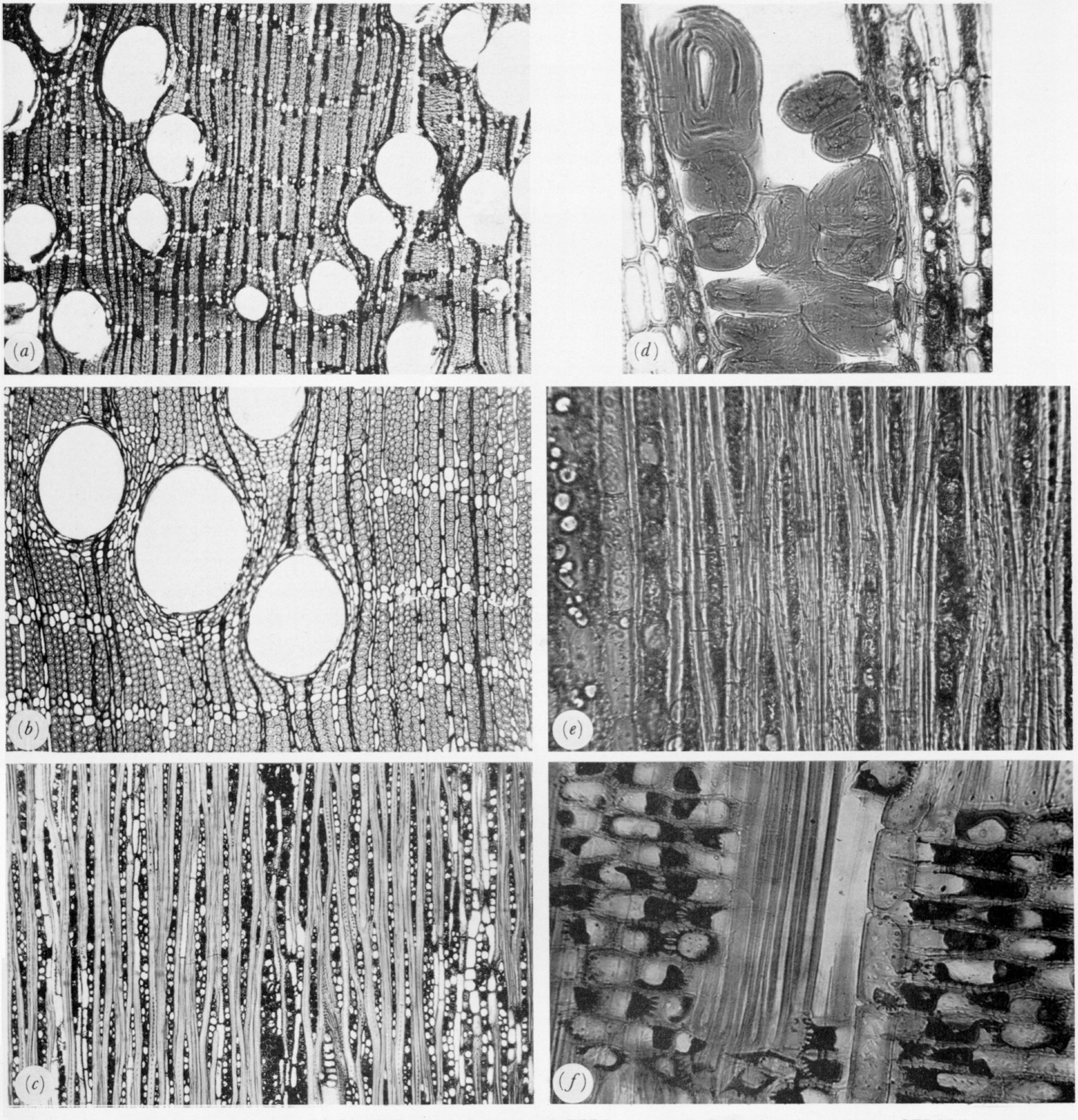

FIGURE 6. Secondary xylem: (*a*) *Licania heteromorpha*, TS (×70, FPRL 7178); (*b*) *Parinari excelsa*, TS (×70, CFI 874); (*c*) *Maranthes corymbosa*, LS (×70, CFI 7722); (*d*) *Licania splendens*, LS showing sclerosed tyloses (×350, CFI 12002); (*e*) *Couepia guianensis* subsp. *glandulosa*, LS showing silica grains (×350, CFI 5353); (*f*) *Chrysobalanus icaco*, LS showing gum deposits in ray cells (×350, CFI 5906).