A TAXONOMIC STUDY

OF THE

CHRYSOBALANACEAE

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by

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A B S T R A C T

The aim of this study has been to prepare a systematic revision of the genera of the family Chrysobalanaceae. At the outset of this research it was apparent that the distinctions between the subgenera and some other groups within the single genus Parinari Aubl. were much greater than the differences between other genera in the family. This is largely because most recent work has been done on a restricted regional basis and generic concepts differ widely in different regions. Most of the earlier workers only had access to incomplete material. For the present study complete material for more than 200 species was assembled. The wood anatomy of species representing all genera except Kostermansia Prance and Hunga Prance was studied. Pollen slides representing all genera were prepared. Seedlings from twenty-six species were also examined. Much useful anatomical information published by other workers has been brought together in this work. Papers on leaf anatomy by Küster (1897); the ovary by Juel (1915), leaf trace anatomy by Morvillez (1918a), and pedicel and floral anatomy by Bonne (1928) have all been of the greatest use.

The first author to give the group its present circumscription was Robert Brown (1818) who recognized it as a family. The last author, however, to monograph this group on a world-wide basis was De Candolle, who, in his 'Prodromus' (1825) placed it as the first tribe of his Rosaceae. Subsequent authors have been approximately equally divided into those who treat it as a family and those who treat it as a tribe or subfamily of the Rosaceae. However, the authors of the most widely used general systems of classification have been unanimous in placing it in the Rosaceae (Bentham & Hooker, 1865; Focke in Engler & Prantl, 1894; Hutchinson 1926, 1959). Focke's is the last work in which all genera

are described.

Focke recognized the following genera:- Chrysobalanus L., Grangeria Comm. ex Juss., Moquilea Aubl., Lecostemon ["Lecostomion"] Moc. & Sessé ex DC. and Stylobasium Desf. in the subtribe Chrysobalanineae, and Hirtella L., Couepia Aubl., Parinari Aubl., Acioa Aubl., Angelesia Korth. and Parastemon A. DC. in the subtribe Hirtellineae. Lecostemon and Stylobasium were included with some doubt and Focke suggested that they might be more closely related to Phytolaccaceae. Subsequent authors have added the genera Afrolicania Mildbr., Geobalanus Small and Magnistipula Engl.

At an early stage of this investigation it was found that Stylobasium and Lecostemon differ from all other Chrysobalanaceae in almost all important respects.

Focke, and all previous and some subsequent authors, have wrongly identified Lecostemon. In this work it is shown that the true Lecostemon is in fact a Sloanea of the Tiliaceae and that Lecostemon sensu Focke is correctly named Rhabdodendron, a genus which has been variously accommodated in Rutaceae and Phytolaccaceae. The present study has shown that Rhabdodendron is not only distinct from all Chrysobalanaceae in external morphology, wood anatomy and pollen morphology, but also differs from the Rutaceae in these respects. In wood anatomy it was found to be very similar to Phytolaccaceae. Its pollen is somewhat different from that of the Phytolaccaceae but not appreciably different from other members of the Centrospermae. In external morphology Rhabdodendron has many distinctive features most of which occur sporadically in the Centrospermae but not in combination. In view of this it seems preferable to treat it as a unigeneric family related to but distinct from the Phytolaccaceae. A Latin description of this new family is given, but it is realized that further work on its relationship to Phytolaccaceae is necessary before it should be published.

Many authors have suggested that Stylobasium does not belong to the Chrysobalanaceae or is an isolated member within it, but only Agardh (1858) described it as a separate family. It is shown in this study that Stylobasium is utterly different from all Chrysobalanaceae in external morphology, wood anatomy, pollen morphology and floral anatomy. In wood anatomy and pollen particularly there are striking similarities to certain members of the Sapindales, and it is suggested that Agardh's family should be recognized and placed near Sapindaceae and Anacardiaceae.

Purged of these two anomalous genera, the Chrysobalanaceae is now a homogeneous entity, whose wood structure and pollen morphology is so uniform that few genera can be discriminated on the basis of these characters. However, wood anatomy and pollen morphology are found to differ constantly and to an appreciable degree from the Rosaceae so much so that, taken in conjunction with the anatomical features described by Küster, Juel, Morvillez and Bonne, they seem to justify the recognition of the group as a family distinct from, although related to, the Rosaceae.

Most previous authors have variously subdivided the group. Their views are briefly summarized, and it is shown that anatomical characters provide no basis for a rational subdivision. In this work, for convenience, two tribes are recognized based on the symmetry of the flower.

In the Chrysobalaneae the ovary is inserted at or near the base of the receptacle-tube.

In the Hirtelleae the ovary is inserted laterally or at the mouth of the receptacle-tube.

Parinari is unique within the family in having its carpels partitioned by a false septum. This character has been used to define Parinari since it was originally described by Aublet in 1775, but visual inspection is enough to show that its uncritical use has given rise to an extremely heterogeneous assemblage. Some components of this are more closely related to genera outside Parinari than to the rest of Parinari. Some species have been assigned to Parinari which do not even have its artificial unifying feature. It was quite clear that currently accepted generic limits were untenable and that there were two alternative taxonomic procedures. Either all species within the family should be united to form a single genus Chrysobalanus or an attempt should be made to discover more natural groupings.

After a detailed study of the external morphology of more than 200 species, the author was satisfied that various segregates of Parinari should be recognized as genera, and that most of the other genera in the Chrysobalanaceae could conveniently be kept apart. However, it was decided to use a computer to demonstrate as objectively as possible the exact correlation of those characters believed by the author to be of greatest taxonomic worth and of all other important characters used by previous authors.

For the tribe Hirtelleae (which includes Parinari sens. lat.) eleven qualitative and ten quantitative characters were used and scored numerically for 124 species. An association-analysis was made for the qualitative data and a principle-component analysis for the quantitative data using programmes devised by Professor W.T. Williams and his associates for a Feranti 'Pegasus' computer. The entire data was analysed by a principle-component analysis programme by Mr. J.N.R. Jeffers for a Feranti 'Sirius' computer. This is possibly the first application of these techniques to a problem concerning generic identities of higher organisms. Although similar methods have been used in discriminating between closely related species, they do not seem to have been used at a higher level. The results of this work are illustrated and discussed at length, and it is shown that the groupings suggested by visual inspection are strikingly confirmed.

Other than Parinari, the limits of the remaining genera are, almost without exception, unaltered, except for Licania. Some authors previous to Focke (1894) had already suggested that Moquilea and Angelesia could not be kept apart from Licania. This is abundantly confirmed by the present study. Geobalanus, a small genus of North American suffrutices, was also found to belong here.

Three species of Parinari from New Caledonia are removed in this work to a new genus Hunga. The fact that all three had been independently described by other authors in Licania, and that yet another species originally placed in Angelesia is undoubtedly congeneric, illustrates the confused state of the genera in the family at the outset of the present study.

The generic changes indicated by this study are as follows:-

New name or new circumscription	Old name
Bafodeya Prance gen. nov.	: Parinari benna
Cyclandrophora Hasskl.	: Parinari subgenus Cyclandrophora
Duckea Prance gen. nov.	: Parinari subgenus Pellegriniella (partly)
Hunga Panch. ex Prance gen. nov.	: The species of Parinari and Licania described from New Caledonia and Angelesia papuana
Kostermansia Prance gen. nov.	: Parinari myriandra and P. heteropetala
Licania	: Licania + Moquilea + Angelesia + Geobalanus
Magnistipula	: Magnistipula + Hirtella subgenus Afrohirtella + Parinari tessmannii
Maranthes Blume	: Parinari subgenus Sarcostegia
Neocarya DC. ex Prance gen. nov.	: Parinari subgenus Neocarya
Parinari sens. strict.	: Parinari subgenus Parinari ["Euparinari"]

As a consequence of these generic changes it is necessary to make thirty-one new combinations. These are made in part 2 of the thesis which is a conspectus of the Chrysobalanaceae. In this conspectus the seventeen genera recognized are briefly described. Explanatory notes are given on such matters of taxonomy and nomenclature as seem pertinent. No attempt has been made in the present study to work out specific limits, but it is hoped to do this as a separate study later. Nevertheless, an attempt has been made to examine specimens of all described species with a view to confirming their generic identity. Specimens have been seen for at least ninety per cent of all previously described species. For all genera other than Hirtella and Licania currently accepted species are listed in the conspectus where the protologue, synonomy, distribution and type specimens are all given. Although detailed work has not yet been done at the specific level, it is the author's belief that the number of species listed approximates to the actual number which would be still recognized after detailed study.

The following list includes all new combinations made in the conspectus:-

Bafodeya (Parinari) benna (Sc. Elliot) Prance
Couepia (Parinari) canescens (Gleas.) Prance
Cyclandrophora (Parinari) asperula (Miq.) Prance
Cyclandrophora (Parinari) elata (King) Prance
Cyclandrophora (Parinari) indica (Bedd.) Prance
Cyclandrophora (Parinari) latifolia (Henderson) Prance
Cyclandrophora (Parinari) travancorica (Bedd.) Prance
Cyclandrophora (Parinari) vilamilii (Merr.) Prance
Duckea (Parinari) barbata (Ducke) Prance
Duckea (Parinari) cordata (Hook. f.) Prance
Duckea (Parinari) coriacea (Benth.) Prance
Duckea (Parinari) gardneri (Hook. f.) Prance

Hunga (*Licania*) *gerontogea* (Schlecht.) Prance

Hunga (*Licania*) *lifouana* (Däniker) Prance

Hunga (*Angelesia*) *papuana* (Bak. f.) Prance

Hunga (*Licania*) *rhamnoides* (Guillaum.) Prance

Kostermansia (*Parinari*) *heteropetala* (Scortech. ex King) Prance

Kostermansia (*Parinari*) *myriandra* (Merr.) Prance

Licania (*Angelesia*) *splendens* (Korth.) Prance

Magnistipula (*Hirtella*) *montana* (Hauman) Prance

Maranthes (*Parinari*) *aubrevillei* (Pellegr.) Prance

Maranthes (*Parinari*) *chrysophylla* (Oliv.) Prance

Maranthes (*Parinari*) *gabunensis* (Engl.) Prance

Maranthes (*Parinari*) *glabra* (Oliv.) Prance

Maranthes (*Parinari*) *goetzeniana* (Engl.) Prance

Maranthes (*Parinari*) *iodocalyx* (Engl.) Prance

Maranthes (*Parinari*) *kerstingii* (Engl.) Prance

Maranthes (*Parinari*) *poggei* (Engl.) Prance

Maranthes (*Parinari*) *polyandra* (Benth.) Prance

Maranthes (*Parinari*) *robusta* (Oliv.) Prance

Neocarya (*Parinari*) *macrophylla* (Sabine) Prance

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P A R T I

1. INTRODUCTION

In connexion with the preparation of certain recent regional floras in Africa a few alterations have been made to the accepted generic limits in the Rosaceae subfamily Chrysobalanoideae (Hauman 1951, Graham 1960). At the outset of this study, it was suggested to me that the distinctions between subgenera and other groups within the single genus Parinari were greater than those separating other genera in the subfamily. Accordingly it was decided to examine the generic limits critically using as much material as possible, and on a world-wide basis.

In recent years data collected from many parts of the plant have been increasingly resorted to in the solution of taxonomic problems (for example, secondary xylem, floral anatomy, pollen grain morphology and seedlings). This is especially true of studies concerning generic and family limits, see for instance Léonard (1957). As extravagant and exaggerated claims are sometimes made for new disciplines by their exponents, it was thought that a critical examination of wood anatomy, pollen morphology, and seedling characters of as many representatives as possible, considered in relation to a critical reappraisal of more orthodox taxonomic features, might both serve to test the value of these newer disciplines, and at the same time contribute to an improved classification of the group.

At an early stage of the investigation it was found that two genera Stylobasium and Lecostemon differ from all other Chrysobalanoideae in almost all important respects. Most previous authors have assigned these genera to the Chrysobalanoideae although sometimes with considerable misgivings. Other workers have suggested that they should be accommodated elsewhere. In chapters 8 and 9 convincing reasons for their exclusion from the group are given in some detail, and some suggestions as to their true relationship are offered. These two genera were found to differ in wood anatomy and pollen morphology to a striking degree from the Chrysobalanoideae.

It was found, however, that the Chrysobalanoideae sens. strict. are very uniform in both wood structure and pollen morphology, so that these features are of little value in the recognition of generic boundaries. Wood anatomy and pollen morphological features were found to differ constantly and to an appreciable degree from the rest of the Rosaceae, so much so that, taken in conjunction with certain other anatomical features described for the leaf anatomy by Küster (1897), for the ovary by Juel (1915), for leaf-trace anatomy by Morvillez (1918a), and for pedicel and floral anatomy by Bonne (1928), they seemed to justify the recognition of the Chrysobalanoideae as a family distinct from, although related to, the Rosaceae. This in fact confirms the view of Robert Brown (1818) and many subsequent authors. It will thus be seen that anatomical characters have been of most value in deciding the rank and contents of the group as a whole.

In the first edition of Engler and Prantl's "Die Natürlichen Pflanzenfamilien", Focke (1894) recognized the following genera in the group: Chrysobalanus, Grangeria, Moquilea, Licania, Hirtella, Couepia, "Parinarium", Acioa, Angelesia and Parastemon. Subsequent authors have added Afrolicania, Geobalanus and Magnistipula. Neither Focke nor other workers have made much use of fruit characters, perhaps because until recently they have been poorly represented in herbaria. A thorough examination of complete material of some 200 species indicated that Parinari could be split into seven homogeneous groups, which are separated by constant differences of greater magnitude than those separating nearly all other pairs of genera in the family.

The Chrysobalanaceae has not been monographed on a world-wide basis since the account in De Candolle's "Prodromus" in 1825. Because of this, some genera, particularly Parinari, have attained their current circumscription by a gradual process of accretion, and are defined differently in relation to other genera in different parts of their range. Parinari is unique within the family in having its carpels partitioned by a false septum. It is the automatic use of this artificial character that has been responsible for the great heterogeneity of this genus. A few of the species assigned to Parinari by various authors do not even have this unifying feature. Present generic limits in the family are clearly untenable. In view of the fact that Parinari contains more structural variation than all other genera put together there are only two taxonomic alternatives. Either all members of the family should be brought together to form a single genus Chrysobalanus, or Parinari should be split. The author was satisfied that these segregates of Parinari should be recognized as genera and that most of the other genera in the Chrysobalanaceae could conveniently be kept apart. However, it was decided to use a computer to demonstrate as objectively as possible the exact degree of correlation of those characters believed by the author to be of greatest taxonomic worth and all other important characters used by previous authors.

For the tribe Hirtelleae (which includes Parinari sens. lat.) eleven qualitative and ten quantitative characters were used and scored numerically for 124 species. An association-analysis was made for the qualitative data and a principle-component analysis for the quantitative data, using programmes devised by Professor W.T. Williams and his associates for a Feranti 'Pegasus' computer. The entire data were analysed by a principle-component analysis programme devised by Mr. J.N.R. Jeffers for a Feranti 'Sirius' computer.

This is possibly the first application of these techniques to a problem concerning generic identities of higher organisms. Although similar methods have been used in discriminating between closely related species, I do not think that they have been used at a higher level. The results of this work are discussed at length in Chapter 10, and it is shown that the groupings suggested by visual inspection are strikingly confirmed.

Other than Parinari the limits of the remaining genera are almost without exception, unaltered, except for Licania. Some authors previous to Focke (1894) had already suggested that Moquilea and Angelesia could not be kept apart from Licania. This is abundantly confirmed by the present study. Geobalanus a small genus of North American suffrutices, described by Small, was also found to belong here.

Three species of Parinari from New Caledonia are removed, in this work, to a new genus Hunga. The fact that all three had been independently described by other authors in Licania, and that yet another species originally placed in Angelesia is undoubtedly congeneric, illustrates the confused state of the genera in the family at the outset of the present study.

Because of the arrangement of chapters in this work, the names of the new genera are used in places in the text before the chapter in which the reasons for their recognition are given. In order to equate the new taxonomy suggested with the old, the following table is now given:-

New name or new circumscription		Old name
Bafodeya	:	Parinari benna
Cyclandrophora	:	Parinari subgenus Cyclandrophora
Duckea	:	Parinari subgenus Pellegriniella (partly)
Hunga	:	species of Parinari and Licania described from New Caledonia and Angelesia papuana
Kostermansia	:	Parinari myriandra and Parinari heteropetala
Licania	:	Licania + Moquilea + Angelesia + Geobalanus
Magnistipula	:	Magnistipula + Hirtella subgenus Afrohirtella + Parinari tessmannii
Maranthes	:	Parinari subgenus Sarcostegia
Neocarya	:	Parinari subgenus Neocarya
Parinari sens. strict.	:	Parinari subgenus Parinari ["Euparinari"]

The second part of this work is a conspectus, where the seventeen genera recognized by me are briefly described. Explanatory notes are given on such matters of taxonomy and nomenclature as seem pertinent. No attempt has been made, in the present study, to work out specific limits, but it is hoped to do this as a separate study later. Nevertheless, an attempt has been made to examine specimens of all described species with a view to confirming their generic identity. Specimens have been seen for at least ninety per cent of all previously described species. For all genera, other than Hirtella and Licania, currently accepted species are listed in the conspectus where the protologue, synonomy, distribution and type specimens are all given. Although detailed work has not yet been done at the specific level, it is the author's belief that the number of species listed approximates to the number which actually exist. The species have not been listed for Hirtella because it would appear that many currently accepted species are in fact synonyms but that thorough future work is needed before they are established as such.

In the case of <u>Licania</u> the reason for not listing the species is different. Most species of <u>Licania</u> have complicated synonomies and the author has had neither the time nor the opportunity to unravel these. For all genera other than <u>Hirtella</u> and <u>Licania</u> all published names are accounted for. Those not provisionally accepted as good species here are either placed in synonomy or reasons for their exclusion are indicated.

2. TAXONOMIC HISTORY

The first edition of the "Species Plantarum" (1753) contains two representatives of the Chrysobalanaceae - Chrysobalanus icaco which Linnaeus placed in Polyandria Monogynia, and Hirtella americana which he included in Triandria Monogynia. Their generic names for purposes of valid publication (Article 13, Note 2 of the current 'International Code of Botanical Nomenclature') are associated with the subsequent descriptions given in the 5th. edition of the 'Genera Plantarum', although both genera had been described in earlier editions of this work, and Hirtella received a full description in the 'Hortus Cliffortianus' (1737).

Aublet (1775) published six generic names later assigned to this group - Licania, Parinari, Couepia, Moquilea, Acioa and Ferolia, the last based on Barrère's pre-Linnean description (1747). Licania was placed in Pentandria Monogynia, Parinari, Couepia and Moquilea in Icosandria Polygynia, Acioa in Monadelphia Dodecandria and Ferolia in a group of plants only partially known. The surprising separation of Licania and Moquilea was due to misinterpretation of the flowers of Licania (see Aublet's figure); Aublet confused the calyx with the corolla and the bracteoles with the calyx. Ferolia which is based on a sterile specimen was later merged with Parinari by most authors, but, in my opinion, is not a member of the Chrysobalanaceae.

Schreber's 8th. edition of the 'Genera Plantarum' (1789) included five of the above genera. Schreber corrected Aublet's description of Licania and re-named it Hedycrea. He placed this genus and Hirtella in Pentandria Monogynia. He also altered Aublet's description of Parinari which he re-named as Petrocarya and transferred to Heptandria Monogynia. Chrysobalanus was placed in Icosandria Monogynia and Acioa (which he called "Acia") in Monadelphia Dodecandra. *Acia* of Schreber included *Couepia* which does not have a staminal ligule, although this is mentioned as a generic character.

Jussieu (1789) collected together all these genera for the first time as part of his family "Rosaceae", which he divided into seven tribes. The tribe *Prockiae* is defined "Germen unicum supernum monostylum. Fructus unilocularis mono aut polyspermus. Arbores aut frutices, interdum petalis carentes." *Prockiae* contains *Tigerea*, *Delima*, *Prockia* and *Hirtella*, only the last of which is still retained in Chrysobalanaceae. The tribe *Amygdaleae* is defined "Germen unicum supernum monostylum. Nux mono aut disperma, nuda aut saepios drupaceae. Arbores aut frutices." This contains eleven genera:- *Licania*, *Grangeria*, *Chrysobalanus*, *Cerasus*, *Prunus*, *Armeniaca*, *Amygdalus*, *Moquilea*, *Couepia*, *Acioa*, and *Parinari* ["*Parinarium*"]. Only the first three and the last four are true Chrysobalanaceae. *Grangeria*, based on a Commerson specimen from Réunion was described for the first time.

Robert Brown (1818) was the first to give family status to this group ["Chrysobalaneae"]. His family contained only true genera of the Chrysobalanaceae:- *Chrysobalanus*, *Moquilea*, *Grangeria*, *Couepia*, *Acioa*, *Licania*, *Hirtella*, *Thelira* and *Parinarium*. *Thelira* was described by Du Petit Thouars (1806), but is, in fact, a Mascarene *Hirtella*. Brown distinguished the family by the basal style, the erect embryo and the tendency to zygomorphy.

Desfontaines (1819) described a new genus *Stylobasium*, which he placed in the order Terebinthales, but it has generally been referred to the Chrysobalanaceae by most subsequent authors. In my opinion *Stylobasium* belongs to a distinct family. Its relationships are discussed in Chapter 9.

De Candolle in his 'Prodromus' (1825) placed the Chrysobalaneae of Robert Brown as the first tribe of his Rosaceae. He included Chrysobalanus, Moquilea, Couepia, Acioa, Parinarium, Grangeria, Licania, Thelira ["Thelyra"] and Hirtella. He also described a new genus, Lecostemon, from a drawing by Mociño* and Sessé 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 Chapter 8.

During the nineteenth century many South American Chrysobalanaceae were badly described and placed in wrong genera - e.g. among many similar instances Hoffmansegg (1825) placed Licania octandra in Hirtella and E. Meyer (1825) similarly misplaced Licania apetala. This led to much confusion. Martius (1826) redefined Moquilea to include Couepia and Acioa. This also led to many species being described in the wrong genus. Zuccarini (1832a, b), in papers describing the species of Chrysobalanaceae ["Chrysobalaneae"] preserved in the Munich herbarium, followed Martius' concept of Moquilea, except that he excluded Acioa of Aublet. He acknowledged that he had not seen Aublet's specimens of Acioa, Couepia or Moquilea. In fact, Moquilea sensu Martius and Zuccarini only included species of Couepia as defined today. Zuccarini defined the generic boundaries between Hirtella and Couepia and by transferring H. polyandra and H. dodecandra to Couepia (or rather Moquilea sensu Zuccarini) gave both genera their modern circumscription. He restricted Hirtella to species with less than ten stamens and a thin endocarp.

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,

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* Mociño and not Moçino as spelt by most authors.

Parinari ["Parinarium"], Grangeria, Licania, Thelyra, Hirtella, Stylobasium and Prinsepia. He also listed the synonyms known to him. Prinsepia was later removed to the Prunoideae by Bentham and Hooker.

Meisner (1836) was the first to make a key to the genera of the Chrysobalanaceae ["Chrysobalaneae"], the first tribe of his Rosaceae. As it includes several misplaced genera it differs from more recent keys. His genera are Roydsia Roxb. (now placed in the Capparidaceae), Trilepisium Pet.-Th. (a genus still of uncertain position), Lecostemon, Stylobasium, Licania, Parinarium, Chrysobalanus, Grangeria, Bartlingia Brongn. (= Pultenaea Sm., Papilionatae), Hirtella, Moquilea (Aubl.) Mart., Balantium Desv. and Thelyra. Balantium is a Parinari. The first four of these were only doubtfully included. He followed Martius in including Acioa and Couepia under Moquilea.

Endlicher (1840), (1842) placed the Chrysobalanaceae ["Chrysobalaneae"] in the order Rosiflorae. He included the genera Chrysobalanus, Hirtella, Licania, Moquilea, "Parinarium", Thelyra, Grangeria and Prinsepia Royle and three 'genera dubia' Lecostemon, Trilepisium and Stylobasium. Like Meisner he followed Martius in citing Acioa and Couepia as synonyms of Moquilea.

Bentham (1840) realized that generic limits in the Chrysobalanaceae were confused and gave a summary of the genera known to him:- Parinari ["Parinarium"], Chrysobalanus, Moquilea, Couepia, Grangeria, Hirtella and Licania. He did not see a good enough specimen of Acioa to decide on its status. He restored Couepia to generic rank, and shows that all the post-Aublet species of Moquilea belonged to it. He said that Thelyra and Prinsepia were unknown to him, and also discussed the affinities of the Chrysobalanaceae with the Leguminosae, and the Rosaceae.

A. De Candolle (1837) described Embelia urophylla

(Myrsinaceae) but later (1842) based a new genus, Parastemon, on it. This he tentatively placed in the Olacineae, but it is in fact a member of the Chrysobalanaceae.

Bentham (1849) when he wrote up the Chrysobalaneae for the 'Flora Nigritana' described two new species of Parinari and divided the genus into three sections - Petrocarya, Sarcostegia and Neocarya.

Korthals (1854) published two new genera, Angelesia and Diemenia, which were soon united by Miquel (1855) into the illegitimate Trichocarya. Angelesia is now placed in Licania and Diemenia is a Parastemon.

C. Mueller (1857) included the following genera in the family - Trichocarya, Coleogyne (now placed in Rosoideae), Pygeum (now placed in Prunoideae), Chrysobalanus, Licania, Moquilea (including Couepia and Acioa), Parinarium, Grangeria, Lecostemon and Parastemon. He included Angelesia and Diemenia among the excluded genera.

In the 'Genera Plantarum' Bentham and Hooker (1865) included the following genera in the "Chrysobalaneae", which they treated as a tribe of the Rosaceae - Chrysobalanus, Licania, Moquilea, Grangeria, Parinarium, Trichocarya, Parastemon, Hirtella, Couepia, Griffonia, Lecostemon and Stylobasium. They correctly placed Prinsepia in the Prunoideae [Pruneae], in spite of its basal style. They described the new genus, Griffonia, which is based on an African species of Acioa. They mistakenly reduced Thelyra to synonymy under Parinari.

Two years later J.D. Hooker (1867) described all the Brazilian species of Chrysobalanus, Licania, Moquilea, Hirtella, Couepia, Parinarium and Lecostemon, and made outstanding contribution to our knowledge of this family. He, however, considered Acioa as part of Couepia.

Baillon (1868) showed that Thelyra is a Hirtella. He also commented on the difficulty of subdividing the

Chrysobalanaceae. In his 'Histoire' (1869) he included it in the Rosaceae. He is the first author to arrange the genera into two groups, based on the symmetry of the flower. "Group a" contains Chrysobalanus, Licania (incl. Moquilea), Lecostemon and Stylobasium. "Group b" comprises Grangeria, Hirtella, Couepia, "Parinari", Acioa and Parastemon. He did not have access to material of Trichocarya. Baillon was the first worker to merge Licania with Moquilea. He also reduced Griffonia to synonymy under Acioa. His views have been largely accepted by later workers, although there are some errors in his work, particularly concerning the figures.

Miers (1880) gave new information about the fruits of Chrysobalanaceae, but the value of his work is reduced by several entirely unacceptable ideas. For example, he placed some South American species of Parinari in Licania; furthermore, his interpretation of the fruit is not entirely correct.

Fritsch (1888) considered the Chrysobalanaceae to be a well defined family, clearly separated from its nearest allies, the Rosaceae and Leguminosae. He made three subfamilies. (1) "Chrysobalaneae" including Chrysobalanus, Licania, Grangeria, Hirtella, Couepia, Acioa, Parinarium, Angelesia, ? Diemenia and Parastemon: (2) "Lecostemoneae" containing Lecostemon: (3) "Stylobasieae" containing Stylobasium. He gives a sketchy key to the genera. In 1889, he published a valuable conspectus of all species of the genus Licania, and gives reasons for uniting Licania and Moquilea. Several other authors have divided the Chrysobalanaceae in various ways. The most widely known of these is that of Focke (1894), in his account for the 'Pflanzenfamilien'. He gave the group the rank of a subfamily of the Rosaceae containing a single tribe which he divided into two subtribes, Chrysobalaninae and Hirtellinae. The genera included in the Chrysobalaninae are Chrysobalanus, Grangeria, Moquilea (kept separate from Licania), Licania, Lecostemon ["Lecostomion"] and Stylobasium. His second group includes _Hirtella_, _Couepia_, _Parinarium_, _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 sub-tribal groupings. He regarded _Lecostemon_ and _Stylobasium_ as anomalous members of the group and suggested a relationship with the Phytolaccaceae. Classifications of the Chrysobalanaceae subsequent to Focke's are dealt with in Chapter 7.

Küster (1894) published an extremely detailed account of the anatomy of the stem and leaf of eleven genera of the Chrysobalanaceae, including _Stylobasium_ and _Lecostemon_, and also of _Prinsepia_. Although Küster himself drew no conclusions from his work it does have some interesting taxonomic implications. Hallier (1903) draws attention to some of these. He was impressed by the fact that the Chrysobalanaceae are very well characterized by a series of anatomical features. He suggested that _Stylobasium_ does not belong there, but in _Prunoideae_ ["_Amygdaloideae_"] somewhere near to _Prinsepia_ and _Dichotomanthes_, that _Moquilea_, _Licania_ and _Angelesia_ should be united and that _Lecostemon_ truly belongs to the Chrysobalanaceae, but is isolated within it. His groupings of the genera are largely supported by the present study and are dealt with in some detail in Chapter 7.

All important generic synonyms are mentioned in the foregoing summary. During the Nineteenth Century many others were published mostly by authors with little knowledge of the group, e.g. at least eleven for the genus _Parinari_. This information is summarized under the appropriate genera in the Conspectus which forms the second part of this work.

During the present century only three new genera have been described. Much work on the floral anatomy of the Chrysobalanaceae has been done. This is discussed in Chapter 3. Authors have been generally divided as to whether the group should be treated as a family or as a subfamily of the Rosaceae. Widely divergent views on its phylogenetic relationships have been expressed. These are discussed in Chapter 6.

In 1903 Engler described Magnistipula from Africa. Most authors since then have united it, at least in part, with Hirtella, but recent work has shown that it is, in fact, distinct. Rhabdodendron was described by Gilg and Pilger in 1905 in Rutaceae. Subsequently, the species of Lecostemon, as defined by Bentham, were transferred to it by authors who believed that the original Lecostemon of De Candolle was a different plant. It has now been established that Lecostemon is in fact Sloanea terniflora (DC.) Standl. (Tiliaceae). Widely divergent views on the affinities of Rhabdodendron have been published. In Chapter 8 it is shown that it must be excluded from Chrysobalanaceae, and its relationships are discussed in detail there. Finally, in 1921 Mildbraed described Afrolicania which is not only distinct from all other genera in certain floral and fruit characters, but has a distinctive wood anatomy as well.

3. ANATOMY

During the last seventy years, a number of important works have been published on various aspects of the anatomy of the Chrysobalanaceae. Many of these are of considerable taxonomic importance, but, for the most part, have been ignored by, or even unknown to, English-speaking botanists. Papers by the following authors are considered at some length below - Küster (1894) on the anatomy of the leaf and primary stem; Juel (1915) on the structure of the gynoecium; Morvillez (1918) on leaf-trace anatomy; Bonne (1925, 1928) on the anatomy of the flower and pedicel. A short paper by Dalziel (1930) draws attention to the taxonomic value of the hairs lining the endocarp of the fruit.

No single author appears to have made a comprehensive study of the anatomy of the secondary xylem. Accounts in general works such as Solereder (1899) and Metcalfe and Chalk (1950) are syntheses of the scattered observation of many workers. In this study, I have examined the secondary xylem of seventy-two species belonging to all genera, as circumscribed by me, except for Hunga and Kostermansia. The details of wood anatomy given below are based entirely on my own observations.

(a) Anatomy of the Primary Stem and Leaf

A detailed study of primary stem and leaf anatomy was made by Küster (1897), in which he gives a description of the family as a whole, and of each genus individually. Küster's account is so detailed and comprehensive that no original work was necessary for the present study. Küster obtained his material from herbarium sheets in the Munich herbarium. I examined all these specimens to confirm their generic identity, during a visit to Munich. Küster studied seventy-six species of eleven genera of the Chrysobalanaceae, three species of Rhabdodendron and one each of Stylobasium and Prinsepia.

All later descriptions of the anatomy of the Chrysobalanaceae are based on Küster's work. Küster himself drew no taxonomic conclusions from his work, some taxonomic implications are discussed below.

Hallier (1903) is the only taxonomist who has considered Küster's work. He gave the group family rank, but did not discuss its relationship to other families.

He pointed out that Küster's work showed the unity of the Chrysobalanaceae as a group. The family is characterized by the following features, which do not occur in the Rosaceae: (1) the abundance of silica deposits. Küster described silica deposited in five ways, silicified membranes, silica-plugs, silica-bodies, silica-sacs and intercellular deposits of silica; (2) the ring of sclerenchymatous fibres in the pericycle which is usually continuous and mixed with stone cells which are thickened only on one side, thus appearing U-shaped in transverse section; (3) the "Rubiaceous" stomata which are confined to the leaf-undersurface. In the Rosaceae the stomata are "Ranunculaceous". Hallier also adds that the Chrysobalanaceae are well characterized by a series of other anatomical features, but he does not list them. Kuster's work shows that there are many differential characters separating the Chrysobalanaceae and Rosaceae. For example, (1) the fibrelike spicular cells in the mesophyll of some genera of the Chrysobalanaceae; (2) the xylem in the form of a cylinder traversed by narrow rays; (3) the cork of superficial origin; (4) the occurrence of hypoderm in the majority of genera.

Hallier showed how Küster's work demonstrated that the genera Prinsepia, Stylobasium and Rhabdodendron ["Lecostemon"] differ from the Chrysobalanaceae in their primary anatomy. In these three genera there are no silica membranes or deposits of intercellular silica; the stomata do not have distinctly different accessory cells; the mesophyll contains much spongy tissue.

In addition to these features, Prinsepia and Stylobasium differ in having no silica of any type; no stone cells, thickened on one side only; no sclerenchymatous ring in the pericycle; the palisade cells are radial, and there is no superficially generated cork. Prinsepia is further different in the transversely divided, paired palisade cells; the chambered medulla; and the occurrence of spiral bands in the wood prosenchyma. Stylobasium has stomata evenly distributed on both sides of the leaf blade, and simple pits in the wood prosenchyma.

Rhabdodendron also differs in possessing peltate hairs, and in the occurrence of fatty bodies in the mesophyll. The fact that Rhabdodendron has silica-bodies in the medullary rays, intercellular silica in the epidermis, and secretory cavities similar to those of Couepia bracteosa led Hallier to believe, at the time of writing, that it belonged to the Chrysobalanaceae but as a separate subtribe Lecostomonineae. In a later publication Hallier (1923) assigned Rhabdodendron to the Rutaceae.

Hallier does not discuss the value of anatomical characters from a generic point of view. For the present study I have tabulated Küster's anatomical data (see Appendix 2) and a number of tentative conclusions emerge.

The Chrysobalanaceae are relatively uniform in their anatomical structure, and hence, the latter is of comparatively small value for determining generic limits. Many of the features, mentioned by Küster, are exceptions that occur in one species only, or in two species from different genera, e.g. secretory cavities occur only in Couepia bracteosa. However, support is lent to the separation of certain genera.

Couepia appears to be a very constant group, as five major features appear in all species. These are, (1) the cells of the outer epidermis are palisade-like and elongated (otherwise only known in _Licania_ and one species of _Maranthes_) and usually with the outer wall thickened; (2) the nerves have both a ring of sclerenchyma and sclerenchyma plates (also found in _Hirtella_ and most _Licania_); (3) when indumentum is present it is arachnoid (also found in _Licania_, _Maranthes_ and _Duckea_); (4) the siliceous bodies in the nerves are globular (also found in 1 _Hirtella_ and most _Licania_); (5) tannin sacs occur in the secondary phloem (also in a species of _Licania_ and in _Maranthes_).

Couepia is well differentiated from _Hirtella_, since they share only one major feature (the occurrence of sclerenchymatous plates together with the sclerenchymatous ring in the leaf nerves). Nearly all species of _Hirtella_ have three positive features, not occurring in _Couepia_ - (1) mucilaginous epidermal cells (also in one species of _Maranthes_ and _Geobalanus_); (2) palisade glands on leaf underside (also in _Acioa_, _Chrysobalanus_ and _Licania_); (3) cone-shaped siliceous bodies in nerves (_Hirtella_ only).

Grangeria is distinct from all _Hirtella_ species in three features: (1) cells of lower epidermis develop a mucilaginous hypoderm (also in _Parastemon_); (2) the nerves do not have sclerenchymatous plates (also in _Licania_, _Parinari_, _Maranthes_, _Duckea_ and _Neocarya_); (3) palisade glands are absent (also in _Couepia_, _Parinari_, _Maranthes_, _Duckea_ and _Neocarya_).
The table shows that there are no anatomical grounds for maintaining _Moquilea_. There is no one character separating from _Licania_ but, on the other hand, there are several features shared by some species of both genera. The anatomy does, however, show variation within this genus.

Parastemon is shown to be closely related to Grangeria. They both have:- (1) mucilaginous hypoderm developing in the cells of the upper and lower epidermis; (2) the nerves have a sclerenchymatous ring but no sclerenchyma plate.

The anatomy gives no positive evidence for, or against, the regrouping of Parinari.

(b) Structure of the Gynoecium

In 1915, Juel published a remarkably thorough study of the structure of the gynoecium of Parinari capensis and Magnistipula bangweolensis. He showed that the gynoecium differs fundamentally from all Rosaceae, and suggested that the Chrysobalanaceae is a group worthy of family rank.

Among the Rosaceae, the Chrysobalanoideae were believed to be most closely related to the Prunoideae. Prinsepia, which has a lateral style was placed in the Chrysobalanaceae, by Lindley (1836), and later removed to the Prunoideae, by Bentham and Hooker (1865). At first sight it appears to form a connecting link between these two groups. Juel showed, however, that the lateral style is actually apical at an early stage of development, and becomes lateral because of unequal growth. The ovules in Prunoideae are pendulous, but in Chrysobalanaceae basal.

Juel showed that the style of Parinari is distinctly 3-lobed at the apex, and that it 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 essentially similar, except that in some flowers a second carpel is also well-developed. Juel suggested that the primitive gynoecium of the Chrysobalanaceae consists of 3 free carpels united by a gynobasic style, similar to that of a trimerous Limnanthaceae. He did not suggest any relationship to that family, contrary to the statements of Bonne (1925) and Hauman (1951). All the plants examined during the present work have at least a shallowly 3-lobed style, and in many the style is deeply lobed. Two or three carpels occur sporadically in flowers of species belonging to about half the genera.

(c) Leaf-trace Anatomy

Morvillez (1918a) described the leaf-trace anatomy of the Chrysobalanaceae. It differs from that of Rosaceae in that at the distal end of the petiole there is an abaxial closed ring of xylem and phloem which shows various modifications towards the adaxial side in different genera and species. He described seven types of modification (which are also listed in Metcalfe and Chalk, 1950); but transitional stages between these types occur. Since he studied only a few species of each genus, and there is a transition between the types, his work is not of use at the generic level. He suggests that the leaf-trace anatomy is much more like the type found in the Caesalpinioideae. His conclusion based on his anatomical work is that the Chrysobalanaceae constitute a separate family to be placed between the Rosaceae and Leguminoseae. His descriptions of the related families are in separate papers. Morvillez (1917) - Rosaceae; (1918b) - Caesalpinioideae; (1918c) - Saxifragaceae; and (1919) - Papilionoideae and Mimosoideae.

(d) Vascular Anatomy of the Flower and Pedicel

A study of the pedicel and of the floral vascular supply was made by G. Bonne (1928). This was a study of the entire Rosaceae including the Chrysobalanaceae. Her work is divided into four sections: (1) a comparison of the pedicel structure with that of the axis of the inflorescence; (2) the structure of the floral articulation; (3) the anatomy of the pedicel; and (4) the floral vascular supply. Bonne's work included many genera of the Chrysobalanaceae. In order to incorporate the information discovered by Bonne into the present work, a small amount of further investigation was made to confirm Bonne's findings, and to examine the genera not discussed by her (Afrolicania, Hunga, Magnistipula, Neocarya and Licania (Geobalanus)). Bonne sectioned the pedicels and flowers, but it was found quicker to use a modern clearing technique for the additional work. That described by Bersier and Bocquet (1960) using chloral-lactophenol acid (CLPA) was chosen. The main difficulty with the Chrysobalanaceae is the initial removal of pigments. A strong bleaching agent must be used in addition to the initial treatment in sodium hydroxide.

The floral articulation is a region on the pedicel with a special structure. It is a constriction noticeable on the pedicels of most Chrysobalanceae. The flowers are mostly caducous, but some pedicels are "sub-articular" and the flowers do not fall. These sub-articular pedicels bear the fruit. The articulation is a meristematic region, which is characterized by the large amount of inclusions in the cells of that region. The details of the structure are described by Bonne. Traces of this articulation occur in the Prunoideae and Sanguisorbeae, but only the Chrysobalanaceae have a well defined articulation which plays a definite role. Stylobasium has an articulation. The region below the articulation has the same structure as the axis of the inflorescence. The region above has a different anatomical structure and constitutes the true pedicel. The Chrysobalanaceae have a very uniform pedicel structure. There are slight differences in the vascular supply between genera with actinomorphic and those with zygomorphic flowers.

Stylobasium, unlike true Chrysobalanaceae, has its cortex divided into two zones.

The most important part of the work for the taxonomist is the study of the floral vascular system. The vascular supply to the various floral organs is illustrated in Plate VI. It can be seen that there is considerable variation, although this is also largely connected with level of ovary insertion.

Bonne shows that there are three main types of vascular arrangements within the Rosaceae sens. lat., and that Stylobasium differs from all Rosaceae sens. strict., and from Chrysobalanaceae, mainly in the following four features. (1) the absence of a disc; (2) the course of the vascular traces in the pedicel and the base of the flower; the staminal bundles do not arise from the perianth trace but from the carpel traces; (3) the gamosepalous calyx; (4) the cortical parenchyma of the pedicel is divided into two zones. It also differs from the Chrysobalanaceae by the unicarpellary ovary.

The Chrysobalanaceae and the Neuradoideae differ from the rest of the Rosaceae in having a different pedicel structure, and by the different courses taken by the vascular bundles. The Neuradoideae are distinct in having a well-developed mucilaginous system in the flowers and pedicel. The status and relationship of this group are not discussed further in this work, but it is interesting to note that the pollen of Grielum was examined and found to be quite different from all other Rosaceae; (Erdtman (1952) also points out that the pollen of Neurada is different from the Rosaceae). Bonne concludes her work by saying that it tends to emphasize the need to separate the Neuradoideae and the Chrysobalanoideae from the Rosaceae.

Bonne proposed a new grouping of the genera of the Chrysobalanaceae which is discussed in Chapter 7. Her conclusions about the arrangement of the genera are very obscurely expressed, and are poorly grounded. She separated Stylobasium into a group on its own.

(e) Hairy Lining of the Endocarp

In a brief note Dalziel (1930) pointed out that three species of *Parinari* (as then circumscribed) have hairs lining the endocarp of fundamentally different types. It is of interest to note that on independent grounds these are now placed in different genera. 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 curled and reduced in length, forming only a velvety cushion lining the inside. In *P. benna* (now *Bafodeya benna*) they are perfectly straight, hollow, needle-shaped "spines" which project stiffly into the cavity.

(f) Anatomy of the Secondary Xylem

The Chrysobalanaceae have a uniform wood structure. The differences between some genera are often no greater than the difference between species in other genera. Since the structure of the wood is so uniform, it has not been necessary to describe it separately for each genus. A few genera have distinctive features, and these are discussed after the family description which follows.

Growth rings are often present, marked by periodic wider spacings of parenchyma bands; present or absent in different samples of the same species. Vessels typically exclusively solitary, occasionally in radial multiples of 2-5 cells, especially in *Acioa*, usually in pairs in *Afrolicania*, typically with an oblique arrangement, moderately large in most genera, mean tangential diameter 200-300 μ; always fewer than 20 per sq. mm. and fewer than 5 per sq. mm. in some species; without spiral thickenings; perforations exclusively simple; intervascular pitting alternate, never minute; ray-vessel pits large, of varying shape, alternate; tyloses frequent, especially in *Magnistipula*, *Maranthes*, Licania and Angelesia, occasionally sclerosed in Licania and in the one sample of Angelesia examined; mean vessel length 0.6 - 0.8 mm. Parenchyma exclusively apotracheal, abundant, in numerous fine continuous bands usually 1 (locally 2) cells wide, 6-11 bands per mm.; less often 2-3 cells wide; less than 6 per mm. in Parinari sens. strict.; bands obscure in Neocarya and Afrolicania; in Afrolicania forming a reticulate pattern of 1-seriate bands; parenchyma strands up to 16 cells high; gum deposits frequent. Rays predominantly uniseriate, exclusively so in Chrysobalanus, Duckea, Grangeria, Hirtella and Licania and with some biseriate in all other genera except Afrolicania in which they are predominatly biseriate; rays never more than 2-seriate; commonly more than 1 mm. high in Couepia, Parastemon, Parinari, Maranthes, Cyclandrophora and Afrolicania; in the latter higher than in any others, commonly over 2 mm. high; usually heterogeneous (Kribs Type III), almost homogeneous in Parastemon; gum deposits abundant; pits to axial parenchyma large. Silica inclusions are present in the ray cells of many species. Fibres usually thick-walled, rather thinner in Parinari and Neocarya and some species of Licania; with numerous distinctly bordered pits on the tangential walls, more numerous and often biseriate in wider cells bordering vessels; pits on radial walls almost entirely limited to areas in contact with rays. Mean length 1.3 - 1.4 mm.

The wood is moderately to very hard and heavy. Specific Gravity 0.75 - 1.10. It is hard 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 in detail by Amos (1952).

The wood of the Chrysobalanaceae is illustrated in Plates I-IVa.

Taxonomic Discussion

All evidence which has been considered, and not only wood anatomy, has shown that Rhabdodendron and Stylobasium do not belong to the Chrysobalanaceae. They are treated separately in Chapters 8 and 9 respectively.

The Chrysobalanaceae are distinguished from the Rosaceae by several important features; 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.

Although the Chrysobalanaceae are thus well distinguished from the Rosaceae, the woods of the two families appear, nevertheless, to be related. The perforations are simple, the parenchyma usually apotracheal, and the fibre pits bordered in both families. The vessels of the Rosaceae are typically small (i.e. less than 100 μ diam.), but they may be moderately large in some genera e.g. Hagenia and Pygeum. The vessels may also be partially solitary as in Eriobotrya, Cydonia and Malus, but in these genera they are usually more crowded than in the Chrysobalanaceae.

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

The Prunoideae are distinct in wood structure from the rest of the Rosaceae, in the fibres that have less distinctly bordered pits which are less numerous on the tangential than on the radial walls, and in the vessels that are commonly arranged in an oblique radial pattern in cross section. The Prunoideae is, in fact, the only tribe of the Rosaceae sens. strict. that can be distinguished from the others by the wood structure. The differences given above are clearly less than those between the Chrysobalanaceae and the Rosaceae. Record and Hess (1943) and Chalk (1950) both point out that the _Chrysobalanoideae_ is distinct enough to be regarded as a family of its own, and that the affinities of the _Prunoideae_ judged by wood structure are within the Rosaceae. Chalk (1950) refers to the Chrysobalanaceae as "_Rosaceae_ - _Chrysobalanoideae_" but describes it separately from the rest of the Rosaceae, and clearly indicates that it ought to be given family rank.

The basic uniformity of the wood within the family is apparent from the description. It is interesting to note that wood structure does not support the subdivisions of the family in a hierarchical manner. For example, the woods of _Chrysobalanus_ and _Maranthes_ or _Licania_ and _Parinari_ sens. strict. are scarcely different. This suggests (contrary to Hauman (1951) and Nakai (1943)) that the subdivisions of the family are only units of convenience. A few genera are distinct in their wood characters:- _Afrolicania_ in the arrangement of its vessels and parenchyma, and the height of its rays (Plate I-C and II-A), _Parastemon_ in its almost homogeneous rays. It is interesting that _Afrolicania_ has such a distinctive wood. This indicates its divergence from _Licania_, and gives extra support for maintaining it as a genus. The wood of _Parinari_ sens. strict. is extremely uniform (Plate I-B, II-C). It is distinguished from wood of other genera by its wider parenchyma bands, a feature which is constant in the samples examined from all parts of its range. _Duckea_ is distinguishable from other _Parinari_ sens. lat. by its exclusively uniseriate rays (Plate II-B). Similarly, _Neocarya_ is distinct on account of the scarcity of its vessels, and the more diffuse, and scarcely banded parenchyma (Plate IV-E).

It is interesting that _Angelesia_, (Plate II-A) and a few species of _Licania_ are the only Chrysobalanaceae with sclerosed tyloses. This is an indication that these two genera, which it is proposed to unite, are closely related to one another. There are no wood characters that are inconsistent with uniting these two genera.

Plate IV illustrates the secondary xylem of five species of Parinari sens. lat. now placed in five different genera (Maranthes, Duckea, Parinari, Cyclandrophora and Neocarya). A comparison with Plate IVa illustrating five widely accepted genera (Chrysobalanus, Grangeria, Hirtella, Licania and Parastemon) clearly shows that the differences between groups of species within the old genus Parinari are often as great as the differences between well-established genera elsewhere in the family.

Various phylogenists during the present century have suggested diverse relationships for the Chrysobalanaceae with other families. Hallier (1923) united the Chrysobalanaceae, Dichapetalaceae and Trigoniaceae to form a single family, which he suggests, is derived from the Linaceae and Polygalaceae. In 1915, Juel correctly interpreted the trimerous ovary of the Chrysobalanaceae for the first time, and compared its essentially gynobasic structure with Limnanthes, but did not suggest that they were in any way related. Bonne (1925) appears to have misread Juel's paper, and suggests a phylogenetic connection between Chrysobalanaceae and Limnanthaceae or Tropaeolaceae. Hauman (1951) suggests relationship with Tropaeolaceae and Geraniaceae. Gutzwiller, (1962), whose knowledge was based chiefly on Stylobasium (now excluded), Parinari and Chrysobalanus, suggested that the Chrysobalanaceae, along with the Connaraceae, should be transferred to the Sapindales, and placed next to the Sapindaceae.

Wood structure does not confirm a close relationship with any of these families. It certainly does not support Hallier's (1923) grouping together of the Chrysobalanaceae, Dichapetalaceae and Trigoniaceae.

The Dichapetalaceae differ from the Chrysobalanaceae in the greater frequency of their much smaller vessels, the occurrence of sclariform perforation plates, the minute intervascular pitting, the predominantly paratracheal parenchyma, the 5 to 6-seriate rays, and the small borders to the fibre pits.

The Trigoniaceae differ in having vessels that are not obliquely arranged, in the rarity of intervascular pitting, the diffuse and unbanded parenchyma, the rays which are commonly up to 4 cells wide, and the occurrence of septate fibres.

From their wood structure the Linaceae belong to a group containing the Humiraceae, Erythroxylaceae, Polygalaceae, Tremandraceae, Trigoniaceae, Zygophyllaceae.

The families that have been grouped with the Linaceae because of their similarities in wood structure, for the most part possess tracheids with conspicuously bordered pit pairs, or have fibres with indistinctly bordered simple pit pairs; their rays are heterogeneous (Kribs types I or IIA); their parenchyma is scanty, paratracheal, or predominantly apotracheal.

The Linaceae differ from the Chrysobalanaceae in their smaller vessels, the occurence of sclariform perforation plates, the scarcity of intervascular pitting, the parenchyma which is extremely varied, and is never of apotracheal bands of the type found in the Chrysobalanaceae, in many genera the parenchyma is paratracheal. The multiseriate rays are generally of Kribs type I-IIB, and there is frequent occurrence of tracheids, which vary from long fibre-tracheids to short vasicentric tracheids.

The Polygalaceae, (excluding Xanthophyllum whose wood is very different from most of the Polygalaceae) differ from the Chrysobalanaceae in their smaller vessels, the scarcity of intervascular pitting in the genera with solitary vessels, the predominantly paratracheal or diffuse parenchyma. In addition to this, various features, which do not occur in the

Chrysobalanaceae, occur in some genera of the Polygalaceae; for example, vasicentric tracheids and included phloem of the concentric type.

Heimsch (1942) points out that the following families have close resemblance in their wood and anatomical structure, the Geraniaceae, Oxalidaceae, Tropaeolaceae, Limnanthaceae and the Balsaminaceae. This is the group which Bonne (1925) and Hauman (1915) have connected with the Chrysobalanaceae.

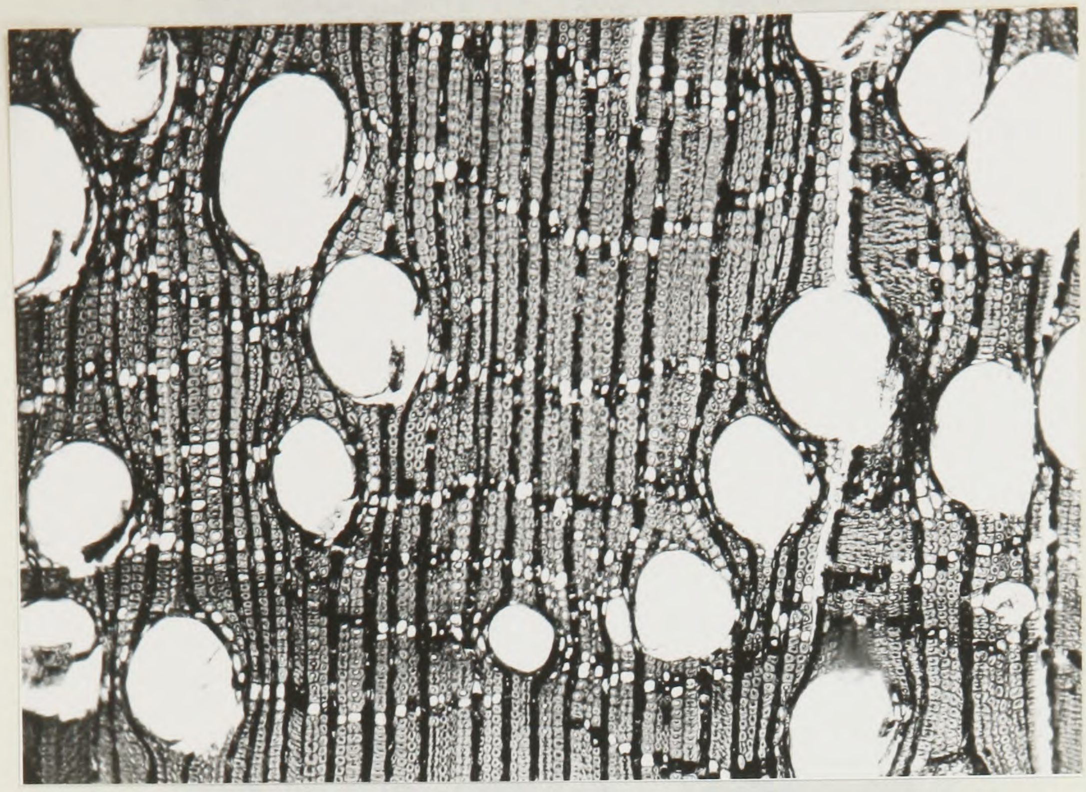
The xylem of the Geraniaceae, and these related families, differs from that of the Chrysobalanaceae in that the vessels are often in multiples, multiperforate plates occur, intervascular pitting is not large, the parenchyma is paratracheal and scanty, the rays are usually few and extremely variable in length and width, the fibres have indistinctly bordered pits and thin walls and are frequently septate. There is thus, no evidence that the wood of the Chrysobalanaceae is related to this group.

Heimsch (1942) also pointed out that the Sapindaceae, Anacardiaceae, Rutaceae, Simaroubaceae, Meliaceae and Burseraceae form a more or less natural group of families judged by wood structure. The wood of Sapindaceae differs from that of the Chrysobalanaceae in the much smaller vessels which are less than 100 μ in diameter, and are more crowded; they are also predominantly in multiples. The intervascular pitting is small to minute. The parenchyma is mostly paratracheal, and never banded. The fibres have simple pits, are rarely thick-walled, and are commonly septate. The only striking similarity between the Sapindaceae and Chrysobalanaceae is the occurrence of uniseriate rays. The wood anatomy indicates that the Chrysobalanaceae do not belong near to the Sapindaceae and these related families. However, it may be observed that Gutzwiller's suggestion that the Connaraceae belong nearer to the Sapindaceae than to the Rosaceae, is certainly supported by wood anatomy.

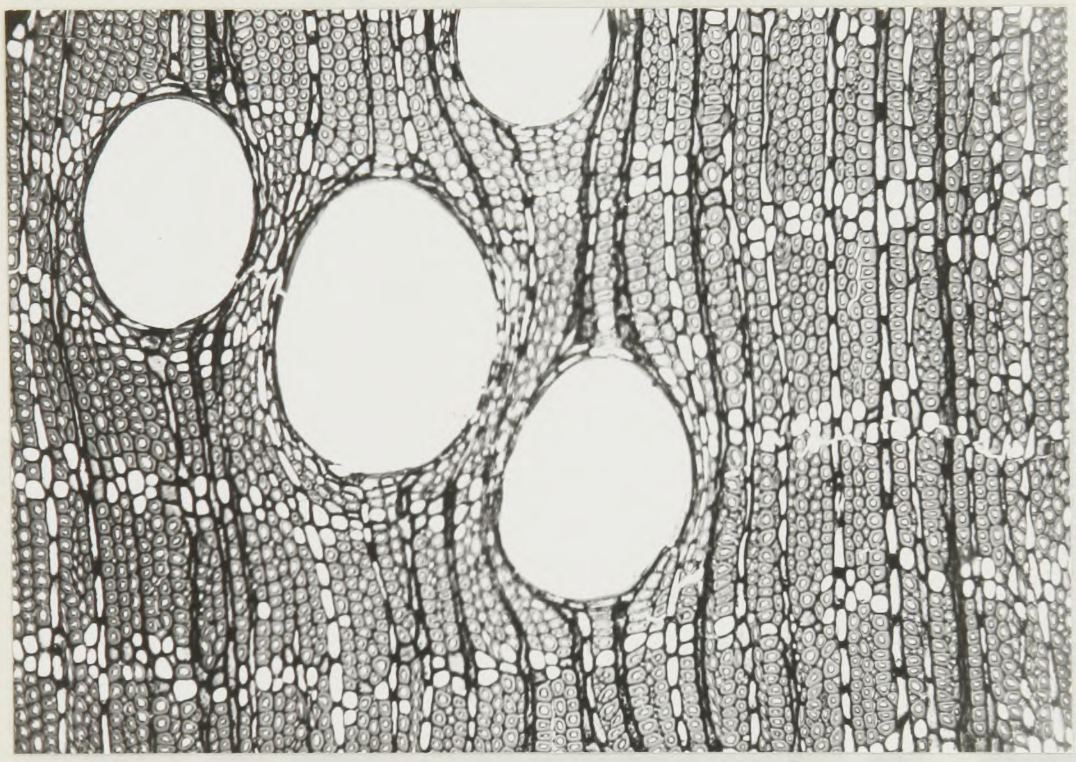
Most taxonomists who have given family rank to the Chrysobalanaceae (for example, Bentham (1840), Fritsch (1888), Wettstein (1933) and Gundersen (1950)) have placed it between the Rosaceae and the Leguminosae. The differences between wood anatomy of Rosaceae and Chrysobalanaceae have already been given.

The wood of the Leguminosae has several characteristic features such as vestured pitting, nevertheless there is considerable variation in other characters. It differs from that of the Chrysobalanaceae in the type of intervascular pitting, which is smaller and vestured, in the predominantly paratracheal parenchyma and the simple fibre pits. Most of the features of the Chrysobalanaceae wood occur in at least several genera of the Caesalpinioideae and Mimosoideae. In common with the Chrysobalanaceae, especially in the Mimosoideae, the vessels are often predominantly uniseriate and the perforations are simple. There are sufficient similarities to justify keeping the Chrysobalanaceae near to the Leguminosae. The woods of the Chrysobalanaceae, Leguminosae and Rosaceae are of about the same level of specialization.

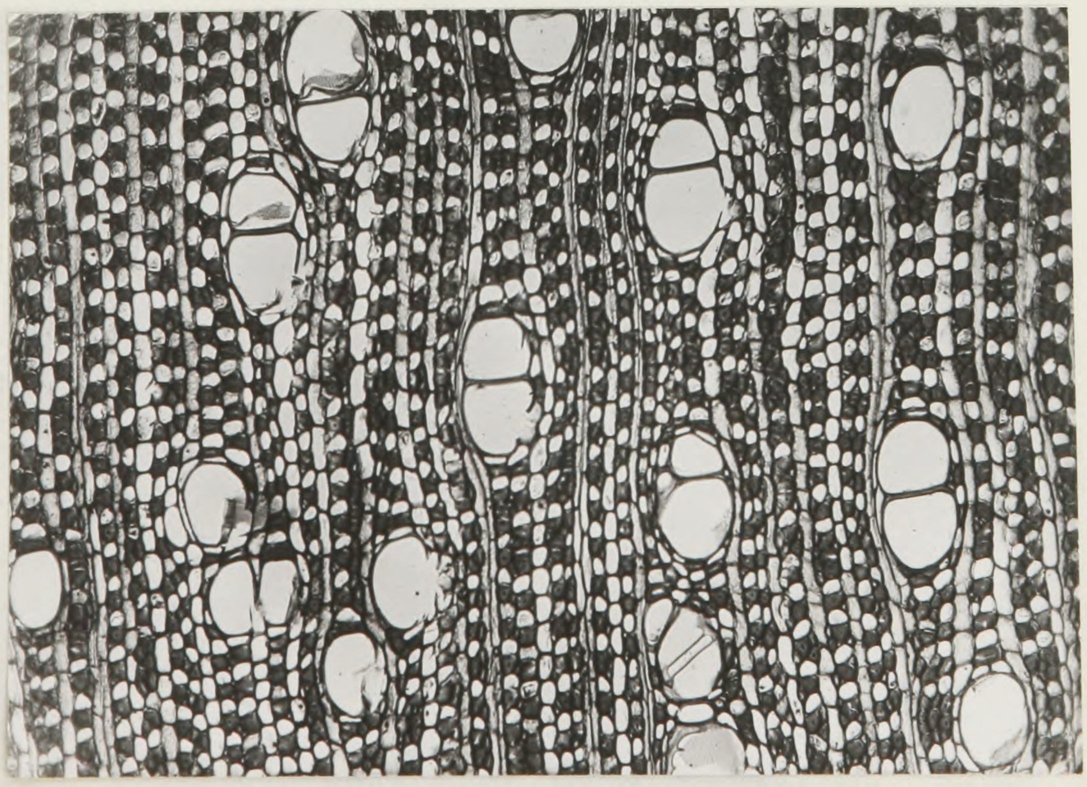
In conclusion it may be said that the wood of the Chrysobalanaceae has equal affinities with that of the Rosaceae and Leguminosae, and in fact provides a connecting link between the two.



A. Licania heteromorpha



B. Parinari excelsa

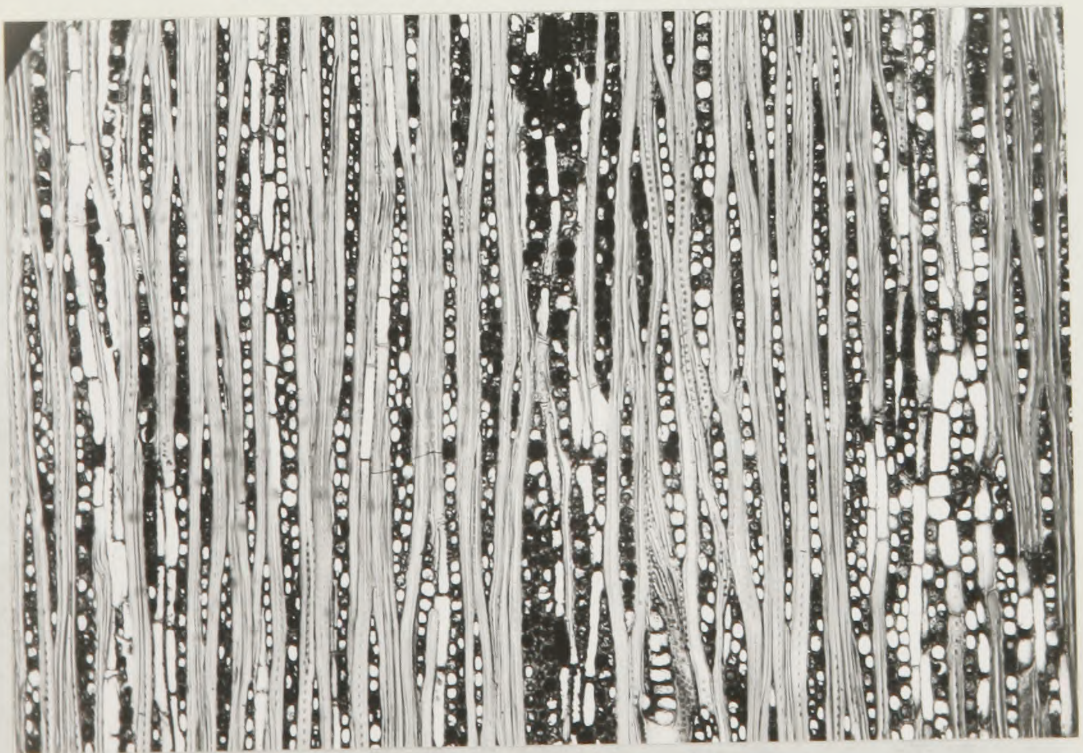


C. Afrolicania elaeosperma

Plate I - The wood of the Chrysobalanaceae X.S. x15.

A. Afrolicania elaeosperma

B. Duckea barbata

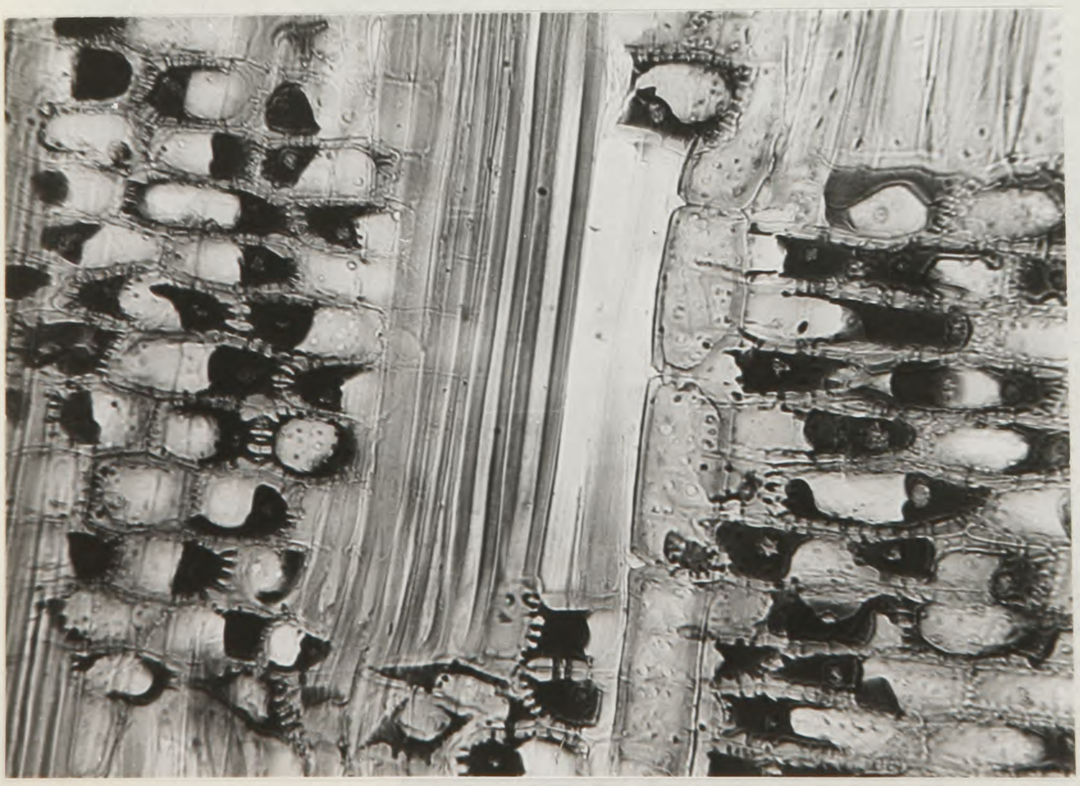


C. Maranthes corymbosa

Plate II- The wood of the Chrysobalanaceae T.S. x15.

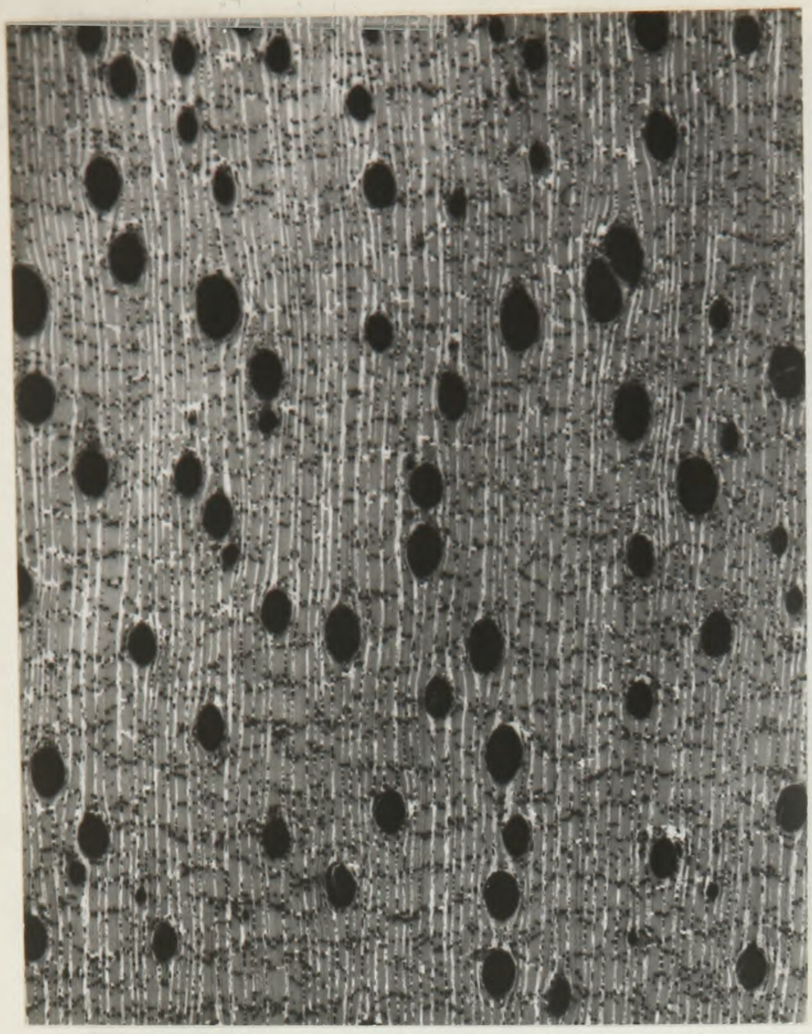
A. Licania (Angelesia) splendens

B. Couepia glandulosa



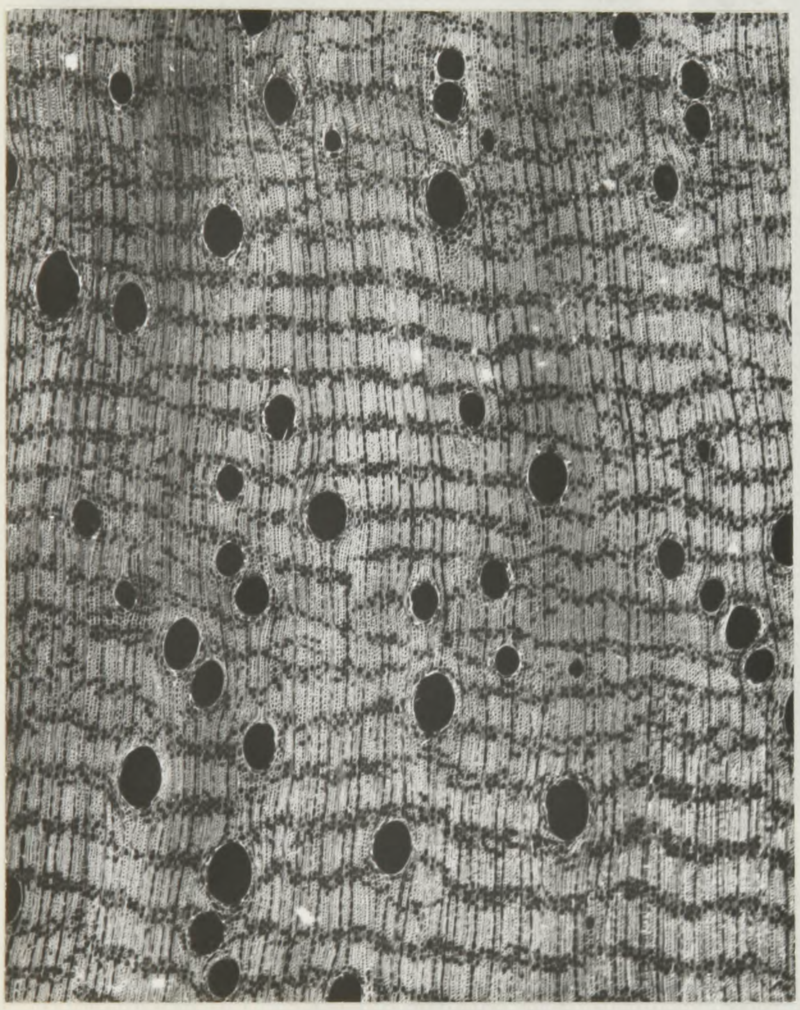
C. Chrysobalanus icaco

PlateIII - The wood of the Chrysobalanaceae T.S. x60.

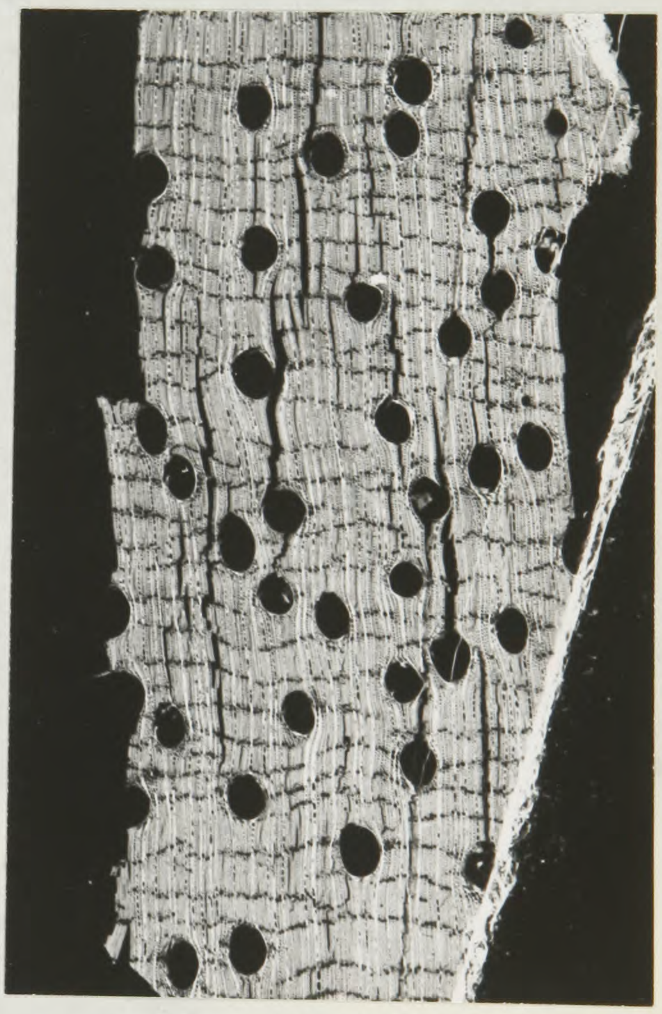


Maranthes corymbosa

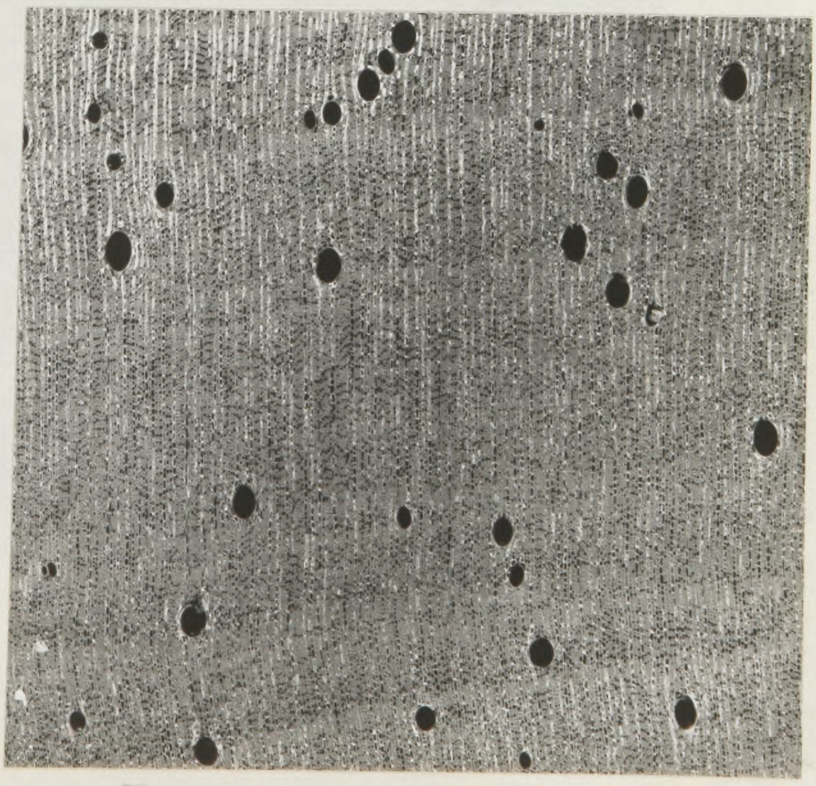
Duckea barbata



Parinari curatellifolia

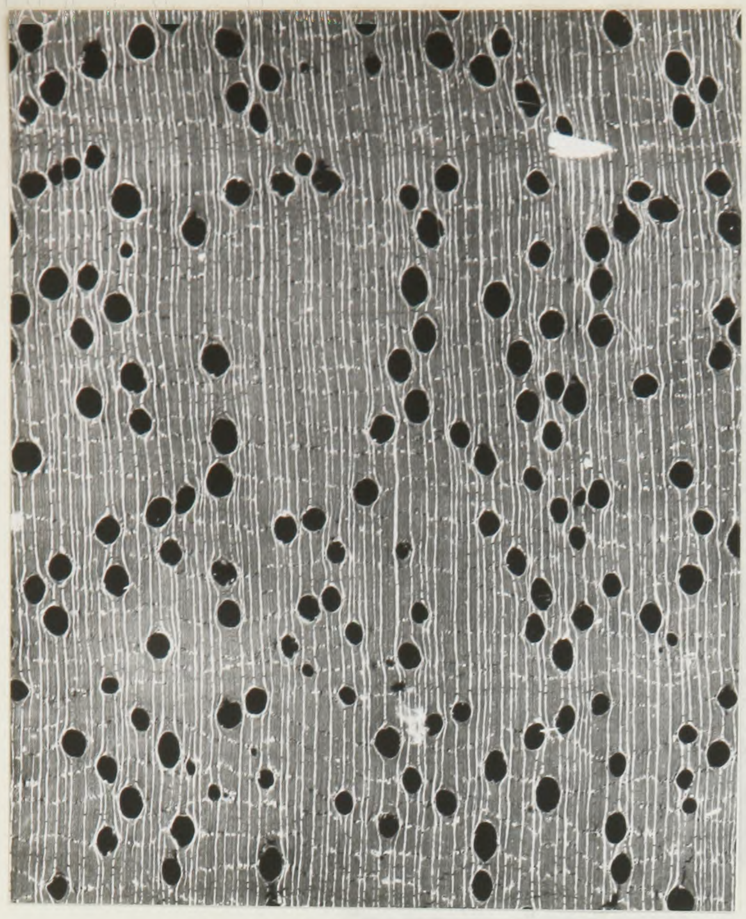


Cyclandrophora asperula



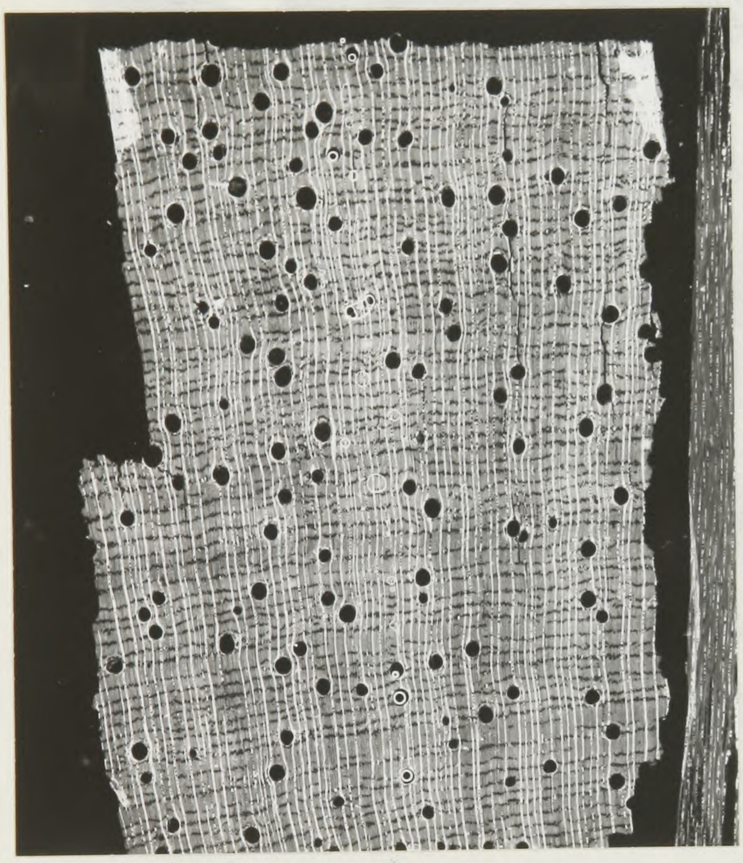
Neocarya macrophylla

Plate IV - The diversity of the wood within the genus <u>Parinari</u> sens.lat. X.S. x15.

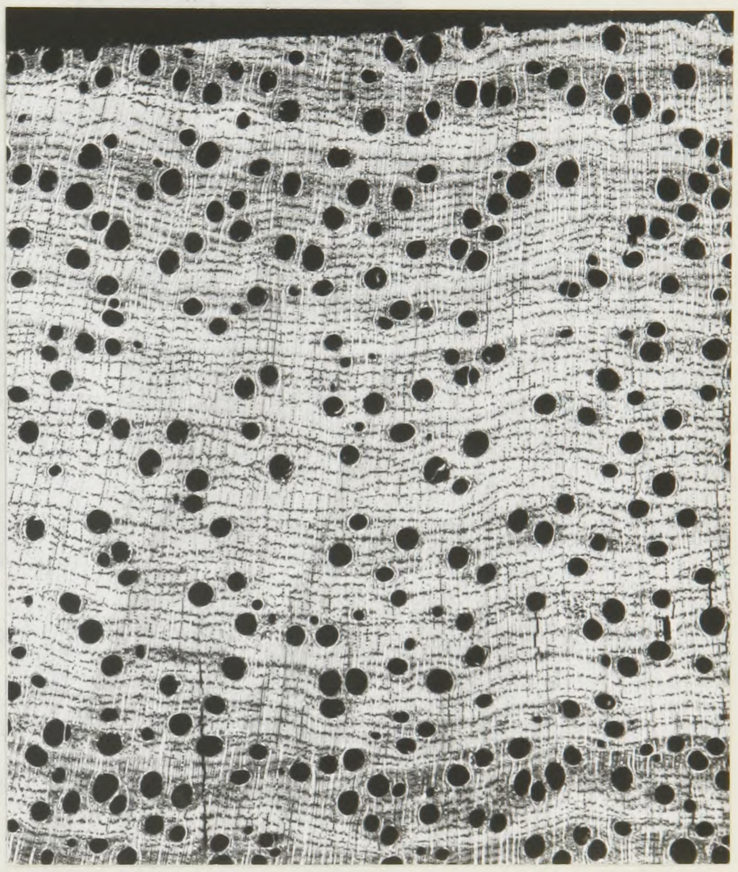


Parastemon urophyllus

Chrysobalanus icaco



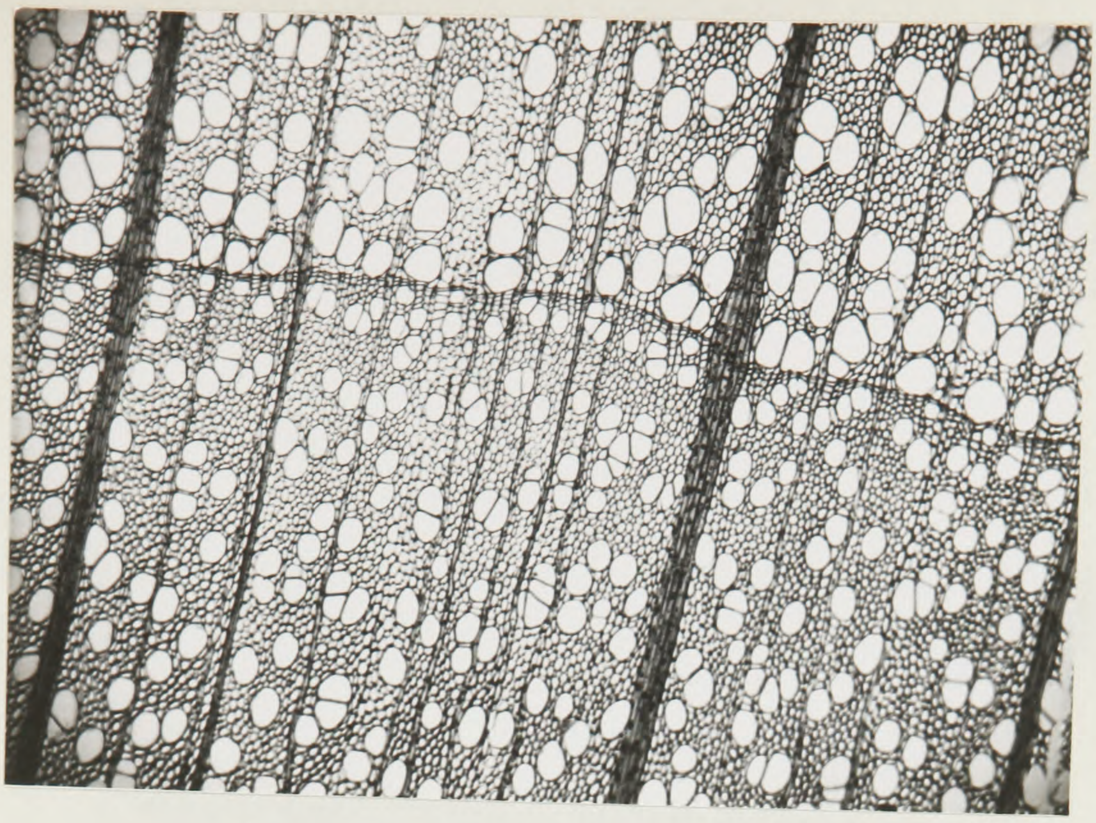
Grangeria borbonica



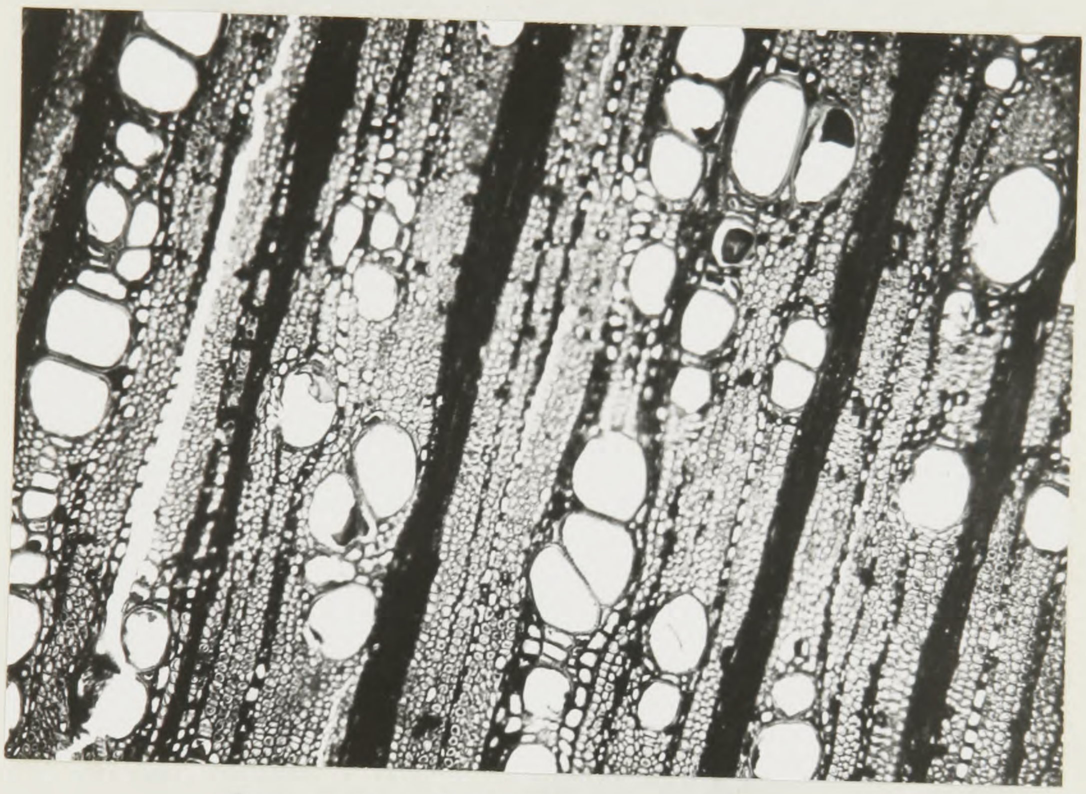
Hirtella triandra

Licania biglandulosa

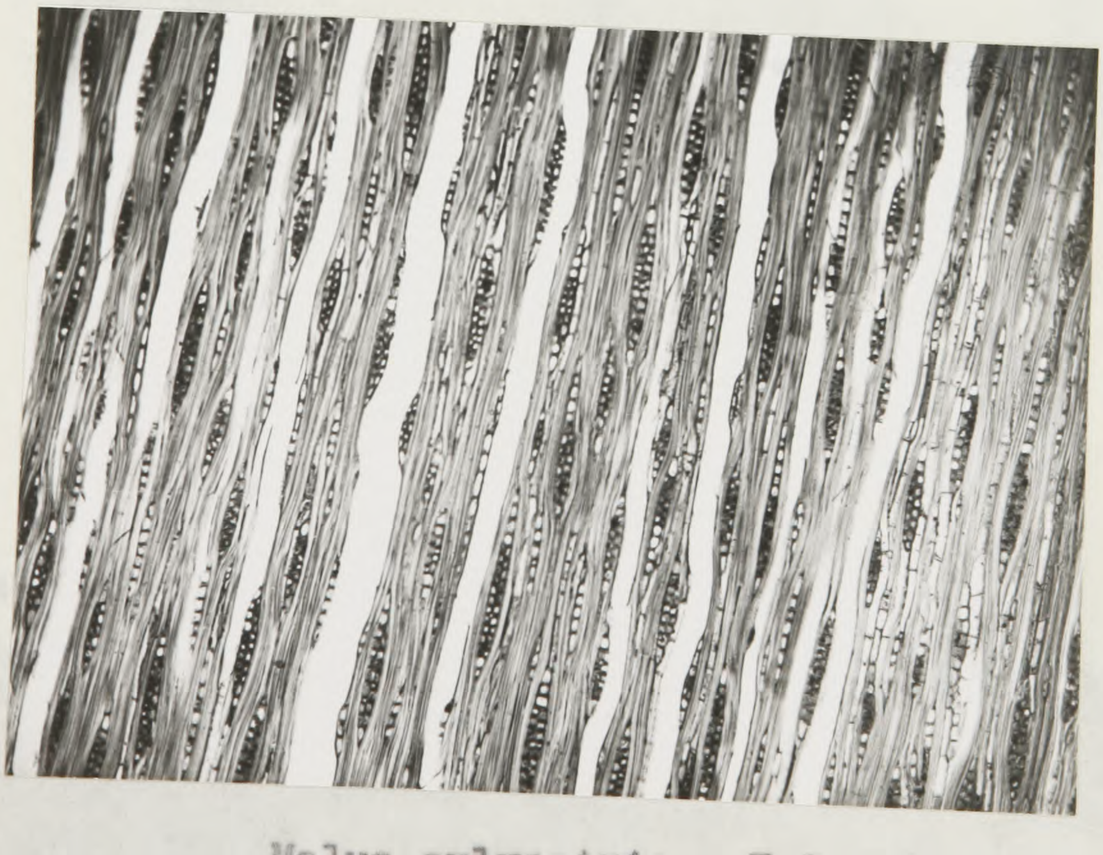
Plate-IVa-The wood of the Chrysobalanaceae X.S. x12.



Prunus demissa - X.S. x15.



Pygeum africanum - X.S. x15.



Malus sylvestris - T.S. x15.

Plate V - The wood of the Rosaceae.

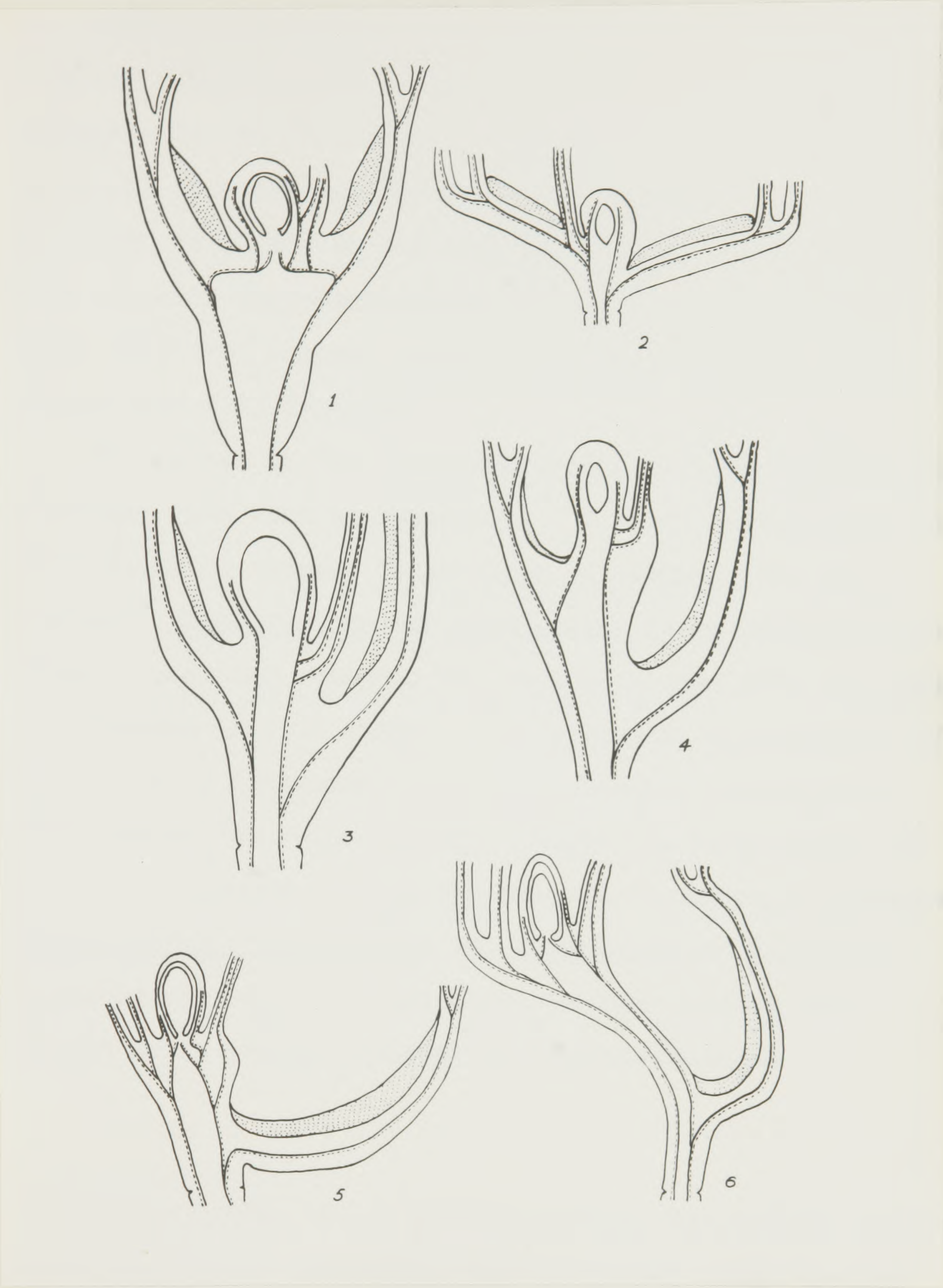


Plate VI - The floral vascular anatomy.

1. *Chrysobalanus icaco* L. (x20) 2. *Afrolicania elaeosperma* Mildbr. (x30) 3. *Geobalanus oblongifolius* (Michx.) Small (X15) 4. *Grangeria borbonica* Lam. (x15) 5. *Neocarya macrophylla* (Sabine) Prance (x10) 6. *Magnistipula bangweolensis* (R.E.Fr.) R.Graham (x10). (1 & 4 after Bonne, 2,3,5 & 6 original).

4. POLLEN MORPHOLOGY

Slides were prepared (by the method used by Dr. G.W. Dimbleby - see Appendix 3) from flowers of 30 species belonging to all 17 genera of Chrysobalanaceae. A further 18 slides from species belonging to genera of Rosaceae, and 14 slides belonging to families with which various authors have believed Chrysobalanaceae to be related, were made. About 35 slides already made in the collections at Kew and Oxford were also examined.

The pollen of the Chrysobalanaceae is very uniform, but different from that of Rosaceae. It is of little value in distinguishing between or grouping the genera, but the pollen of _Rhabdodendron_ and _Stylobasium_ is so different that strong supporting evidence for excluding them from the group was obtained in this study. The taxonomic significance of the pollen is discussed after the following description which covers the whole family. Plate VII illustrates the grains of 4 genera of Chrysobalanaceae, 5 genera of Rosaceae, _Rhabdodendron_, _Stylobasium_, and _Tropaeolum_ and _Serjania_ (Sapindaceae), two families which various authors have thought to be closely related to Chrysobalanaceae.

Pollen grains with 3 furrows without any special features except occasional equatorial constrictions; some species have both grains with 3 and 4 furrows; without distinct pores; usually distinctly triangular in shape in polar view, except when 4 furrowed, elliptical to circular in equatorial view; oblate-spheroidal, prolate-spheroidal or subprolate in shape as indicated by the ratio - 100 polar length : equatorial length = 85-150. Size very variable from one genus to another, polar area usually small, sometimes medium, but never large. Exine medium to rather thick, very little patterning on the walls, usually scabrate to verrucate, never striate.

Chrysobalanaceae pollen is easily distinguishable from that of the Rosaceae but is clearly similar to it. It is different in the markedly triangular shape in polar view in the expanded grain. The Rosaceae are rounder to 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." The present study of Rosaceae pollen (sens. lat.) confirms that three main types of pollen occur. The Rosaceae sens. strict., the Chrysobalanaceae and the Neuradoideae types. The latter tribe of the Rosaceae has a very different pollen from the rest. Pollen study, and indeed many morphological features, indicate that it does not belong to the Rosaceae.

Various phylogenists during the present century have suggested diverse relationships between the Chrysobalanaceae and other families. Hallier (1923) united Chrysobalanaceae, Dichapetalaceae and Trigoniaceae to form a single family which he suggests is derived from Linaceae and Polygalaceae. In 1915 Juel correctly interpreted the ovary of Chrysobalanaceae for the first time and compared its essentially gynobasic structure with Limnanthes, but did not suggest that they were in any way related. Bonne (1925) appears to have misread Juel's paper and suggests a phylogenetic connection between Chrysobalanaceae and Limnanthaceae and Tropaeolaceae. Hauman (1951) suggests relationship with Tropaeolaceae and

Geraniaceae. Gutzwiller (1962) whose knowledge was chiefly based on Stylobasium (now excluded) Parinari and Chrysobalanus suggested that Chrysobalanaceae, along with Connaraceae, should be transferred to Sapindales and placed next to Sapindaceae. I have examined pollen from all these families and find no important similarities between them and Chrysobalanaceae. It is of interest, however, to note that in the case of Stylobasium Gutzwiller appears to be correct (see Plate VII 8 & 20, pollen of Stylobasium and Serjania (Sapindaceae) and Chapter 9).

The differences between Chrysobalanaceae and the Rosaceae are, however, comparatively small, whilst the pollen of the Tropaeolaceae, Geraniaceae, Limnanthaceae, Linaceae, Polygalaceae and Sapindaceae are all distinctive and very different from the Rosaceae type. Pollen thus supports the reasons for keeping the Chrysobalanaceae near to the Rosaceae in the Rosales, and not removing it to the Geraniales or Sapindales as has been suggested by various botanists.

The plate shows typical Chrysobalanaceae pollen 1-7, Rosaceae 10-18, families to which relationship with the Chrysobalanaceae has been suggested 19 and 20. It also shows that the pollen of Stylobasium 8, and Rhabdodendron 9 is quite different from that of the Chrysobalanaceae and supports their exclusion. The pollen of these two genera is described separately in chapters 8 and 9 since they do not belong to the Chrysobalanaceae, and so must be considered in more detail individually.

The pollen of all Chrysobalanaceae is so similar that it does not provide good generic characters. Neocarya (Parinari) macrophylla is distinguishable from other Parinari sens. lat. by the size of the grain (50-100 µ). Afrolicania (15-25 µ) is conspicuous in having the smallest pollen grain. 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_. _Kostermansia_ (_Parinari_) _myriandra_ is distinct from all other Chrysobalanaceae examined, including African and South American _Acioa_, in having three swellings on each of the triangular sides of the exine walls visible in polar view. Apart from _Kostermansia_ no other genus is clearly definable on pollen characters.

Plate VII - The pollen of the Chrysobalanaceae and related families. (x600).

1-7.CHRYSOBALANACEAE: 1.Parinari myriandra 2,3,7. Hirtella glandulosa 4.Chrysobalanus icaco 5,6.Grangeria borbonica. 8.STYLOBASIACEAE:-Stylobasium spathulatum. 9.RHABDODENRACEAE: -Rhabdodendron sylvestris. 10-18.ROSACEAE: 10,11.Cliffortia nitidula 12,13.Rubus caesius 14,15.Pyrus communis 16,17. Pygeum africanum 18.Grielum sp. 19.TROPAEOLACEAE:- Tropaeolum peltophorum. 20. SAPINDACEAE :- Serjania caracasana.

5. BLASTOGENY

The use of seedling characters in systematic botany has been very much neglected, but where it has been applied it has usually yielded useful information, especially at the generic level, as exemplified in Léonard's recent work (Léonard, 1957). Seedling characters are useful to the taxonomist have been clearly defined by Léonard, and so it is unnecessary to discuss them further. Many difficulties are encountered in the use of blastogeny, for example lack of herbarium material, difficulty in obtaining viable seed, and sometimes difficulty in germinating the seed. This was especially true of the present work because of its comparatively short duration. A list of material used is given in Appendix 1-D, and it can be seen that much of the information has been gathered from herbarium material from two sources; (1) the Herbarium Plantularum Yangambiense collected under the direction of Prof. M.G. Gilbert, and (2) the seedling collections made by D.B. Fanshawe from British Guiana and Northern Rhodesia from the forest nurseries. I have, however, germinated at Oxford seeds of as many species as it has been possible to obtain over the past three years. The results are incomplete, and it is hoped, in the future to accumulate additional seedling information from species of all genera of the Chrysobalanaceae. Nevertheless the results already gathered give extra information, which both demonstrates the value of blastogeny as a part of systematic botany and confirms some of the taxonomic decisions made on other grounds.

Table 1 summarizes the most important differences between seedlings of different members of the Chrysobalanaceae. From this it can be seen that the majority of genera have the same basic type of germination; that is hypogeal and with the first leaves alternate. So far this has been recorded in Chrysobalanus, Licania, Afrolicania, Couepia, Hirtella, Parinari, Cyclandrophora and Neocarya. Within this group Parinari is distinct in the number of persistent appendages on the epicotyle (Plate VIII). Perhaps the most interesting fact yielded by blastogeny is the heterogeneity within the group formerly considered as Parinari. The subgenus Sarcostegia (elevated to the genus Maranthes in the present work) has epigeal germination and opposite first leaves, in this it is different from all the rest of Parinari sens. lat. and indeed from all the rest of the Chrysobalanaceae observed so far (Plates IX, X). This gives strong support for removing Maranthes from Parinari. As Couepia is probably the closest genus to Maranthes, it is interesting to observe that it does not have the same type of germination as Maranthes. This type of germination has been observed in species of Maranthes from both Africa and Asia, indicating the constancy of this character within the genus. The third main type of germination is found in Magnistipula and Acioa. These two genera have hypogeal germination and opposite first leaves. In Magnistipula there are four first leaves arising at about the same level, in fact they are sub-verticellate. This has not been observed in any other genera of the Chrysobalanaceae. All the species of Magnistipula whose seedlings have so far been examined have been placed in Hirtella by Hauman (1951). Blastogeny gives supporting evidence for the separation of Hirtella and Magnistipula in the way proposed in the present work. It would be of great interest in the future to observe the type or germination in members of Magnistipula placed in that genus by Hauman (1951). The first leaves of Acioa are paired, and are not of the sub-verticellate type found in Magnistipula; otherwise these two genera come very close on seedling characters. This is not surprising considering their similarities in fruit structure. The tomentum of the epicotyl, the shape and aspect of the young leaves all indicate that these two genera are closely related.

It is possible to give additional characters to the ones already mentioned, but most of these are really dependent upon the position of the cotyledons and first leaves, (for example length of hypocotyl and epicotyl) and can hardly be considered as generic characters without determining their constancy by observation of a large number of species from each genus. It is, however, of interest to note that the first leaves have the type of undersurface characteristic of the genus to which they belong, except that they may be more hairy (as in *Afrolicania elaeosperma* and *Acioa dewevrei*). The first leaves of *Parinari* have the stomatal cavities so characteristic of that genus, those of *Couepia comosa* and *C. versicolor* have a tomentum similar to the adult leaves, those of *Hirtella paniculata* have long, stiff, brown hairs which serve to diagnose the genus from *Couepia*, and those of *Acioa* have two glands at the base of the lamina.

The seedlings of *Stylobasium* (Plate XXIV) have epigeal germination and alternate first leaves. A combination of characters which has not been observed in the Chrysobalanaceae.

It must be emphasized that only a few species of each genus have been observed to date, but it is hoped to gather additional material in the future, since blastogeny yields such useful taxonomic information.

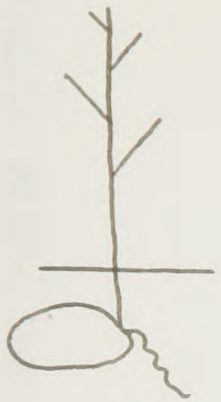
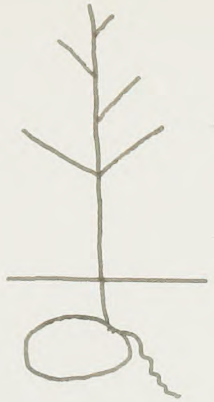
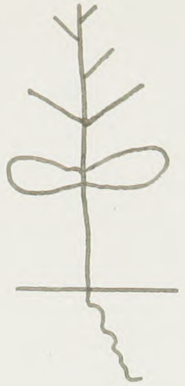
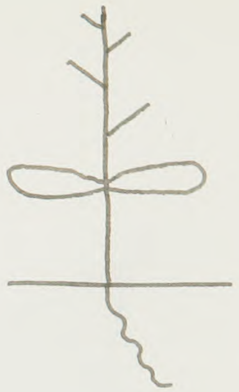
 HYPOGEAL 1° LVS-ALT	 HYPOGEAL 1° LVS-ALT	 EPIGEAL 1° LVS-OPP	 EPIGEAL 1° LVS-OPP
Chrysobalanus icaco Chrysobalanus atacorensis Licania divaricata Licania buxifolia Licania heteromorpha Licania kunthiana Licania venosa Afrolicania elaeosperma Couepia exflexa Couepia comosa Couepia versicolor Hirtella paniculata Hirtella racemosa Parinari excelsa Parinari parvifolia Parinari campestris Cyclandrophora glaberrima Neocarya macrophylla	Magnistipula bangweolensis Magnistipula butayei Magnistipula montana Magnistipula sp. II Acioa dewevrei Acioa sp.	Maranthes glabra Maranthes corymbosa	Stylobasium spathulatum

Table I - Types of Germination in the Chrysobalanaceae

Plate VIII- The seedling of Parinari campestris Aubl. ($X\frac{1}{2}$).

Plate IX - The seedling of <u>Maranthes corymbosa</u> Blume (x $\frac{1}{2}$).

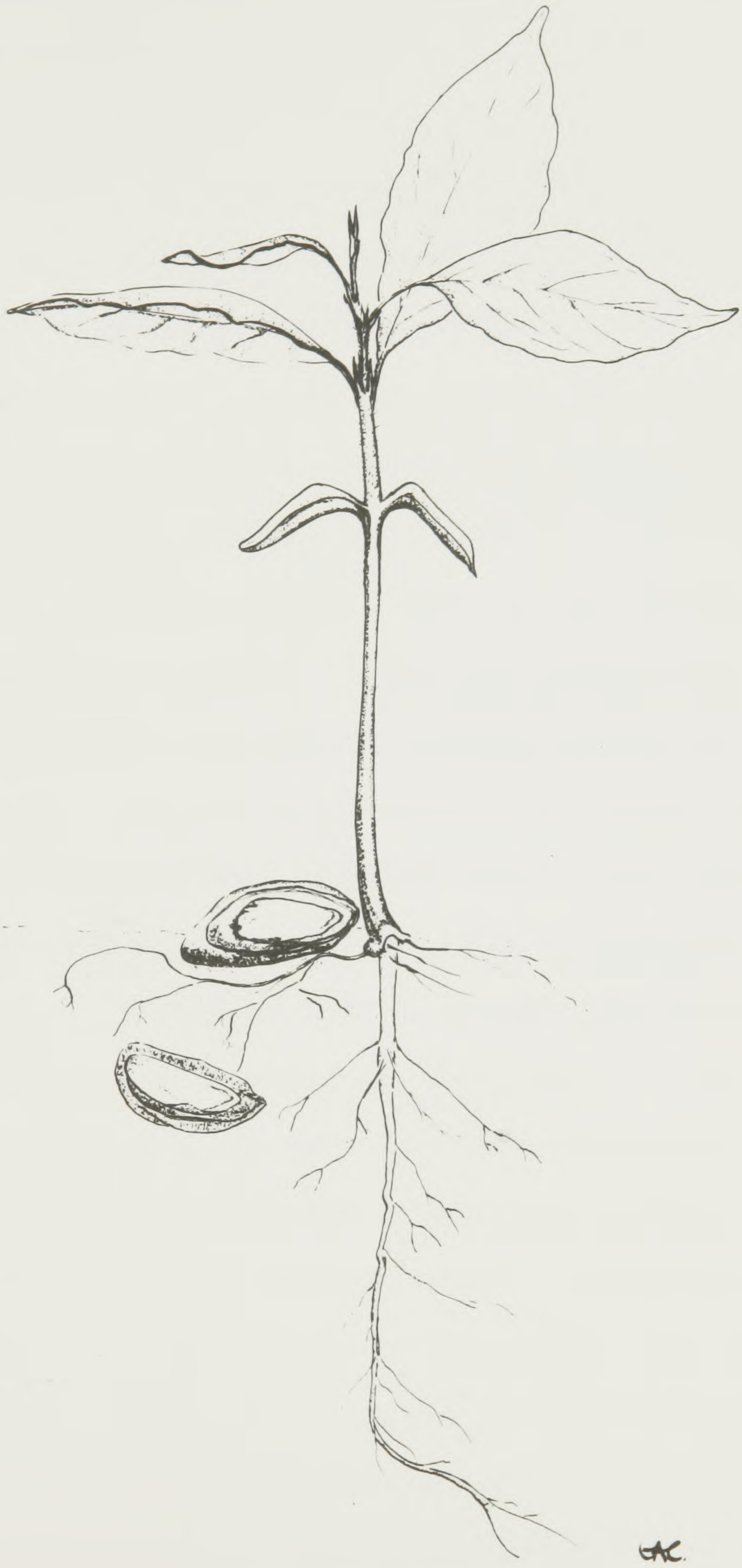


Plate X - The seedling of Maranthes corymbosa Blume (x $\frac{1}{2}$).

6. THE STATUS AND POSITION OF THE CHRYSOBALANACEAE

The group was first described as a family by Robert Brown (1818). Since then several systematic botanists have accepted the Chrysobalanaceae as a family. The following is a list of authors of general works who have followed Brown. Bartling (1830), Zuccarini (1832b), Lindley (1836), Endlicher (1836), Bentham (1840), Walpers (1843), Miquel (1855), Agardh (1858), Warming and Mobius (1911), Wettstein (1933), Exell (1944), Gundersen (1950), Dandy (1960). All of these authors have placed the family next to the Rosaceae.

However, the author's of the most widely used system of classification have treated the group as a subfamily of Rosaceae - De Candolle (1825), Bentham and Hooker (1865), Focke in Engler and Prantl (1894) and Hutchinson (1926, 1959).

Fritsch (1888) who made a careful study of the group regarded it as a family which should be placed between Rosaceae and Leguminosae, and his views have been reiterated by nearly all subsequent workers with a detailed knowledge of the group. Wettstein (1933) placed the Chrysobalanaceae in this position, and commented that part of his reason for regarding it as a family was the characteristic anatomy.

In 1957 Küster published a detailed account of the anatomy of the leaf and primary stem. He drew no taxonomic conclusions but in 1903 Hallier concluded from Küster's data that the group should be separated from the Rosaceae as a family. Juel (1915), who correctly interpreted the ovary of the Chrysobalanaceae, considered it to be so different from that of the Rosaceae that he thought the group should be elevated to family rank, but remain near Rosaceae. On the basis of differences he discovered in leaf-trace anatomy Morvillez (1918a) reached a similar conclusion. Bonne (1928) on the basis of a detailed study of the pedicel and floral vascular anatomy concluded that the Chrysobalanaceae are quite

Chrysobalanaceae	Rosaceae
Primary stem and leaf anatomy	
Silica deposits abundant in five different forms	Silica absent
The stone cells in the pericycle are thickened only on one side thus appearing U shaped in T.S.	No pericycle cells thickened only on one side
Stomata "Rubiaceous"	Stomata "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
Pedicel anatomy	
Pedicel articulate at an active meristematic zone	Pedicel inarticulate or if articulate no active meristem
Wood anatomy	
Vessels oblique, infrequent usually 200-300 μ diam.	Vessels not oblique, abundant, usually less than 100 μ diam.
Parenchyma banded, composed of long strands	Parenchyma sparse, not banded, composed of short strands
Rays predominatly uniseriate	Rays multiseriate
Intervascular pitting large	Intervascular pitting never large, usually minute
Silica abundant in rays	Silica absent
Pollen	
Pollen markedly triangular in expanded grain	Pollen usually not triangular or only weakly triangular
No protrusion in mouth of the furrow	Often with a wedge-shaped protrusion in mouth of furrow
Grain scarcely patterned	Grain often distinctly patterned
Floral anatomy	
Ovary basically of 3 carpels with gynobasic style	Ovary never gynobasic
Ovule erect	Ovule pendulous
Flowers at least slightly zygomorphic in all genera except Chrysobalanus.	Flowers actinomorphic

distinct from the rest of the Rosaceae. Both Metcalfe and Chalk (1950) and Erdtman (1952) imply that no objections could be raised against treating the group as a family on the basis of wood anatomy and pollen-grain structure respectively. Details of the anatomical differences between Chrysobalanaceae and Rosaceae are discussed at some length in Chapters 3 and 4 and are summarized in the table below.

There are also several characters which are common to all, or most, Chrysobalanaceae which are only of sporadic occurrence in Rosaceae.

From the characters tabulated above, and the discussion in Chapters 3 and 4, it is clear that the Chrysobalanaceae, although sufficiently distinct from Rosaceae in enough characters to be treated as a separate family, is nevertheless still closely related to it.

There are no grounds for placing the Chrysobalanaceae in any order other than the Rosales as is done by various authors. It has been suggested that the Chrysobalanaceae is related to Linaceae, Polygalaceae, Limnanthaceae, Dichapetalaceae, Trigoniaceae, Gerianiaceae, Tropaeolaceae and Sapindaceae. In gross morphological features of basic flowers and fruits the Chrysobalanaceae does not even remotely resemble any of these. In anatomy and palynology they are (almost without exception) utterly different. This is discussed in Chapters 3 and 4.

7. THE REGROUPING OF GENERA WITHIN THE CHRYSOBALANACEAE

A summary of previous attempts to group the genera is given below.

BAILLON (1867)

"Group a" Chrysobalanus, Licania (incl. Moquilea), Lecostemon and Stylobasium.

"Group b" Grangeria, Hirtella, Couepia, Parinari, Acioa, Parastemon.

FRITSCH (1889) did not attempt to group the genera except by making separate subfamilies for the anomalous genera Stylobasium and Lecostemon.

FOCKE (1894)

Subtribe Chrysobalaninae - Chrysobalanus, Grangeria, Moquilea, Licania, "Lecostomion" and Stylobasium.

Subtribe Hirtellinae - Hirtella, Couepia, "Parinarium", Acioa, Angelesia and Parastemon.

HALLIER (1903)

Subtribe Lecostominae - Lecostemon.

Subtribe Chrysobalaninae - Chrysobalanus, Licania (incl. Moquilea and Angelesia), Parastemon.

Subtribe Hirtellinae - Grangeria, Hirtella, Couepia, "Parinarium", Acioa.

BONNE (1928)

Subtribe Chrysobalaninae

Group* (a) - Chrysobalanus.

Group (b) - Stylobasium.

Subtribe Hirtellinae

Group (c) - "Parinarium", Hirtella, Couepia, Acioa.

Group (d) - Grangeria, Licania, Moquilea, Angelesia.

HAUMAN (1951)

Rosaceae - Chrysobalanoideae - Chrysobalanus, Moquilea, Licania, Afrolicania.

Hirtellaceae (placed in Geraniales by Hauman).

"Section" Hirtellinae - Hirtella, Magnistipula, Acioa, Couepia, Angelesia, Grangeria ?, Parastemon ?.

"Section" Parinariinae - Parinari.

The above summary shows that there has been a good deal of difference of opinion as to how the genera should be grouped. This is probably due to the fact that the Chrysobalanaceae is a well defined family which cannot be subdivided into taxa of any real significance above the generic level. The uniformity of the pollen and wood structure has been emphasized in previous chapters. It is definitely impossible to divide the family into any two major groups on pollen, wood or seedling characters.

The floral vascular structure, which is discussed in Chapter 3, is the only anatomical feature which would indicate any useful sub-division. This is largely due to differences in the level of ovary insertion on the receptacle, which determines whether the flower is actinomorphic or zygomorphic. A summary of the ovary position is given below:-

* It is not clear what rank Bonne intended these "groups" to have.

Exactly Central - *Chrysobalanus*.

Nearly Central - *Geobalanus*, *Licania*, *Afrolicania* and *Parastemon*.

Lateral - *Grangeria*, *Hunga*, *Hirtella paniculata*, *H. myrmecophila* and *H. caudata*.

Terminal - *Hirtella*, *Couepia*, *Acioa*, *Parinari*, *Maranthes* etc.

This shows the complete gradation of this character. The intermediate condition of *Hunga* and *Grangeria* has been recognized previously, but the fact that it occurs in some species of *Hirtella* has not been pointed out before, and this considerably reduces the value of dividing the group into tribes. The fact that in *H. myrmecophila* there is disc tissue above the level of the ovary definitely places it in the same group as *Grangeria*. There is also a complete gradation in the symmetry of the stamens. For example in *Grangeria borbonica* the stamens form a complete circle, in *G. porosa* they are grouped to one side. It is thus impossible to draw a clear cut distinction between the actinomorphic and zygomorphic Chrysobalanaceae. It is not possible to divide the family into two separate ones as is done by Nakai (1942) and Hauman (1951).

In the present work the two tribes *Chrysobalaneae* and *Hirtelleae* are maintained for convenience, but the distinction between them is rather arbitrary.

Tribe *Chrysobalaneae*:- ovary inserted at or near the base of the receptacle.

This contains the genera - *Chrysobalanus*, *Licania*, *Afrolicania*, *Geobalanus* and *Parastemon*.

Tribe _Hirtelleae_:- ovary inserted at least mid-way up the receptacle, or at its mouth.

This contains the genera - _Hirtella_, _Couepia_, _Parinari_, _Maranthes_, _Cyclandrophora_, _Neocarya_, _Duckea_, _Bafodeya_, _Kostermansia_, _Acioa_, _Magnistipula_, _Grangeria_ and _Hunga_.

This is in fact, the way in which Hallier (1903) divided the genera, as far as he had seen them. If _Grangeria_ and _Hunga_ are not included in the same tribe as _Hirtella_, the _tribes_ would be impossible to separate because of the species of _Hirtella_ with the ovary insertion mid-way up the calyx-tube. The tribes defined as proposed here do not cut across any generic limits which would happen if they were delimited on any other characters, but the difference between them is of insufficient importance to warrant the recognition of two subfamilies and is quite inadequate for the separation of the Hirtellaceae as a distinct family. I agree with Baillon (1868) who said, "il est difficile de sectionner les Chrysobalanées d'une manière nette et précise, au moyen du mode d'insertion de l'ovaire sur le réceptacle." It is also impossible to divide them satisfactorily in any other way.

8. THE HISTORY AND SYSTEMATIC POSITION OF THE GENUS RHABDODENDRON

Rhabdodendron Gilg. & Pilg. in Verhand. Bot. Ver. Brandenb. 47:152 (1905); Huber in Bol. Mus. Goeldi 5:425-31 (1908); Krause in Engl., Nachtr. 4:157 (1915); Engler in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 19A:357 (1931).

Lecostemon* sensu Benth. in Hook. Journ. Bot. 5:293 (1853); Focke in Engl. & Prantl, Nat. Pflanzenfam. 3(3):58 (1894) non Sessé & Moc. ex DC.

A. History

The genus Rhabdodendron has usually been included in the Chrysobalanaceae, often under the name Lecostemon. I hope at a later date to deal more fully with its systematic position but it seems advisable to indicate here my reasons for excluding Rhabdodendron from the Chrysobalanaceae, and to give the history of its confusion with Lecostemon, especially since the literature gives a confused picture of both the taxonomy and wood structure of the former genus.

The foundation for Lecostemon is a drawing by the Spanish botanists Sessé and Mociño. Sessé returned to Spain with Mociño after their exploration in Mexico in 1804 and when Sessé died in 1809, Mociño was left with their manuscripts (including 'Flora de Guatemala', 'Flora Mexicana' and 'Plantae Novae Hispaniae'), their colour drawings (about 1,400) and their herbarium. Because of continual changes of government in Spain, he was unable to obtain money to publish the proposed works and finally, after some time in prison, he fled to Montpellier in 1813 with his drawings and

* There seems to have been much doubt amongst later authors as to the spelling of the name Lecostemon. Some of the variations in spelling observed are: Lecostomon - Endlicher (1836), Meisner (1840); Lecostomion - Focke (1894); Lycostomon - Hauman (1951).

manuscripts in a cart. Although a soldier confiscated his cart he was able to keep his botanical possessions. After being destitute for some time he was helped by French scientists and eventually met De Candolle in Montpellier. De Candolle realized the value of his drawings and assisted him in naming his new species. A few years later with the adoption of a new constitution in Spain, Mociño was given permission to return and hastily decided to do so. De Candolle, who had by then moved to Geneva, gathered together more than 200 artists and young ladies of that city to make tracings of those drawings which he had not already copied. About 1,100 were made in 10 days. Copies of some of these were later distributed to ten major herbaria by De Candolle's son, A.L.P.P. de Candolle under the title "Calques des dessins de la flore de Mexique de Moçino et Sessé qui ont servi de type d'espèces dans le Systema ou le Prodromus." No. 311 is a tracing of the drawing of the plant named Lecostemon and is the type of that genus described seven years later by De Candolle and published in his Prodromus (2:639.1825). In all, De Candolle described 271 new species and 17 new genera from these tracings and does not seem to have been aware of the existence of the corresponding dried specimens which he certainly did not use. The Sessé and Mociño specimens were incorporated in the Madrid Herbarium in 1820 and are at present on long loan to the Field Museum, Chicago. This collection should always be consulted in order to interpret the descriptions. Certain specimens in the Delessert Herbarium, Geneva are not so well authenticated. Some may be duplicates of the originals but some, e.g. Mimosa hirsuta, were evidently collected later. Others at Kew and the British Museum bear the name of Pavon who did not visit Mexico. These historical notes have been prepared from information given by Lasègue (1843), Colmeiro (1858,1892), Hemsley (1879), A. de Candolle (1880), Urban (1902), Leon (1902) and Sprague (1926).

Mociño gave his original drawings to the physician who attended him in his final illness and these have never come to light.

The type of Lecostemon is thus the tracing from which De Candolle described the genus and it must be interpreted from the dried specimen in the Madrid Herbarium.

De Candolle named the species L. terniflorum almost certainly supplying the epithet himself and placed the genus under "Genera Rosaceis affinis". Later Meisner (1836) and Endlicher (1840) both placed it as a doubtful member of the tribe Chrysobalanoideae in the Rosaceae.

At this point it is probably better to anticipate a little and to say at once that Lecostemon terniflorum is a Sloanea, in the Tiliaceae and that it is conspecific with Sloanea quadrivalvis Seem., now S. terniflora (DC.) Standl.

The confusion with Rhabdodendron was due to Bentham (1853) who decided that four new species in his possession collected by Gardner and Spruce, belonged to the Chrysobalanaceae, and that they were congeneric with De Candolle's description of Lecostemon. He gave an accurate and detailed description of a genus purporting to be Lecostemon as an amplification of De Candolle's account and described the four new species: L. gardnerianum, L. amazonicum, L. crassipes and L. macrophyllum. He was in fact describing an entirely different genus which I have referred to at the beginning of this account as Lecostemon sensu Bentham.

Carolo Mueller in Walpers Annales 4:646 (1857) placed this genus in Chrysobalaneae and amplified Bentham's description. He listed only Bentham's four species but added as a note to L. gardnerianum "Species proxima L. terniflora". These four Brazilian species reappeared in J.D. Hooker's account (1857) in "Flora Braziliensis". Baillon (1867) included Lecostemon (presumably sensu Bentham) in his first group of the Chrysobalanoideae but pointed out its differences from the other genera of the group. His figure of the style is incorrect. Fritsch (1888) made it a separate tribe of the Chrysobalanaceae and Focke (1894) included it as a member of his subtribe Chrysobalanineae mentioning its anomalies and suggesting an affinity with the Phytolaccaceae.

Gilg and Pilger (1905) described a new genus Rhabdodendron which they placed in the Rutaceae, tribe Cusparieae. Rhabdodendron was based on a single gathering from Brazil which they called R. columnare. This clearly belongs to Lecostemon sensu Bentham and is in fact conspecific with L. macrophyllum. As Lecostemon sensu Bentham had, up till then, no valid generic name, Rhabdodendron is the correct name for it and is now maintained but this was merely a matter of good luck for the authors as a long time had still to elapse before the identity of the type species of Lecostemon was discovered.

It was not long, however, before the relationship between Lecostemon sensu Benth. and Rhabdodendron was recognized. Huber (1909) realized that these were congeneric and transferred L. macrophyllum, L. amazonicum and L. crassipes to Rhabdodendron rightly considering that L. terniflorum belonged to a different genus though he had not seen the Mocino herbarium specimen. He gave a parallel summary of the characters of Lecostemon Sessé & Moc. ex DC. and Rhabdodendron Gilg & Pilg. to establish the fact that they are different genera. Unfortunately he made no reference to Bentham's paper on Lecostemon (1853) but apparently took his facts from J.D. Hooker's account in the 'Flora Brasiliensis' which he cites. He made no reference to L. gardnerianum of which Hooker (1857) said that it seemed to come nearest to the Sessé and Mociño specimen, nor does he include it in his key. It is known solely from the type gathering and is certainly congeneric with the other three species as is shown both by floral structure and the wood anatomy, although it differs strikingly in vegetative characters. Huber's assumption that Lecostemon

Sessé & Moc. ex DC. was different from Lecostemon sensu Benth. was correct though not the result of a full and critical examination. His transfer of three Lecostemon species to Rhabdodendron stands and he described four new species in the latter genus: R. duckei, R. paniculatum, R. longifolium and R. arirambae all of which have later been reduced to synonymy under the previously published species. Furthermore, he created a new tribe: Rhabdodendreae in the Rutaceae instead of placing it in the tribe Cusparieae of the same family. The Rhabdodendreae was later elevated to subfamily Rhabdodendroideae by Engler (1931).

Most later authors except Gleason (1927) accepted Huber's reasoning and used Rhabdodendron as the correct name. Gleason (1927), however, described Lecostemon sylvestre from British Guiana although he was evidently familiar with Huber's work since he says that "The genus Lecostemon is one of the most poorly known members of the Chrysobalineae ..... it has even been placed in the Rutaceae." Sandwith (1942) transferred L. gardnerianum to Rhabdodendron. He said that the identity of Rhabdodendron with Lecostemon Sessé & Moc. ex DC. had been fully discussed by Huber. Maguire (1948) transferred L. sylvestre to Rhabdodendron.

In 1903 Hallier placed Lecostemon in the Chrysobalanoideae but kept it as a separate rather isolated tribe. Later, however, he seems to have investigated the problem further and to have discovered the true identity of Lecostemon Sessé & Moc. ex DC. as he wrote on the herbarium sheet of Lecostemon amazonicum, Spruce 473 in the Munich Herbarium, "Chrysobalaneae Lecostemoniae Hallier f., Engler's Rosalen etc. (Hamburg 1903) p. 10. (Lecostemon Moc. & Sessé = Sloanea sp.) Lecostemon Spruce et Benth. incl. Rhabdodendron Gilg et Pilger. H. Hallier 16.VI.1914." He does not appear to have published this anywhere, although Hallier (1923) p. 71 mentions that Lecostemon Moc. & Sessé is different from Lecostemon Spruce.

Standley (1944) apparently arrived independently at the same conclusion, i.e. that Lecostemon Sessé & Moc. ex DC. is a Sloanea (Tiliaceae). His evidence is based on an herbarium specimen from the Mociño Herbarium. This specimen of Sloanea so closely resembles the drawing of Lecostemon used by De Candolle that Standley concludes that the drawing was of this actual specimen. I have examined a photograph of the Mociño specimen (Plate XIII), kindly supplied by the Field Museum, Chicago), and the tracing of the Sessé and Mociño plate (Plates XI & XII) and am sure that both Hallier and Standley came to the correct conclusion. It is indeed fortunate that the Sessé and Mociño Herbarium is still intact. Standley made the necessary new combination Sloanea terniflora (Moc. & Sessé) Standl. His author citation is in fact wrong and it should be Sloanea terniflora (DC) Standl., for although Sessé and Mociño supplied the name Lecostemon, De Candolle seems to have been responsible for the epithet and the description.

The species of Rhabdodendron are very distinct from the Chrysobalanaceae, and it would be hard to see why Bentham should have placed them there except for the fact that the basal style provides an obvious similarity. Other floral features such as the linear stamens, the long stigmatic surfaces etc., are quite unlike the Chrysobalanaceae, as are the wood structure, leaf anatomy and pollen morphology.

B. Description

The genus consists of high shrubs with entire, alternate, gland-dotted, coriaceous leaves, with small peltate hairs on the undersurface, Stipules small, subulate or obscure. Bracts and bracteoles reduced to scales. Inflorescence of supra-axillary racemose panicles.

Flowers hermaphrodite, with a broad slightly concave receptacle. Calyx very short; lobes 5 with entire margins, or indistinct. Corolla of 5 caducous, broad to elongate oblong-elliptic petals, apex rounded or minutely apiculate, minutely punctate, aestivation imbricate, inserted on the receptacle. Disc absent. Stamens numerous (about 45) not inserted in any special order, filaments short, flattened, persisting after the anthers fall, and then curving over the margin of the receptacle and the calyx; anthers linear, erect, basifixed, caducous, 4 locular dehiscing longitudinally, Ovary sessile, globose, glabrous, uniloculer, inserted at the base of the concave receptacle. Ovule 1, erect, basally attached, anatropous. Style arising from the base of the ovary to one side of it, fairly thick, elongated; stigmatic surface on the outermost side ascending from the base or the middle. Fruit a small drupe, globose, at the top of the thick, broad, woody stipe in the cup-shaped receptacle; exocarp crustaceous when dry, thin, slightly fleshy-coriaceous; endocarp slightly woody. Seed 1, reniform-globose, exalbuminous, with a thin testa; cotyledons thickly fleshy, conferruminate; radical small and bent inwards towards the hilum.

Five species of high shrubs in British and French Guiana and the northern provinces of Brazil (Plate XVIII).

Published names and probable species

R. crassipes (Spruce ex Benth.) Huber in Bol. Mus. Goeldi 5:427 (1909).

R. macrophyllum (Spruce ex Benth.) Huber loc. cit.

R. amazonicum (Spruce ex Benth.) Huber loc. cit.

R. gardnerianum (Benth.) Sandw. in Jo. Arn. Arb. 24:224 (1943).

R. sylvestre (Gleason) Maguire in Bull. Torr. Bot. Cl. 75:397 (1948).

R. arirambae Huber loc. cit. = R. crassipes

R. columnare Gilg & Pilg. in Verh. Bot. Ver. Brand. 47:152 (1905) = R. macrophyllum

R. duckei Huber loc. cit. = R. crassipes

R. longifolium Huber loc. cit. = R. crassipes

R. paniculatum Huber loc. cit. = R. crassipes

C. Pollen morphology

Slides were prepared from the following herbarium specimens:

R. sylvestris (Gleas.) Maguire - Fanshawe & Maguire F.D.B.G. 32141, (K); R. macrophyllum (Spruce ex Benth.) Huber - Ule 8986, (K).

The grains have 3 furrows, 3 pores, ora circular or slightly lalongate. Large polar area, exine of medium thickness. Grains finely reticulate, 18-25 μ. 100 P/E = 100. (This agrees with Erdtman's (1952) description of R. amazonicum (Plate VII-9)).

The pollen differs from that of the Chrysobalanaceae in three important features: The presence of distinct pores, the large polar area, and the fine reticulation. Since the Chrysobalanaceae are very uniform palynologically this is a strong indication that it belongs elsewhere.

Erdtman (1952) says that it differs from the Rutaceae by cause of the circular ora. The Rutaceae have distinctly lalongate ora. Thus Rhabdodendron seems misplaced there. He also says that palynologically there is no support for placing it in the Phytolaccaceae.

The pollen, thus, indicates that the genus has not yet been correctly placed.

D. Wood structure and leaf anatomy

a) Material used

1. Mature wood

R. amazonicum - CFI 7012 Col. Dr. Ducke 220 Via Record (F; NY); X 1406 from Inst. Nat. Pesq. Amaz. Brasil.

R. macrophyllum - CFI 11,051 Col. Dr. Ducke Via Record, Yale n. 23649A; X 1396 from Inst. Nat. Pesq. Amaz. Brasil (INPA).

R. crassipes - CFI 6707 Col. Monteiro da Costa Via Chicago Field Mus. Nat. Hist. No. 613237 (F).

R. sylvestre - CFI 13,046 Col. For. Dept. Brit. Guiana No. 2747 (F; K; FHO).

2. Twig slides

R. gardnerianum from Gardner 2814 (OXF).

R. amazonicum from For. Dept. Brit. Guiana 2497 (K).

R. sylvestre from Tutin 243 (K).

R. macrophyllum from Spruce 82 (NY); Ducke 163 (NY); Spruce s.n. (E).

R. amazonicum)
R. macrophyllum) Via Metcalfe, Kew.
R. crassipes)

3. Leaf anatomy

R. amazonicum - Ducke Ser. No. 25466 (K).

b) Description of mature wood

1. R. amazonicum, R. crassipes and R. sylvestre

The wood is characterized by the anomaly of successive bundles of xylem and phloem repeating the structure of the young stem, separated by a band of conjunctive parenchyma.

Vessels abundant, particularly near the anomalous parenchyma, solitary (except where crowded together in R. amazonicum), radial and oblique arrangement. Size variable, mean diameter, R. amazonicum = 68 µ. Vessels up to 100 µ frequent, vessels larger infrequent (up to 135 μ). Perforation porous, semi-circular in shape. The area of the perforation generally oblique to almost vertical. Intervascular pits minute, alternate, often coalescent, 3.5-4.5 μ. Vessel to parenchyma pits larger, alternate. Some vessels filled with gum in R. amazonicum and R. sylvestre.

Fibres thick to moderately thick walls. In R. amazonicum thick-walled next the anomalous phloem and thinner away from it. With simple or bordered pits, few on the tangential walls, few to numerous on the radial walls. Bordering most marked near the rays. The bordering caused Heimsh to describe the fibres as tracheids.

Parenchyma apotracheal very sparse, a few cells scattered between the fibres. There is also some paratracheal parenchyma which does not completely surround the vessels, but is confluent in R. amazonicum where the vessels are more crowded. In addition to this are the masses of parenchyma between the successive phloem and xylem groups.

Rays. There is great variation in size between the species studied. Milanez (1932) points out that great variation in ray size according to the height above ground level studied. Up to 10 cells wide and 50-75 cells high in R. amazonicum, 1-5 wide, 5-50 high in R. crassipes, 1-3 wide, 8-25 high in R. sylvestre. Hetergeneous type II A in all species, with gum inclusions in many cells. Pits scattered, moderately large (Plates XIV, XV).

2. R. macrophyllum

Both wood specimens seen of this species differ vastly from the above in that they do not possess anomalous structure. This species has been described by Heimsch (1942) and Chalk (1937) and (1950). It has further important differences from the other species. The parenchyma is abundant, in apotracheal bands continuous or broken, and paratracheal which is aliform or confluent. The rays are all narrow, 1-2 cells wide, and short, heterogeneous II B to homogeneous I. The vessels have simple perforations. The one similarity with the other Rhabdodendrons is that the fibres have bordered pits and so are "fibre-tracheids". (Plate XVI).

c) Twig specimens

The nine twig slides examined show that they have a similar structure to the mature wood. Only one species, R. gardnerianum, has anomalous structure in the young wood. In this species a distinct new cambium has developed. The other samples are too young to show it. The five species examined show great similarity in the young wood and the bark. Inside the bark has a layer of thin walled cells and then a layer of stone cells. Furthermore the leaf trace patterns are all similar. There are definite spirals in the vessels. On vessel characters they would be hard to separate at all. The only difference in R. macrophyllum is that it has more parenchyma and less fibres, which is also true of its mature wood (Plate XVII).

d) The diverse wood structure

The fact that this genus contains several species with anomalous structure and one without it has drawn the attention of several authors, Heimsch (1942), Chalk (1937, 1950). Previously the wood of R. macrophyllum was known from one sample only. Although this is a correlated sample, the possibility of a confusion of samples could not be ruled out. Heimsch suggested this possibility, and at one time it seemed to me to be the most likely explanation. However, it has now been possible to obtain a second independent sample. This was kindly collected and sent to me by the Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil. This sample also lacks the anomalous phloem, and proves, without doubt, that the original sample is correctly determined, and belongs to the correlated herbarium material at Chicago, which I have seen. If I had not seen this second wood sample I would have refrained from drawing any conclusions about this genus. Heimsch, however, pointed out that all species of Rhabdodendron have fibrous elements as tracheids which is an important unifying feature. It is not unknown for a genus to have some members with included phloem, and others without. e.g. Combretum. The differences in wood anatomy between R. macrophyllum and the other species of the genus are far greater than that between the majority of genera. Some botanists might be tempted to split Rhabdodendron into two genera on the basis of wood structure. However, in all other respects, R. macrophyllum resembles the other species of the genus. The floral morphology, vegetative characters and pollen structure are as in the other species and they unquestionably belong in the same genus.

e) Leaf structure

Küster (1897) made a detailed description of the leaf anatomy for three species (R. amazonicum, R. crassipes and R. macrophyllum). His work is part of a detailed study of the anatomy of the Chrysobalanaceae. It thus tends to emphasize the differences between them. Some of the more outstanding leaf features are given here.

The leaf has a distinctively bifacial mesophyll. The mesophyll contains abundant fatty bodies. It is traversed by fibre-like 'spicular cells', both simple and branched. These begin at the vein endings. Silica, in the form of silica bodies, is abundant in the mesophyll. Silica in other forms does not occur in the Rhabdodendron leaf. It has a true hypoderm. The palisade tissue is on the upper side of the leaf only. It is from 1-4 cells thick. The cells are very short. Characteristic of the leaves are the secretory cavities which occur on both sides of the leaves. They are filled with resinous contents. The stomata have no accessory cells. The only type of hairs are peltate hairs.

Their shield has a jagged margin owing to the projecting ray cells, which have thin walls and a narrow lumina. Each one contains a silica body. The ray cells do not reach the central part of the shield. The nerves are enclosed in a continuous ring of sclerenchyma. In addition to this they are encircled by a ring of silica rich parenchyma.

B. Taxonomic observations

The descriptions given show that in both wood structure and leaf anatomy Rhabdodendron is completely different from the Chrysobalanaceae. They indicate that it was certainly incorrectly placed there. Anatomists have considered it in two other families: the Rutaceae by Heimsch (1942), Milanez (1943) and Metcalfe (personal communication), also by several systematic botanists; the Phytolaccaceae by Record (1933) and by Chalk (1950).

Record (1933) placed it in the Phytolaccaceae because of the occurrence of anomalous structure in several genera of that family. He particularly compares it with Gallesia. He points out that the only important difference of Rhabdodendron from the Phytolaccaceae is in the small distinctly bordered pits of the fibres. All Phytolaccaceae genera with anomalous structure have fewer, smaller, simple or indistinctly bordered fibre pits. Normal Phytolaccaceae woods, however, also have small distinctly bordered fibres pits. Chalk (1937)and (1950) supports Record's placing of the genus. Heimsch (1942) included it in the Rutaceae (Rhabdodendroideae) but concludes that on anatomical evidence it does not belong there. It is the tracheid fibrous elements that bring him to this conclusion. He emphasized that the Rutaceae are relatively consistent in their wood structure, so that it would be unexpected to find such a divergent form within that family.

Milanez (1943) gives a description of the wood of R. amazonicum. He is convinced that it belongs to the Rutaceae. Some of his reasons are very weak. For example his three main arguments are:- (1) that the wood has more differences from the Phytolaccaceae than from the Rutaceae. (2) that more systematic botanists place it in the Rutaceae. (3) anomalous structure is not a character of any one particular family, but is a common attribute of various ones. The first argument seems to be incorrect in any case. His main reason is based on the fact that Rhabdodendron pits are very different from those of Gallesia, whilst very similar to Rutaceae. He considers pits a primary character and that the similarities with the Phytolaccaceae are due to secondary developments which by chance have led to a resemblance, rather than through a true affinity. He points out that Rhabdodendron differs from Gallesia in several other ways. It has no tyloses, more crystal deposits and a different arrangement and attachment of the anomalous phloem.

The majority of differences and similarities of Rhabdodendron wood to the two families are apparent from the summary of the opinions of previous workers. The resemblance of the wood to the Phytolaccaceae seems more apparent to me. The wood differs from the Rutaceae in several other features, besides the tracheid fibre elements and the anomalous structure. In particular is the vessel arrangement and the stone cells. The leaf structure is completely different from the Phytolaccaceae. In this it is near to the Rutaceae. The Rutaceae also have secretory cavities, the same general lamina structure, and the same type of crystal inclusions.

Since there are so many differences from both Rutaceae and Phytolaccaceae it seems questionable whether Rhabdodendron belongs to either of these families. A list of families having anomalous structure of this type does not help. Those families are:-

Amarantaceae, Buxaceae, Caesalpiniaceae, Capparidaceae, Chenopodiaceae, Connaraceae, Convolvulaceae, Dilleniaceae, Flacourtiaceae, Hippocrateaceae, Menispermaceae, Nyctaginaceae, Papilionaceae, Phytolaccaceae, Polygalaceae and Verbenaceae.

The Rutaceae are a very uniform group anatomically and as Record (1933) has pointed out it would be unlikely that Rhabdodendron belongs here. Anomalous structure is in several cases the character of only one genus in a family (e.g. in Verbenaceae, Buxaceae and Dilleniaceae). The other differences, however, mean that it would be a very anomalous Rutaceae.

The combination of characters which Rhabdodendron possesses make it anomalous. The most important features are listed. The minute calyx lobes, the absence of a disc, the long linear anthers with short persistent filaments, the basal style, the single unilocular, uniovulate carpel, the gland-dotted leaves, the peltate hairs, the anomalous secondary phloem and the conspicuously bordered fibre pits. It appears that the combination of the above characters exclude it from any known family.

It is beyond the scope of this work to consider in detail the affinities of Rhabdodendron, but it seems most convenient to elevate it to family status, since it does not fit readily into any family. I would place the Rhabdodendraceae in the Centrospermae since from the facts already given it appears most probable that it is a primitive member of this order. Apart from the wood structure, certain morphological features, e.g. the long anthers and the shape of the stigma, are suggestive of members of the Phytolaccaceae and related families. Mr. H.K. Airy-Shaw of the Kew Herbarium tells me that he has independently reached the same conclusion.

RHABDODENDRACEAE Prance

Flores regulares hermaphroditi parvi. Calycis tubus brevis turbinatus; lobi 5 minuti vel obsoleti. Discus nullus. Petala 5 sub margina tubi calycis inserta oblongo-elliptica sepaloidea decidua minute punctata aestivatione imbricata. Stamina indefinita (c. 45) sub margine tubi calycis inserta; filamenta brevissima complanata libera persistentia; antherae longae lineares 4-loculares longitudinaliter dehiscentes deciduae. Ovarium sessile liberum ad basin calycis tubi concavi insertum globosum; ovulus 1 basalis erectus; styli basi ovarii insertus, stigmate lineari ab apice ad mediam vel etiam ad basin styli per laterem exterius decurrenti. Fructus drupaceus parvus, exocarpio tenue, endocarpio tenue sub-lignoso. Semen erectum; embryo exalbuminosus.

Frutices Americae australis tropicae. Folia alterna simplicia integra exstipulata glanduloso-punctata subter peltato-pilosa. Inflorescentiae axillares anguste paniculatae vel racemiformes.

Typus familiae: Rhabdodendron Gilg & Pilger in Verh. Bot. Ver. Prov. Brandenb. 47:152 (1906), cujus holotypus Rh. columnare Gilg & Pilger idem es ac Rh. macrophyllum (Benth.) Huber, adhuc inter Rosaceas (sub nomine Lecostemonis) vel Rutaceas interpositum.

Syn. Rutaceae tribus Rhabdodendreae Huber in Bol. Museu Goeldi 5:425 (1909); subfam. Rhabdodendroideae Engler in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 19A:358 (1931).

F. Herbarium material consulted

1. Rhabdodendron amazonicum - Spruce 377 Type, fl. (K; OXF; P); Ducke 794 fl. (F; NY); 10826 fr. (B); 9950 fr. (BM); 9964 fl. (BM); 10938 fr. (BM); 14986 fl. (BM); 10339 fr. (BM); 10525 fl. (BM); 15933 fr. (BM); 11370 fr. (BM); 15618 fl.

(BM); 11606 fr. (BM); 10216 fr. (BM); 8854 fl. (BM) (Type of R. paniculatum); Froes 20461 fr. (NY); Black 49-8174 fr. (NY); Cowan 38643 fr. (NY); 38656 fr. (NY); Egler 1314 fr. (NY); Monteiro da Costa 213 fr. (F); Riedel 1355 fr. (NY).

2. R. crassipes - Spruce 1497 Type, fl. (P; OXF); Killip & Smith 30588 fl. (NY); Leprieur s.n. st. (F); Fanshawe F.D.B.G. 5233 fr. (K; NY); ? 7406 (Cayenne) fr. (NY); Ducke 220 fr. (F; NY); 8546 fl. (BM); Ule 8882 fl. (NY); Chagas INPA 389 st. (FHO); Rodrigues 3401 fr. (FHO).

3. R. gardnerianum - Gardner 2814 Type, fl. (BM; K; OXF; NY; P).

4. R. macrophyllum - Spruce 82 Type, fl. (K; OXF; NY; P); Ducke 163 fl. (F; NY); 177 fl. (F); 177 additional fr. (F); fl. (NY); 8595 fr. (BM); 12198 fr. (BM); 13623 fl. (K); Ule 8986 fl. (K); Riedel 1436 fr. (NY); Rodrigues & Chagas 2787 fl. (FHO); Rodrigues & Coehlo 1190 fr. (FHO); Rodrigues & Lima 2647 fr. (FHO); Rodrigues 47 fr. (FHO).

5. R. sylvestre - Fanshawe & Maguire 23558 fr. (F; NY); 32141 fl. (K; NY); Sandwith 1237 fl. (K; NY); F.D.B.G. 2747 fl. (F; FHO; K); Tutin 243 fl. (K).

Plate XI - Photograph of the tracing of <u>Lecostemon terniflorum</u> made at Geneva. (Neotype of <u>Sloanea terniflora</u> (DC.) Standl.).

Plate XII - Photograph of the tracing of *Lecostemon terniflorum* made at Geneva. (Neotype of *Sloanea terniflora*(DC.) Standl.).

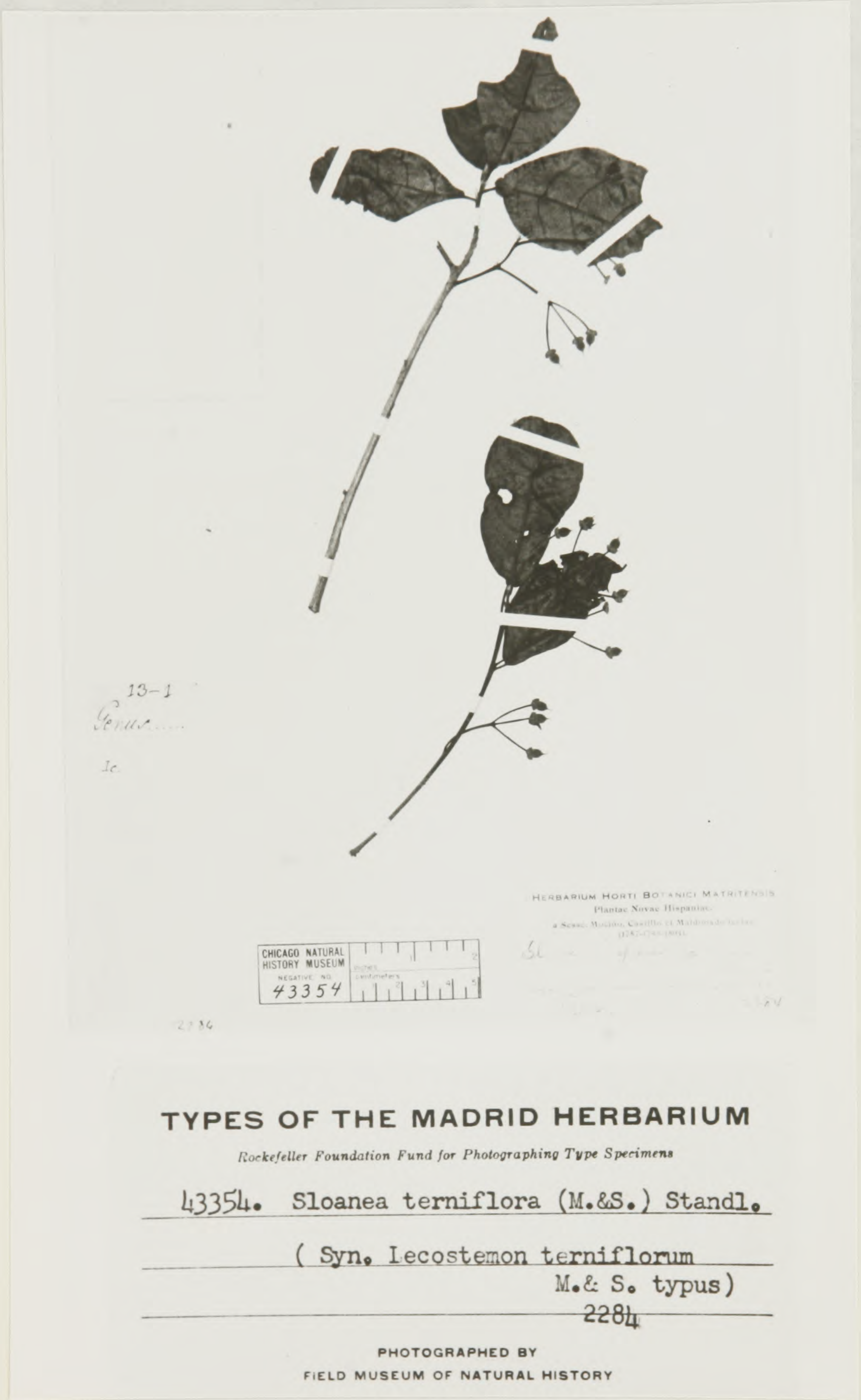


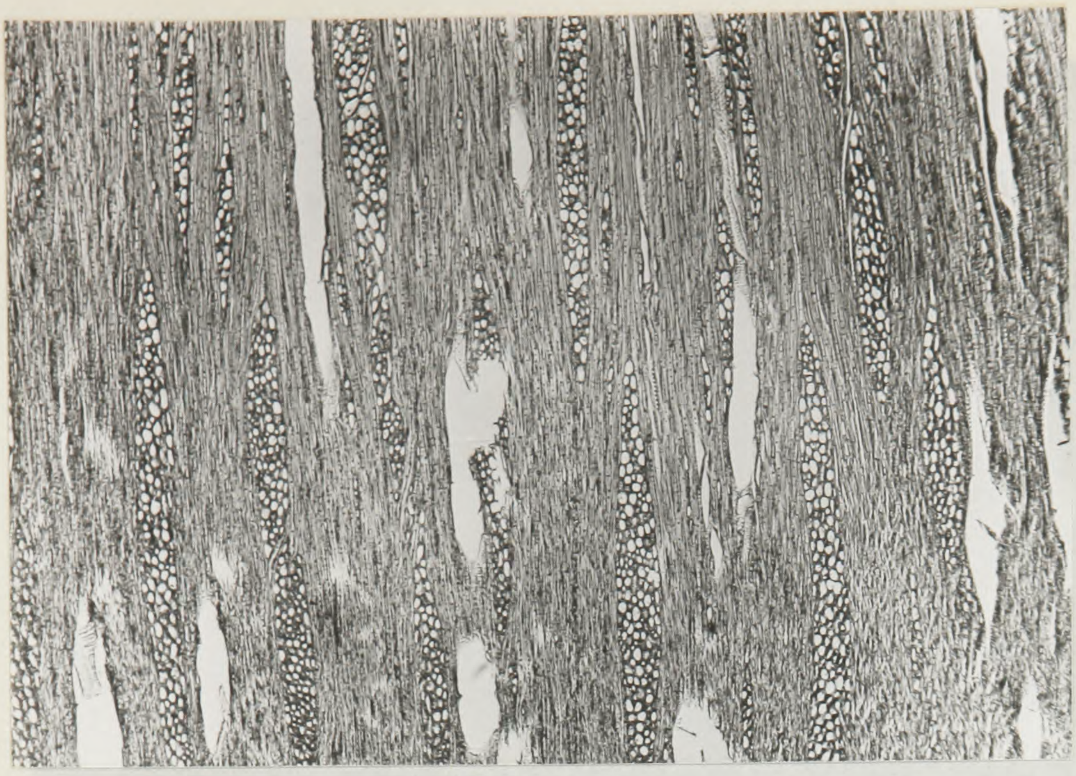
Plate XIII - The specimen of Sloanea terniflora (DC.) Standl. in the Mociño & Sesse' herbarium.

X.S. (x 12)

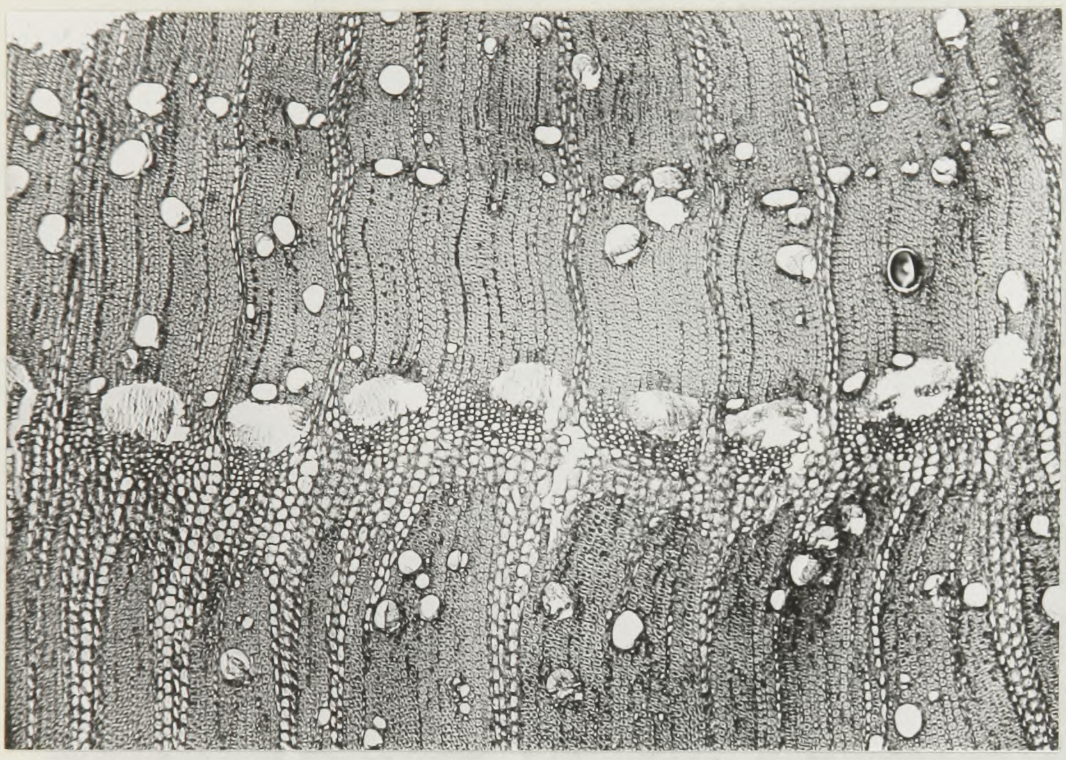
T.S. (x 12)

T.S. (x 60)

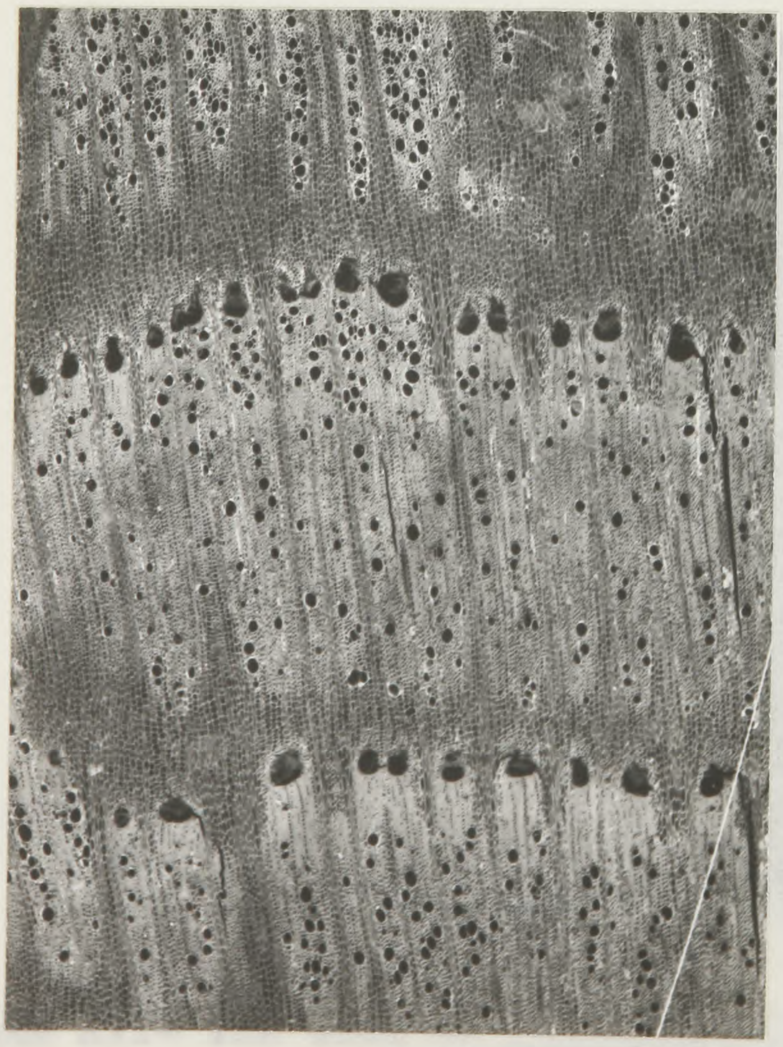
Plate XIV- The wood of Rhabdodendron crassipes.



T.S. (x20)

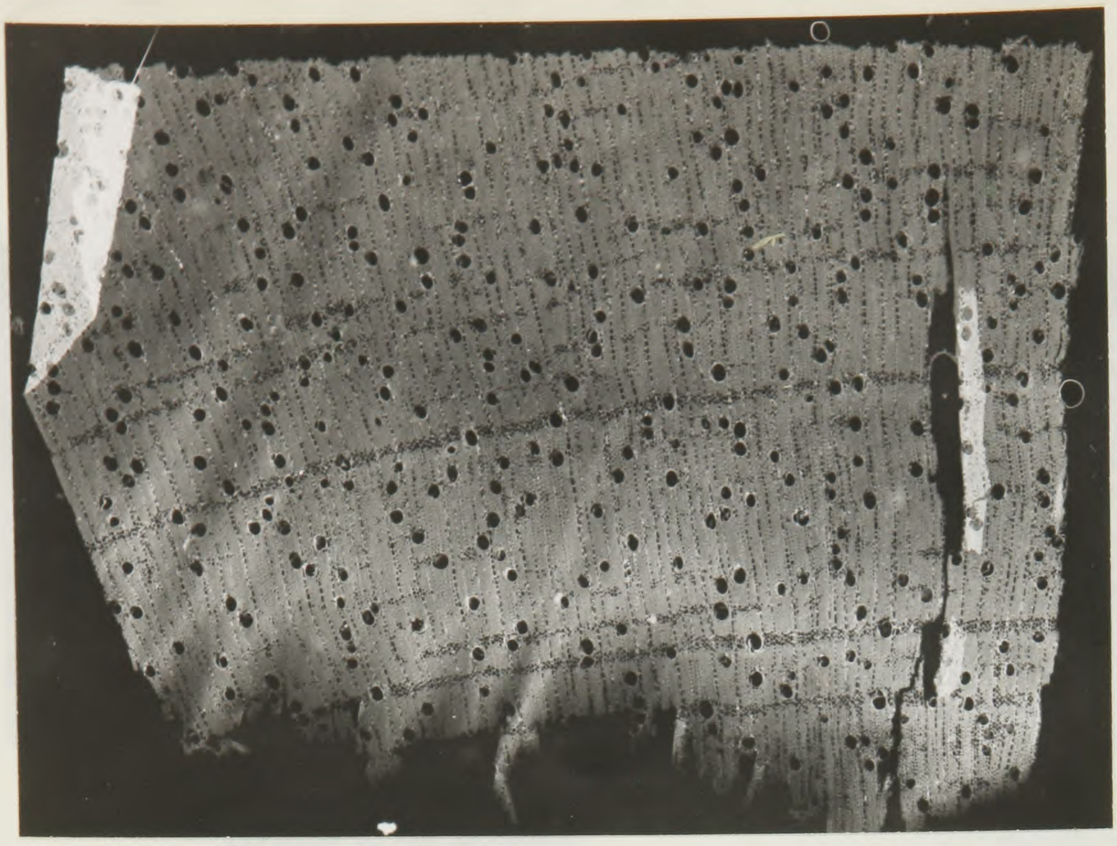


X.S. (x20)

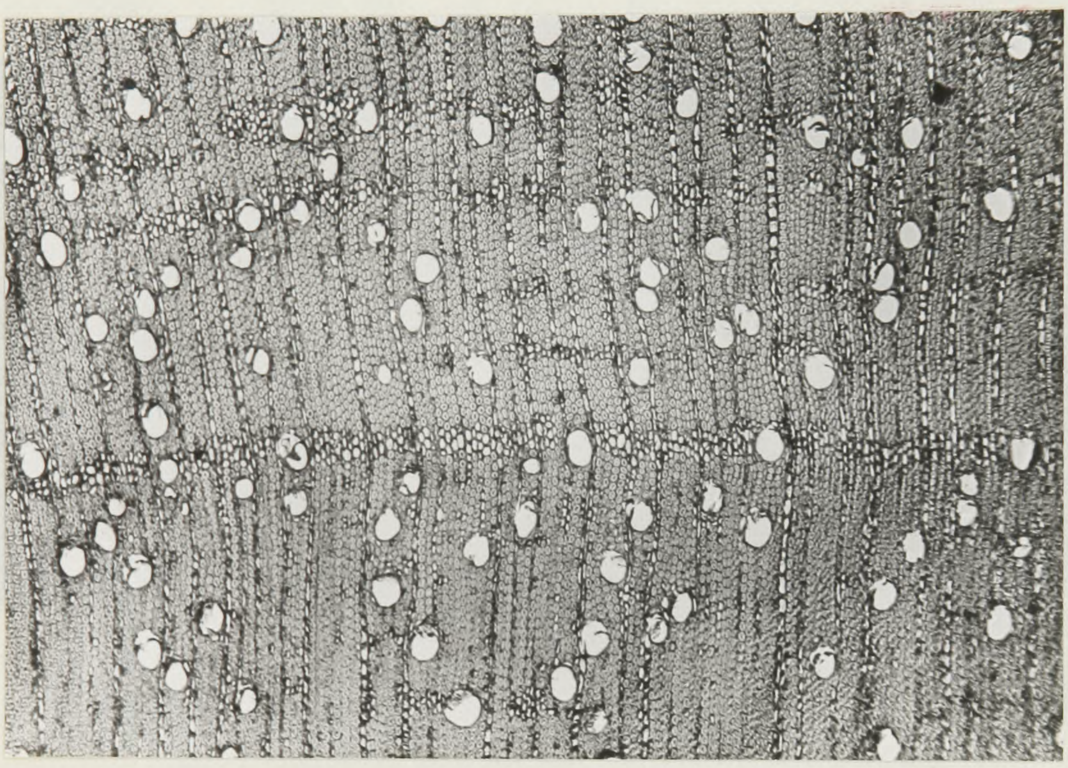


X.S. (x15)

Plate XV - The wood of Rhabdodendron amazonicum.



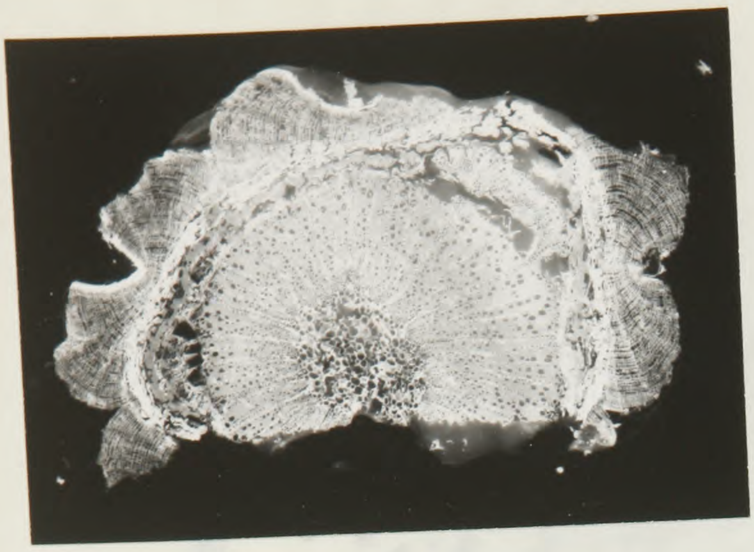
X.S. (x15)



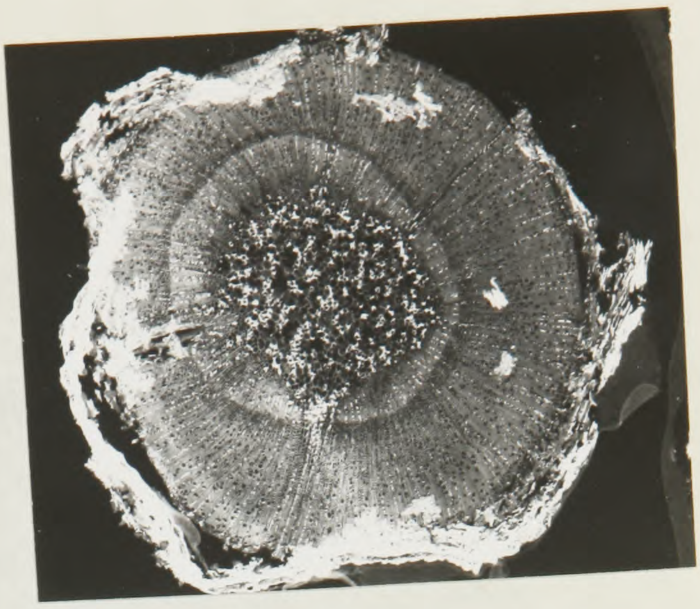
X.S. (x20)

T.S. (x15)

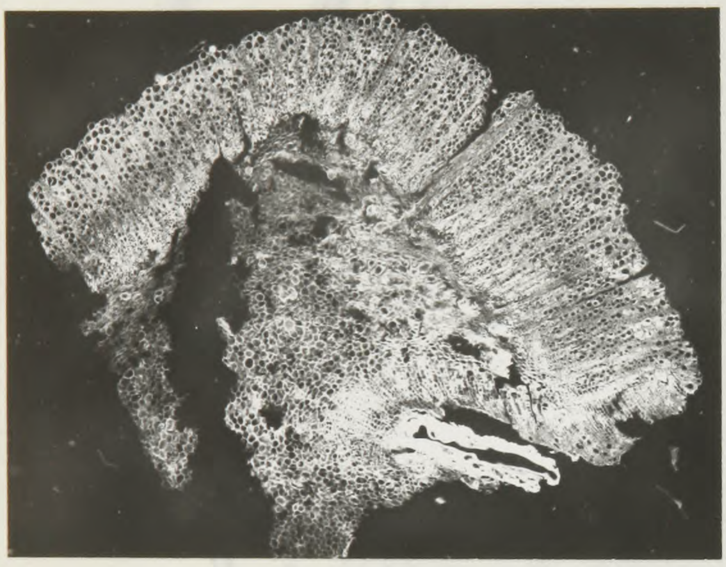
Plate XVI- The wood of Rhabdodendron macrophyllum.



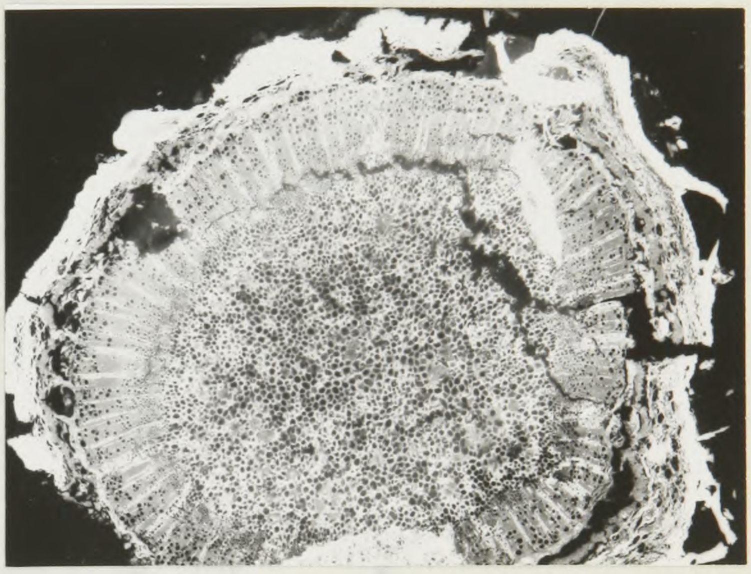
R.gardnerianum



R.macrophyllum



R.amazonicum



R.sylvestre

R.amazonicum

Plate XVII - The twig anatomy of Rhabdodendron. (x11)

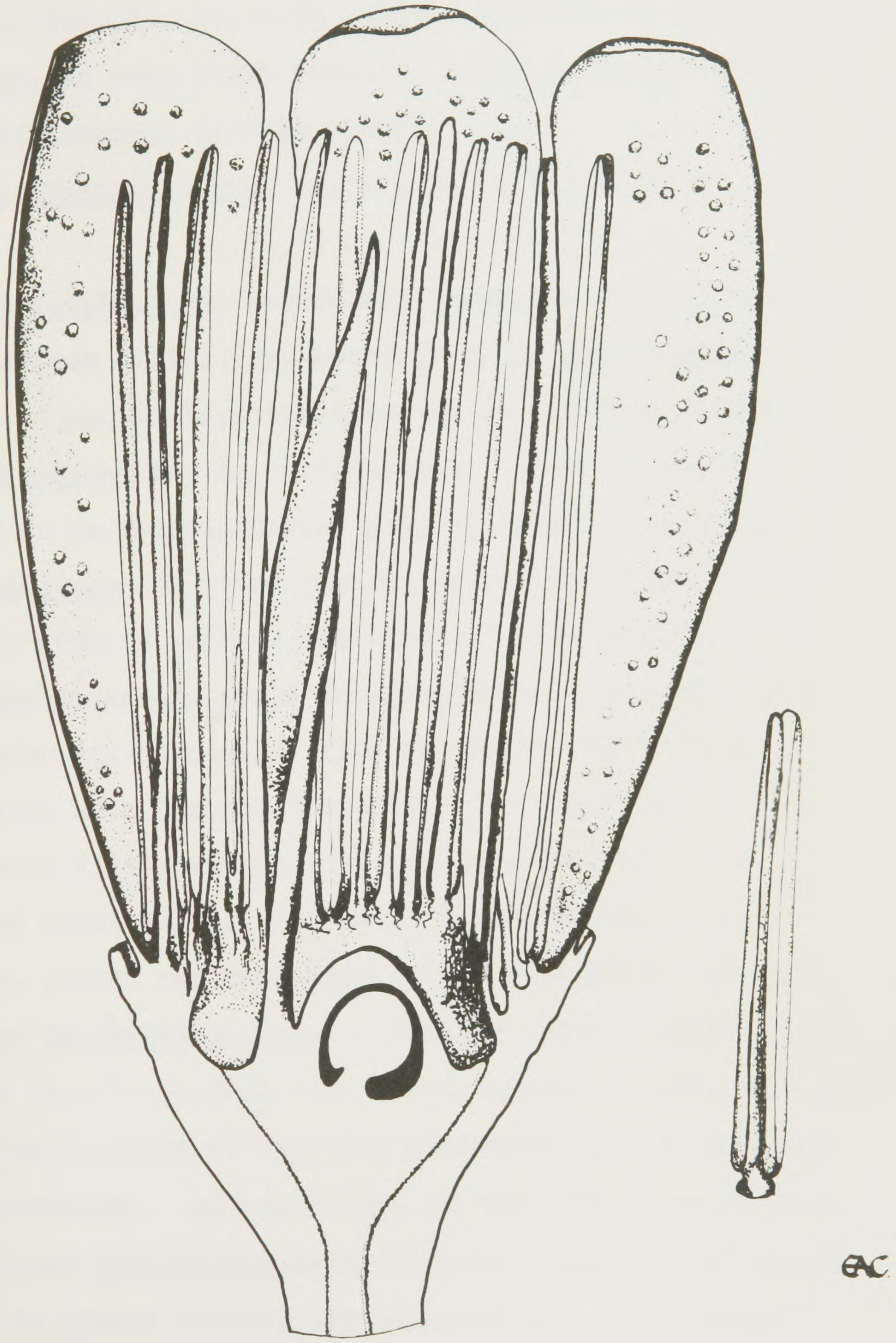


Plate XVIII - The flower of Rhabdodendron macrophyllum.

(x20)

9. THE SYSTEMATIC POSITION OF *STYLOBASIUM*

Stylobasium Desf. in Mém. Mus. Paris 5:37, t. 2 (1819); DC., Prodr. 2:92 (1825); Meisner, Plant. Vasc. Gen 1:101 (1836); Endlicher, Gen. Pl. 2:1253(1840); Benth. in Benth. & Hook., Gen. Pl. 1(1):609 (1865); Fritsch in Verh. Zool-Bot. Ges. in Wein 38:93 (1888); Focke in Engl. & Prantl, Nat. Pflanzenfam. 3(3):58 (1894).

Macrostigma Hook., Ic. Pl. 5, t. 412 (1842).

Stylobasium was accurately described in some detail by Desfontaines (1819), who based it on *S. spathulatum*. He placed it in the Terebinthaceae as he saw some affinity with *Heterodendron* (now in Sapindaceae). A.P. de Candolle (1825) placed in in Terebinthaceae but, together with *Suriana*, *Heterodendron* and other genera, it was in "Genera Terebinthaceis affinia sed non satis nota." He also commented, "An Terebinthaceis prope Heterodendron an Rosaceis Chrysobalaneis adjungendum." Thus he was the first to suggest any connexion with Chrysobalanaceae. Bartling (1830) placed it in "Genera dicotyledonea dubia v. incertae sedis." His comment about it was, however, "Chrysobalaneis inser." Meisner (1836) and Endlicher (1840) both placed it as a dubious *Chrysobalanoideae*. Lindley (1836), Bentham and Hooker (1865), Bentham (1865) and Baillon (1867), all referred to it as a member of the Chrysobalanaceae, without any qualification. Agardh (1858) is the only botanist that has considered *Stylobasium* as a separate family Stylobasieae, which he placed between the Rosaceae and Surianaceae.

Hooker (1842) based a new genus *Macrostigma* on *M. australe*. He did not suggest a systematic position for it; it is in fact *Stylobasium*. Nees (1844) described a new species, *Stylobasium lineare*. Bentham in the 'Genera Plantarum' (1865) merged *Macrostigma* with *Stylobasium* and treated its only species as _S_. _spathulatum_ var. _parvifolia_ Benth. Fritsch (1888) commented on the considerable difference between _Stylobasium_ and the Chrysobalanaceae and suggested that further research, in particular on the anatomy, would show its correct relationship. He tentatively retained it in the Chrysobalanaceae, but as a separate subfamily the _Stylobasieae_. Focke (1894) retained _Stylobasium_ in the _Chrysobalanoideae_ but pointed out that two characters alone, the basal style and the erect ovule, indicated this relationship. He suggested a possible relationship with the Phytolaccaceae. Hallier (1903) discussed the taxonomy of the Chrysobalanaceae on the basis of the detailed anatomical work of Küster (1897), and concluded that _Stylobasium_ does not belong to the Chrysobalanaceae. He placed it in the Rosaceae, _Amygdaloideae_ and pointed out, in particular, its similarities with _Prinsepia_. Twenty years later the same author (Hallier, 1923) retains _Stylobasium_ in Rosaceae. _Prunoideae_ and places it next to _Dichotomanthes_. All other authors since Focke have retained _Stylobasium_ as an anomalous member of the Chrysobalanaceae.

Shrubs. _Leaves_ entire, alternate. _Stipules_ minute, subulate, or none. _Flowers_ solitary in the axils of the leaves, or in short, few-flowered, terminal false racemes. _Flowers_ mostly polygamous, the females with long filiform staminodes, the male with a small abortive ovary, some hermaphrodite. _Calyx_ rather narrow, obconical, persistent in fruit; lobes 5, obtuse, imbricate. _Corolla_ absent. _Stamens_ 10, hypogynous; filaments short and thin, persistent in male flowers, as long as the exserted staminodes in female flowers; anthers large, linear, erect, longer than the calyx and supported by it, bilocular, dehiscing longitudinally. _Style_ 1, basally attached, as long as the calyx but curved inside it, with deflexed stigma in male flowers, longer in female flowers; stigma large and peltate. Ovary superior, of a single carpel, attached centrally to the receptacle, glabrous, unilocular; ovules 2, basally attached, erect with the micropyle facing towards the style. Fruit a small drupe, obovoid or globose, unilocular and one seeded, glabrous inside; mesocarp thin, fleshy; endocarp thick, hard, bony, with a very smooth exterior, on germination splitting into two equal halves; seed with a little endosperm; radical pointing downwards; cotyledons 2, thick, transversally induplicate.

An exclusively Australian genus, found only in Western Australia and the Northern Territory in dry sandy areas. (Plate XXIII).

The small inconspicuous nectarless flowers, without petals, but with very large anthers producing copious pollen, and the considerably expanded stigmatic surface suggest that the flowere are wind pollinated. But there is no field evidence of this.

The most important floral and fruit differences from the Chrysobalanaceae are the absence of a disc, the large linear anthers, the hypogynous stamens, the large peltate stigmatic surface, the endocarp which splits into two equal halves on germination and the presence of a thin layer of endosperm in the seed. Furthermore, the geographical distribution does not overlap with that of the Chrysobalanaceae.

Stylobasium differs as much from the Rosaceae in the absence of a disc, the large linear anthers, the hypogynous stamens, the gynobasic style, the erect ovules, the large peltate stigmatic surface and the polygamous flowers.

Leaf Anatomy

All the following characters are recorded by Küster (1897). During the investigation I cut sections of the leaves from the following specimens to confirm Küster's findings - S. spathulatum Royce 6452 and Chippendale 20927; S. lineare Müller s.n.

The epidermal cells are flat, tubular, isodiametric and in surface view polygonal. The cuticle often appears to have parallel raised ridges. The stomatal cells are uniform and distributed over the whole of the leaf surface: they have no accessory cells. The other two or three cell layers consist of elongate palisade cells. There is spongy mesophyll tissue only in the centre and near the nerves where there is thickened collenchyma. The 4-8 lateral nerves develop no ring of sclerenchyma. There are no trichomes, palisade glands or crystals. Silica in any form is absent.

The six main differences between Stylobasium and the Chrysobalanaceae are as follows: (1) The symmetrical stomata are evenly distributed on both surfaces of the lamina. In Chrysobalanaceae the stomata are asymmetrical and confined to the lower surface. (2) The stomata do not have accessory guard cells. In Chrysobalanaceae these are always present. (3) There is no continuous sclerenchymatous ring round the leaf nerves and no cells thickened only on one side, both characteristic features of the leaf nerves in Chrysobalanaceae. (4) The narrow assimilatory cortex of the axis. In Chrysobalanaceae the axis does not have assimilatory tissue. (5) The spongy mesophyll tissue is considerably less than that of the Chrysobalanaceae. (6) There are no silica deposits of any sort. In Chrysobalanaceae silica in one form or another is always abundant.

Floral Anatomy

The figure (Plate XXII) shows the path of the vascular traces to the various floral organs. This has been described in detail by Bonne (1925), in her study of the Rosaceae. Her work serves to show how different the vascular anatomy of Stylobasium is from any of the Chrysobalanaceae or Rosaceae. Bonne considered the differences sufficient to place it in a separate "group" of the Chrysobalanaceae - Stylobasieae.

The main difference from the Chrysobalanaceae is that the staminal traces do not arise from the perianth traces but from the carpellary traces. This does not occur in Chrysobalanaceae and is rare in Rosaceae. Bonne suggests, that because the three groups of vascular traces to perianth, stamens and gynoecium all arise lower than the flower there has been a fusion of a central gynophore with the receptacle tube. She gives as further evidence that there is no receptacle tube, the absence of a disc, the hypogynous stamens and the complete absence of calcium oxalate crystals, which are abundant in the tube of the Chrysobalanaceae. As there are no petals in Stylobasium and the stamens are inserted at the base of the calyx-lobes, there is no external evidence which can be used to decide whether the tissue between the sepals and the stamens represents calyx-tube or receptacle.

There are 10 vascular traces in this tissue, five of which enter the sepals and five of which terminate near their base. Bonne regards this as evidence for "fusion" of sepals and petals. This explanation might not be acceptable to modern developmental anatomists but Bonne has at least shown that Stylobasium does differ anatomically from the Chrysobalanaceae in this respect.

Bonne also showed that Stylobasium is truly monocarpellary, a very important difference from Chrysobalanaceae; where there is always a trace of abortive carpels. The cortical parenchyma of the pedicel is divided into two zones whereas it is homogeneous in Chrysobalanaceae.

It has thus been demonstrated that Stylobasium is basically very different from the Chrysobalanaceae in floral anatomy. Bonne herself observed that the only three similarities which she could find were the articulated pedicel, the presence of a gynophore and the gynobasic style.

The Pollen

Slides were prepared from the following herbarium specimens:- S. spathulatum Desf. Perry 2480; S. lineare Nees; R.D. Royce 6633.

The grains have three furrows, 3 pores, and a small polar area. The exine is rather thin in relation to grain size. The pattern is verrucate to reticulate. Grain size is 38-42 μ. 100 polar length: Equatorial length = 88-100. The furrows are protruding. (Plate VII-8).

The grain is distinguished from the Chrysobalanaceae in having distinct pores which lie in distinctly protruding furrows. The mouth of the furrow in polar view is quite unlike that of Chrysobalanaceae pollen. (see Plate VII-8, 1-7).

The Stylobasium type of pollen occurs frequently in the Sapindaceae e.g. in Serjania (Plate VII-20), in Aceraceae and in other members of the Sapindales. The Sapindaceae is a eurypalynous family, and so other strikingly different pollen types are found within it, nevertheless, on pollen characters Stylobasium seems to fit into the Sapindales better than into the Rosales.

Wood Structure

The wood anatomy of Stylobasium does not appear to have been described previously. No wood samples were obtainable from any known timber collection. The samples used in this work were kindly collected by Dr. G. Chippendale from Alice Springs and Dr. Royce from Western Australia.

As the wood is very different from that of all Chrysobalanaceae and has never been described before it is described in detail below.

The following species were sectioned and macerated - S. spathulatum: Chippendale 8032 - C.F.I. Wood Col. 20927; Royce 6452 - C.F.I. Wood Col. 21068; S. lineare: Royce 6633 - C.F.I. Wood Col. 21069.

Growth rings present but not very conspicuous, marked by a change in fibre-wall thickness and by terminal parenchyma in S. spathulatum.

Vessels commonly in radial multiples of 2-9 cells. Perforation simple. Intervascular pitting alternate, large, with hexagonal borders. Average vessel diameter 65 μ, average member length 315 μ.

Fibres moderately thick-walled. Pits simple, indistinct on the radial walls. Septate fibres occur in S. spathulatum but not in S. lineare. Average fibre length 825 μ.

Parenchyma predominantly paratracheal, varying from a condition in which a few cells partially or completely surround the vessels to aliform and confluent types, where the parenchyma is more abundant. The confluent bands may be regular or irregular and 1-3 cells in width. Occasional groups of cells detached from these bands give the appearance of being apotracheal. Terminal bands 1-3 cells wide occur in S. spathulatum. Fusiform parenchyma cells present.

Rays mostly uniseriate but with a few biseriate, mostly 3-11 cells and 150-550 μ high. Many rays 10 cells high, a few higher (up to 16 cells). The rays are heterogeneous of

Kribs type IIA, with cells mostly rather elongate and containing numerous inclusions. Ray-vessel pitting alternate, and large.

The wood is rather soft. Silica granules are absent. (Plates XIX, XX, XXI).

The vessel arrangement of Stylobasium is entirely different from that of the Chrysobalanaceae. Stylobasium vessels are small and in multiples, and they lack the typical oblique arrangement of the Chrysobalanaceae. The parenchyma is not in continuous bands except at the end of the ring. Where there are broken bands in S. lineare they are quite distinct from the Chrysobalanaceae in that they are confluent. That some of the parenchyma cells are fusiform is an important basic difference. Fusiform parenchyma never occurs in the Chrysobalanaceae. The fibres of Stylobasium do not have bordered pits and septate fibres occur in S. spathulatum. Both these features are unknown in the Chrysobalanaceae. The pits of the ray cells are quite unlike those of the Chrysobalanaceae, whose ray cells are distinct by their thick walls and vary numerous and obvious pits, also the end walls of the cells are nodular. This is not so in Stylobasium. The absence of silica is an important distinguishing feature of Stylobasium, also the ray cells are not filled with the abundant gum deposits typical of the Chrysobalanaceae.

The only basic similarity between the two woods is found in the rays. The uniseriate rays of S. spathulatum and 1-3 seriate rays of S. lineare resemble those of the Chrysobalanaceae. Some of the pits connecting vessels and rays of Stylobasium are large and elongate as in the Chrysobalanaceae.

Several characters of the wood of Stylobasium, for example the vessel member length and the occurrence of fusiform parenchyma cells, indicate a higher level of specialization than in the Chrysobalanaceae.

The wood of Stylobasium differs from that of the Rosaceae in as many features. The intervascular pitting is large whereas in Rosaceae it is never large. The fibre pits are simple and are indistinct on the radial walls; but in Rosaceae they are bordered and usually equally numerous on the radial and the tangential walls. The parenchyma is predominantly paratracheal in Stylobasium but usually apotracheal only in Rosaceae. The rays are predominantly uniseriate in Stylobasium whereas they are multiseriate in Rosaceae. Fusiform parenchyma cells and terminal bands of parenchyma are important features of the wood of Stylobasium, but neither of these features occur in Rosaceae.

Discussion of the Systematic Position as indicated by Wood Anatomy

The wood structure clearly indicates that Stylobasium should be removed from the Chrysobalanaceae. The wood of Stylobasium does not correspond exactly to that of any of the families represented in the wood collection of the Commonwealth Forestry Institute, Oxford. At Oxford there is a punched-card system for storing information taken from slides of the woods represented there. The wood of Stylobasium was compared with other woods by use of this punched-card system, but this did not lead to the continuous selection of any one particular family. However, the Anacardiaceae and Sapindaceae appeared frequently. Initially the following characters of the wood of Stylobasium were chosen for comparison: (1) vessels in radial multiples; (2) fusiform parenchyma cells; (3) fibres with simple pits; (4) predominantly paratracheal parenchyma in bands; (5) predominantly uniseriate rays. The selection for cards using these five characters does not leave any punched-cards with such a combination of features. However, when as many variations as possible of the characters of Stylobasium wood were used, the Anacardiaceae and the Sapindaceae were the only families that appeared to have comparable woods.

The wood of Stylobasium does have close affinities with these families, but has enough differences to suggest that it does not belong to either of them. Wood structure gives further evidence that the relationship of Stylobasium is with the Sapindales, although not as a member of any existing family. Some of the most important features of the wood of Stylobasium are listed below, together with some of the families of the Sapindales in which these features also occur in at least several genera.

Vessels in radial multiples	- Sapindaceae, Aceraceae, Melianthaceae, Hippocastanaceae, Anacardiaceae, etc.
Vessel perforation simple	- Sapindaceae, Aceraceae, Hippocastanaceae, Melianthaceae, Anacardiaceae, etc.
Fusiform parenchyma cells	- Sapindaceae, Aceraceae, Melianthaceae, Corynocarpaceae.
Fibre pits simple	- Sapindaceae, Aceraceae, Hippocastanaceae, Melianthaceae, Sabiaceae.
Septate fibres	- Sapindaceae, Akeniaceae, Melianthaceae, Sabiaceae.
Rays mostly uniseriate	- Sapindaceae, Hippocastanaceae, Anacardiaceae, etc.

From this it can be seen that on wood anatomy Stylobasium fits better into the Sapindales than into the Chrysobalanaceae.

Hallier suggested that Stylobasium should be placed in the Rosaceae in his subfamily Amygdaloideae (which corresponds closely to the currently accepted Prunoideae). There are several anatomical features against this. The Rosaceae have small intervascular pitting, multiseriate rays and fibres with distinctly bordered pits. They never have fusiform parenchyma cells.

Blastogeny

The seedling escapes from the seed by splitting the endocarp into two equal halves. The germination is epigeal. The first pair of leaves are alternate, as are the later leaves. The young leaves have a short and sparse pubescence and all have stipules which are small and linear. The germination of Stylobasium is illustrated in Plate XXIV.

The combination of epigeal germination with first leaves alternate has not been observed in any Chrysobalanaceae examined so far. Seeds of Stylobasium were kindly collected by Dr. G. Chippendale of Alice Springs, Northern Territory, Australia. A high rate of germination was obtained from them.

Taxonomic Discussion

The fact that Stylobasium is not a member of the Chrysobalanaceae is apparent from the anatomical and morphological descriptions already given. Apart from Agardh (1858) Hallier (1903) was the only botanist to remove it from Chrysobalanaceae; he placed it in the Rosaceae sens. strict. His main reasons were the large disc-shaped style like the small disc-shaped one of Prinsepia (Prunoideae), the basally thickened bud scales, the phyllotaxis, the solitary rather large flowers at the end of the branches forming a raceme, the cuneate leaves gradually narrowed to the petiole, the cup shaped, five lobed, ciliate calyx, the 10 stamens and the thin layer of endosperm. Throughout this chapter attention has been drawn to the morphological and anatomical differences from the Rosaceae. Stylobasium certainly does not fit into the Rosaceae.

It has already been shown that in wood anatomy and pollen structure Stylobasium is very similar to certain members of the Sapindales. Many of its morphological features also occur there. There is little against placing it there. Polygamo-dioecious flowers, the absence of a corolla and a disc, rather linear anthers, a thin endosperm, a single carpel all occur in various families of the Sapindales. The style is not always terminal. It is often subterminal in both the Sapindaceae and Anacardiaceae. Stylobasium does not fit well into any one family of the Sapindales. The absence of a disc and the presence of endosperm would exclude it from the Sapindaceae.

In this study I am more concerned with the relationship of Stylobasium to Chrysobalanaceae than with establishing its correct position in a general system of classification. However, the foregoing evidence does seem to indicate that Agardh (1858) was correct in giving it family status (see Bullock in Taxon 7:32, 1958), and that it is best accommodated in the Sapindales, where it seems to be most closely related to Sapindaceae and Anacardiaceae. This is in fact returning the genus to the position originally suggested for it by Desfontaines (1819) and maintained by De Candolle (1825).

Gutzwiller (1961), in discussing the systematic position of Suriana, decided that it should constitute a separate family close to Chrysobalanaceae, Connaraceae and Sapindaceae in the "Geraniales sens. lat." However it is apparent that her knowledge of Chrysobalanaceae was superficial and probably based as much on a knowledge of Stylobasium as on its true members. The present study has shown that Stylobasium is quite different from the rest of the Chrysobalanaceae, and that the latter shows no important resemblances to Geraniales (see pp 29,33); it does however confirm Gutzwiller's incidental observation that Stylobasium is related to Sapindaceae.

The species of Stylobasium

The two species can be distinguished as follows:

Leaves cuneate-oblong or obovate; drupe twice as long as calyx 1. S. spathulatum

Leaves linear; drupe scarcely exceeding the calyx 2. S. lineare.

1. S. spathulatum Desf. in Mém. Mus. Paris 5:37, t. 2 (1819).

Type: Baudin s.n. (1801) W. Australia, fl. (P).

Distribution: Western Australia, Northern Territory.

2. S. lineare Nees in Lehm., Pl. Preiss 1:95 (1844).

Type specimens: Preiss 2383, W. Australia; 2384, W. Australia (not seen).

Distribution: Western Australia.

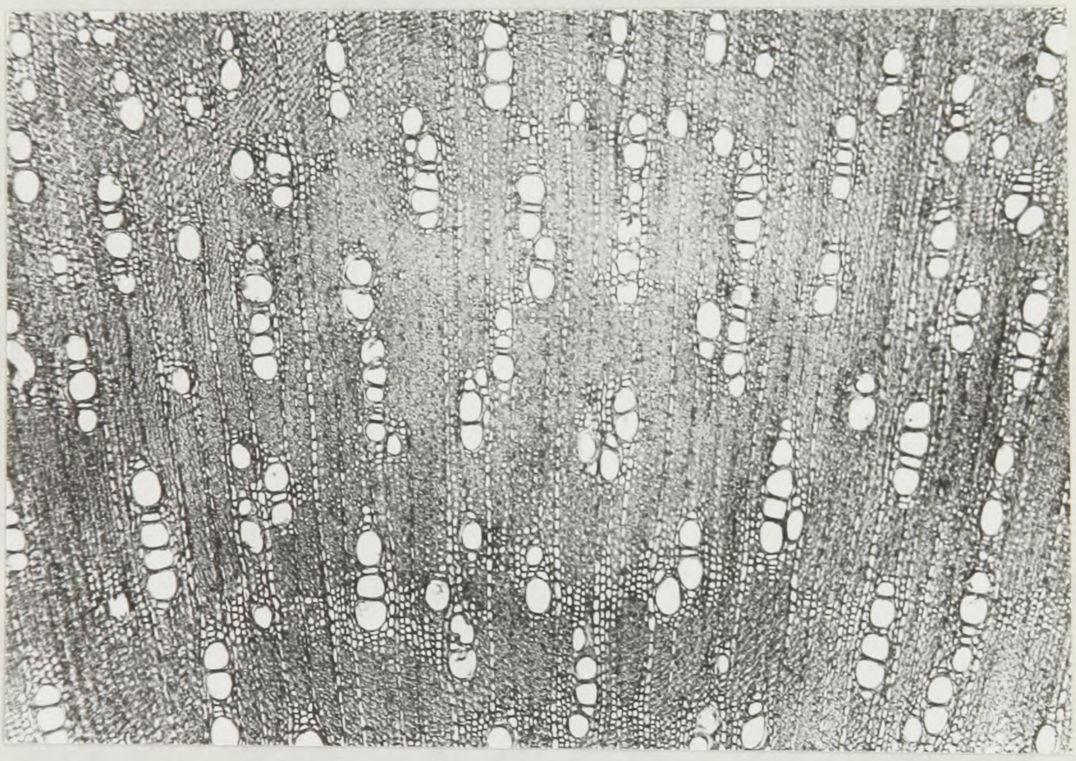
Macrostigma australis Hook., Ic. Pl. 5, t. 412 (1842) = S. lineare Desf. var. parvifolia Benth., Fl. Austral. (1864).

Herbarium material consulted

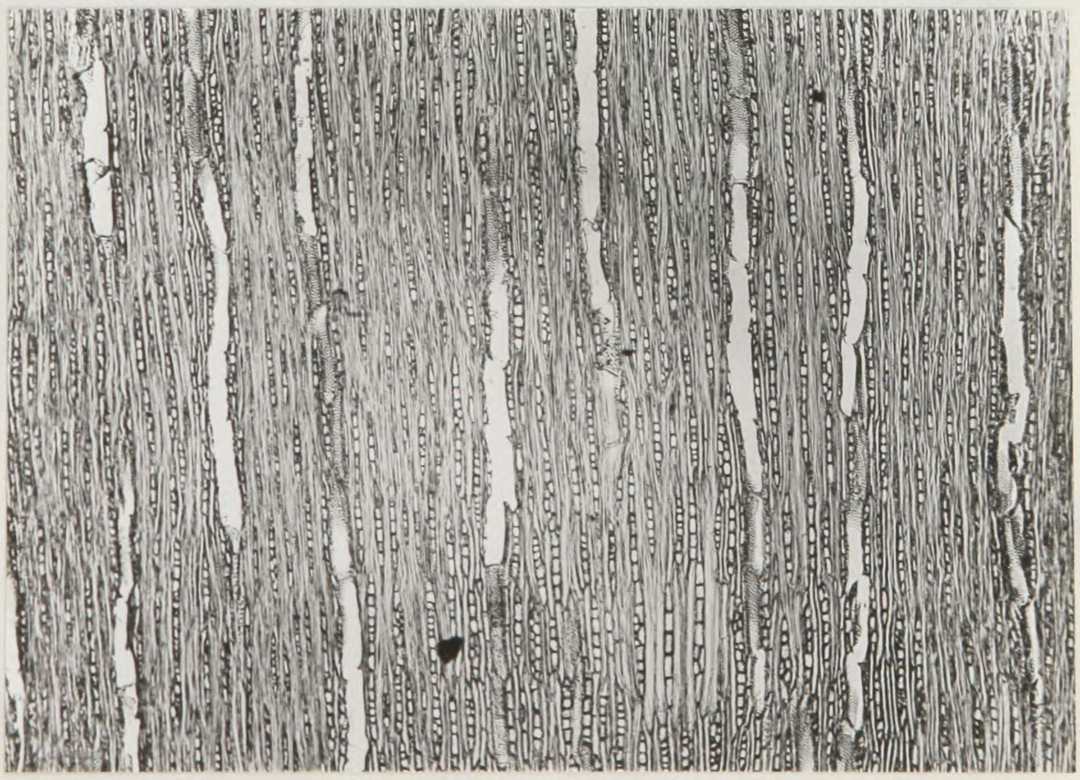
S. spathulatum - Baudin s.n. Type, fl. (P); Morrison s.n. fl. (K; E); Lazarides 5808 fr. (K); Speck 1019 fl. (K); Perry 2482 fr. (K); 2480 fl. (K); Royce 6452 fr. (FHO); Allen 590 fl. (K); Chippendale 8874 fr. (FHO); 8032 fr. (FHO); Hill 423 fl. (K).

S. lineare - Pritzl 620 fl. (M; BR; E); 9 fl. (K); Blake 18063 fl. (K); Royce 6633 fl. (K; FHO); Oldfield s.n. fl. (K); Pemberton 2841 fr. (K); Morrison s.n. fl. (K; P); Mueller 262 fl. (M); Molloy s.n. fl. (CGE).

X.S. x15



X.S. x 20



T.S. x 20

Plate XIX - The wood of Stylobasium spathulatum.

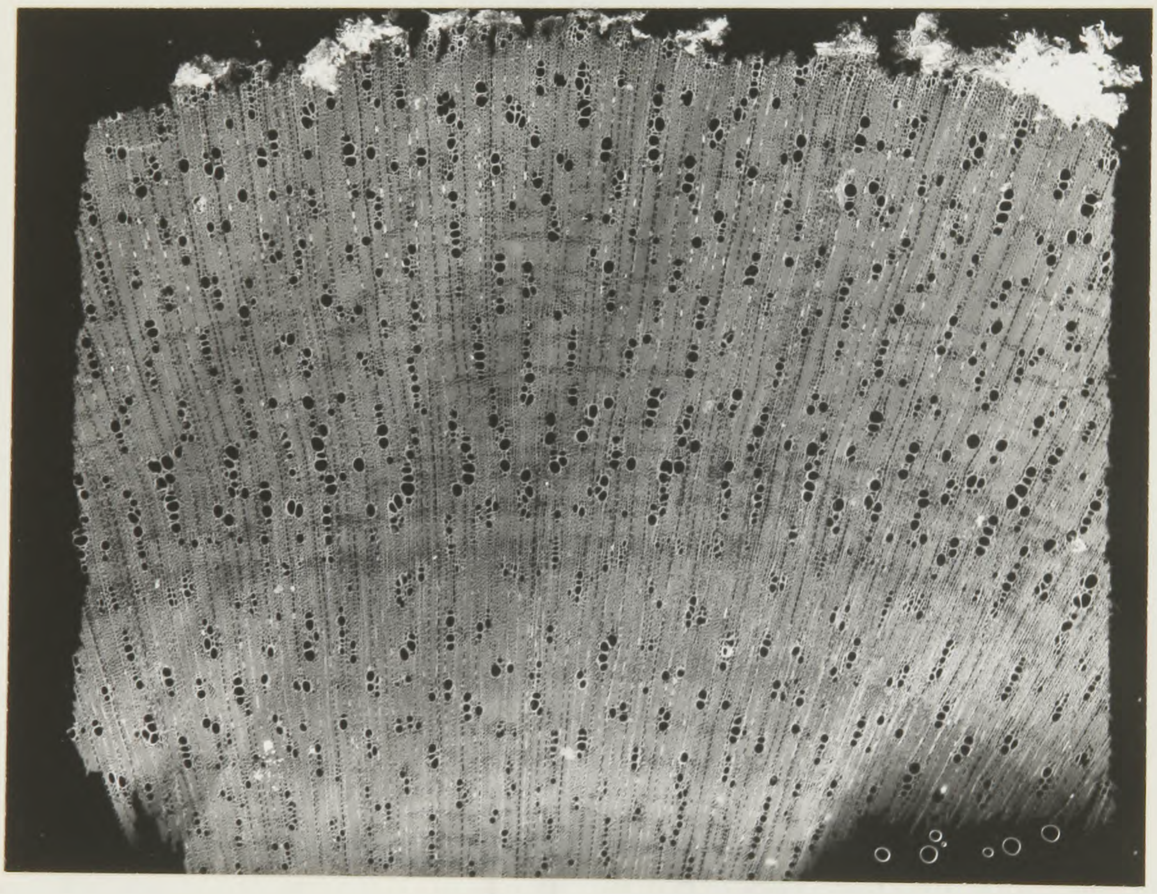
T.S. x 20

T.S. x 60

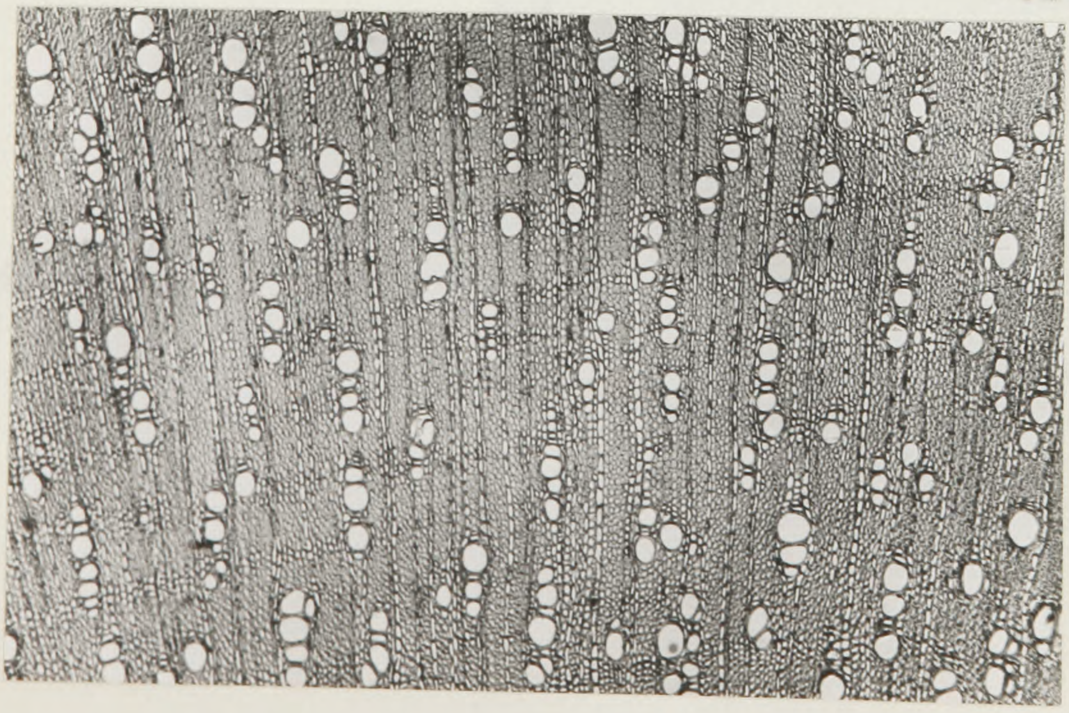
T.S. x 60

Plate XX - The wood of Stylobasium spathulatum.

T.S. x 15.



X.S. x 15.



X.S. x 20.

Plate XXI - The wood of Stylobasium lineare.

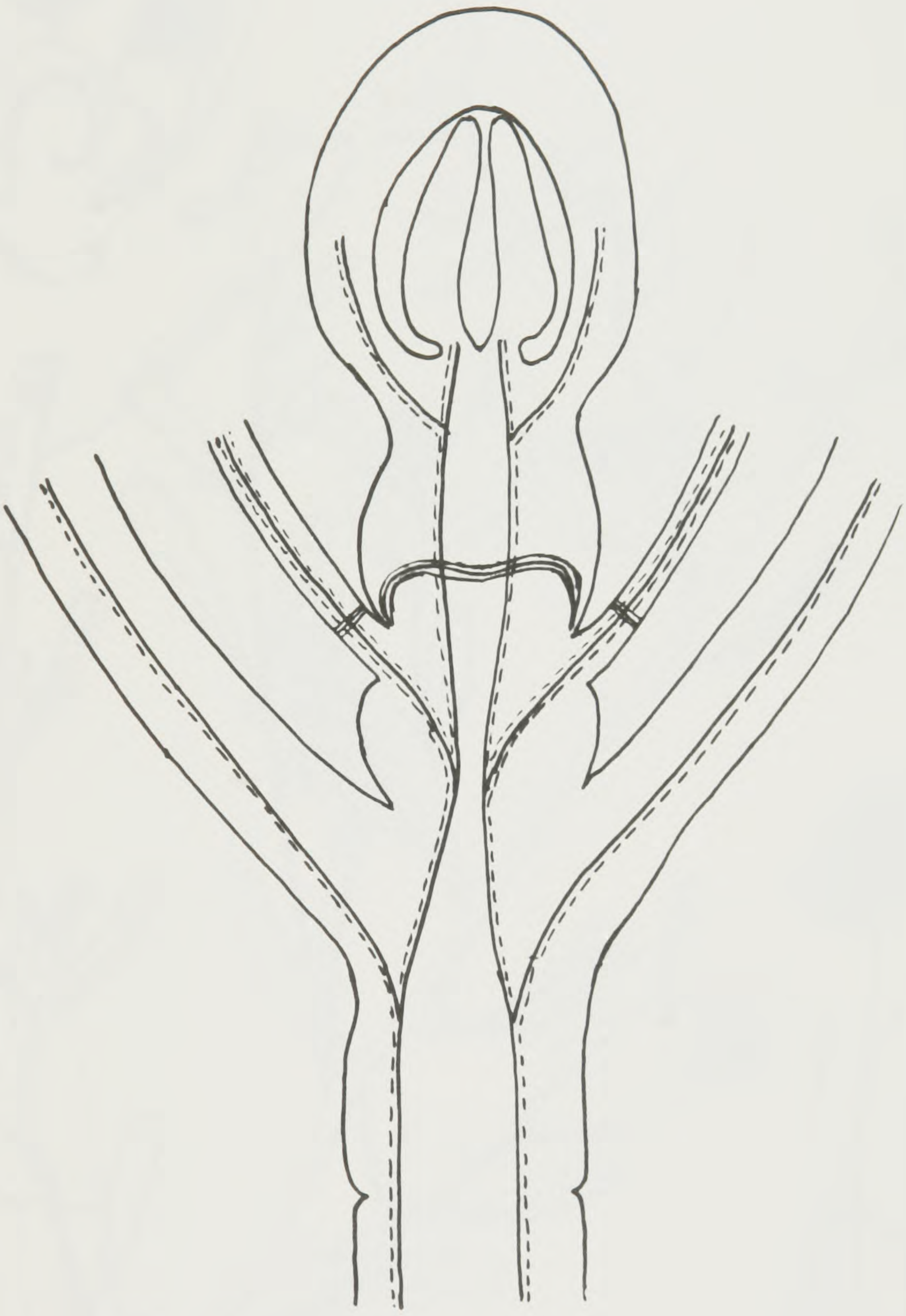


Plate XXII - The floral vascular anatomy of Stylobasium spathulatum Desf. (x25, after Bonne).

Plate XXIII.- STYLOBASIUM SPATHULATUM Desf.

A, flowering branch (x1); B, young flower (x5); C, ⚥ flower (x10); D, ♀ flower (x10); E, fruit (x5).

Plate XXIV - The seedling of Stylobasium spathulatum Desf. (X $\frac{3}{4}$).

10. STATISTICAL CONFIRMATION FOR THE RECOGNITION OF GENERA IN THE CHRYSOBALANACEAE

In Chapter 7 the genera were grouped into two tribes Chrysobalaneae and Hirtelleae. Within these tribes there are different problems concerning the definition of boundaries between the genera, therefore the two tribes are considered separately in the present chapter. The genera Hunga and Grangeria are, however, considered in relation to both tribes because of their intermediate position. The Hirtelleae is considered first because it contains a greater number of species and genera, and the definition of the genera was found at the outset of the present work, to be more confused than in the Chrysobalaneae.

a) The Hirtelleae

Several botanists have already pointed out that the genera within this group are badly defined. Juel (1915) said, "Es scheint mir indessen zweifelhaft, ob die im allgemeinen angenommenen Gattungen en der Chrysobalanoideen wirklich gut begründet sind, und ob nicht etwa die Gattungen Hirtella, Couepia, Parinarium und Acioa zu vereiningen sind, oder auf andere Weise aufzuteilen." Hauman (1952) said of Parinari "Très hétérogène, il conviendra sans doute de le diviser." Early in this study it was apparent that currently accepted generic limits were unsatisfactory. It was apparent that the distinctions between some genera were less than the distinctions between subgenera and other groups within the genus Parinari. This is largely because this tribe is pantropical and has not been monographed since 1825. All recent work has been done on a restricted regional basis, and generic concepts differ widely in different regions.

The main cause of the confusion is the undue emphasis given to a single character, the false partition of the ovary, which was used to diagnose _Parinari_. All species of the Chrysobalanaceae with a bilocular ovary have automatically been placed in _Parinari_, regardless of the fact that frequently the partition is incomplete, and that traces of a partition occur within other genera of the _Hirtelleae_. A critical examination of the whole family has in fact shown that certain plants with a unilocular ovary (_Parinari myriandra_ and _P. heteropetala_) have been placed in _Parinari_ and some with a bilocular ovary have been placed in different genera. Four species of _Licania_ (now _Hunga_) from New Caledonia and one species of _Angelesia_ (also now _Hunga_) from Papua have a bilocular ovary.

It soon became obvious that _Parinari_ was heterogeneous. Most species have been assigned to their genera on the basis of incomplete material. Early in this investigation an attempt was made to assemble complete material for as many species as possible. A special effort was made to obtain fruiting specimens as they had been neglected to a large degree by previous workers, and they showed promise of providing useful characters.

It appeared that _Parinari_ could be divided into seven groups, five of which almost exactly corresponded to the subgenera _Parinari_, _Sarcostegia_, _Cyclandrophora_, _Pellegriniella_ and _Neocarya_. The differences separating these groups in nearly all cases seemed to be greater than those separating the long-established genera _Hirtella_, _Grangeria_, _Acioa_ and _Couepia_. Four species of _Licania_ and three of _Parinari_ from New Caledonia and one species of _Angelesia_ from Papua appeared to be congeneric and distinct from all other genera.

At this stage it was decided to test the validity and relationships of these "genera" using a digital computer. Recent authors have differed as to the circumscription of

Magnistipula and the relationship of its species were also investigated with the computer. The genus Acioa is not easily confused with the others, and was not included in the first two statistical analyses.

(1) The Characters used

In order to make a statistical examination of this group the data had to be scored numerically. For computer analysis all characters must be recorded for each sample, which means that enough gatherings of each species must be obtained to observe all characters. It was possible to gather complete data for 124 species from the five genera originally concerned. A varying number of herbarium sheets of each of the 124 species were seen (see Appendix 1). The characters used include all those used by previous taxonomists to define the subdivisions of the group, plus additional characters that I thought were significant. In all twenty-one features were used. Obviously some of the characters included were in my opinion of little taxonomic value, but if the analysis gives a true picture it should not make any difference to include them because in the analysis poorly correlated characters are given no weight. Some of the characters used are qualitative (i.e. with only two alternatives) and some quantitative (i.e. numerical features or ones where there are more than two possibilities). There were eleven qualitative and ten quantitative characters used. A list of these characters is given:-

Qualitative

1. Calyx lobes pointed (1) or rounded (0).
2. Receptacle hairy inside right to base (1) or not (0).
3. Ovary bilocular (1) or unilocular (0).
4. Bracts and bracteoles enclosing flowers in small groups (1) or not (0).
5. Stamens far exserted (1) or not (0).
6. Staminodes united into a "comb" (1) or not (0).

7. Ovary insertion terminal at mouth of receptacle (1) or not (0).

8. Stipules enlarged (1) or not (0).

9. 2 glands at the leaf base or on petiole (1) or not (0).

10. Prominent lenticels on young flowering stem (1) or not (0).

11. Stamens joined into a single ligule (1) or not (0).

Quantitative

12. Receptacle shape elongate, symmetrical, hollow (1), elongate symmetrical solid (2), ventricose (3), saccate (4).

13. Fertile stamens occupying complete (1), two thirds (2), or less than half (3), of the perimeter.

14. Leaf-undersurface with stomatal cavities (1), softly and densely hairy (2), glabrous (3), with stiff and not dense hairs (4).

15. Bracts and bracteoles with many sessile or stalked glands (1), two sessile basal glands (2), or none (3).

16. Epicarp verrucose (1), smooth (or with a few hairs) (2), with a dense rusty tomentum (3), dense covering of crustaceous warts (4).

17. Endocarp smooth (1), v. rough and fibrous (2), hard and roughish (3), soft with thin fibres only (4).

18. Seedling Escape basal stoppers or plates (1), a single line (2), three or more lines (3), no special mechanism (4).

19. Inflorescence panicle (1), corymbose panicle (2), elongated raceme (3), short, subcorymbose raceme (4).

20. Stamen number.

21. Flower size - measured in centimetres from articulation to apex of calyx-lobe.

The complete data for every species used, as scored numerically is given in appendix 4.

At this stage some discussion on the type of character selected and the value of these twenty-one characters is necessary. It has already been pointed out that all characters used previously for division of genera within this group were included. Thus, although I did not consider characters six, eight and ten to be significant, they were included to give them a fair test. For example, character six, whether the staminodes form an elevated tongue or not, is used by Hauman as one of the characters to define Magnistipula. As can be seen from appendix 4 this character occurs occasionally in other genera, and it is not diagnostic of Magnistipula in the sense that I would define it.

Obviously floral morphology is extremely important for generic characters. It can be seen that eleven out of the twenty-one characters are floral (characters 1-3, 5-7, 11, 12, 13, 20 and 21). Most of the floral characters are self-explanatory from the list but characters five, twelve and thirteen, the length of the stamens, the shape of the receptacle and the insertion of the stamens, need further explanation. Character five has two alternatives, whether the stamens are far exserted or not. Far exserted was defined as where the filaments are at least twice as long as the calyx-lobes. The descriptions of the different genera given in the Conspectus show that there is considerable variation in the shape of receptacle. As with several of these characters the problem is how to express this accurately for the computer. The majority of species in the Hirtelleae have subcampanulate-turbinate, hollow receptacles, this is symbolized by a 1. (as in Plates XLI, LI, etc.). A survey of the whole tribe showed that certain of the putative genera differed from the basic type of receptacle. The solid type found in Parinari subgenus Sarcostegia is symbolized by 2 (see Plate LIII), the oblique ventricose type, found in Magnistipula, Parinari benna and P. tessmannii, by 3 (see Plates XLV, XVVI), and the distinctive saccate type found in P. macrophylla by 4 (see plate L). Character thirteen is based on the insertion of the fertile stamens. These may be attached round the whole perimeter of the receptacle (see Plate XLII), or they may be unilateral (3) (see Plate XXXIX), in the extreme cases; but many are intermediate (2), often with only a few anantherous stamens (see Plate XLI).

Fruit characters are extremely important, especially because they have been neglected in the past. After enough fruiting material had been obtained it was found that the fruits yielded many extra characters. For the purpose of the statistical analysis this is summarized into three categories (characters sixteen to eighteen), the type of epicarp, endocarp and dehiscence. The diversity of the fruit structure in the Hirtelleae is illustrated in plates XXV and XXVI. The type of fruit exterior is comparatively constant within certain genera (e.g. Hirtella and Magnistipula), and within the subgenera of Parinari. It may be verrucose as in Parinari subgenera Parinari and Neocarya (1) (Plates XXV-A, XXVI-H); smooth, unwarted and glabrous as in Hirtella or Parinari subgenus Sarcostegia (most spp.) (2) (Plates XXVI-I and L); densely tomentose as in most of Magnistipula and Acioa (3) (Plate XXVI-K) or of a crustaceous appearance, due to the density of warts, as in Parinari subgenus Cyclandrophora (4) (Plate XXV-D). Likewise, the endocarp was divided into four categories, which are easily observable. It may be completely smooth and bony as in Parinari benna (1) (Plate XXVI-J), very rough, hard and channelled as in Parinari subgenus Parinari (2) (Plate XXV-A and G, XXVI-H), hard and roughish, with a granular exterior, as in Couepia (3) (Plate XXVI-M), or soft and scarcely differentiated as in Magnistipula (4) (Plate XXVI-K). The most interesting feature of the fruit concerns the different mechanisms which allow the seedling to escape from the hard endocarp. This has been discussed briefly by Hill (1937), but has not been applied in the past as a taxonomic character within the group. These mechanisms are illustrated in the plates. The most striking is found in Parinari subgenera

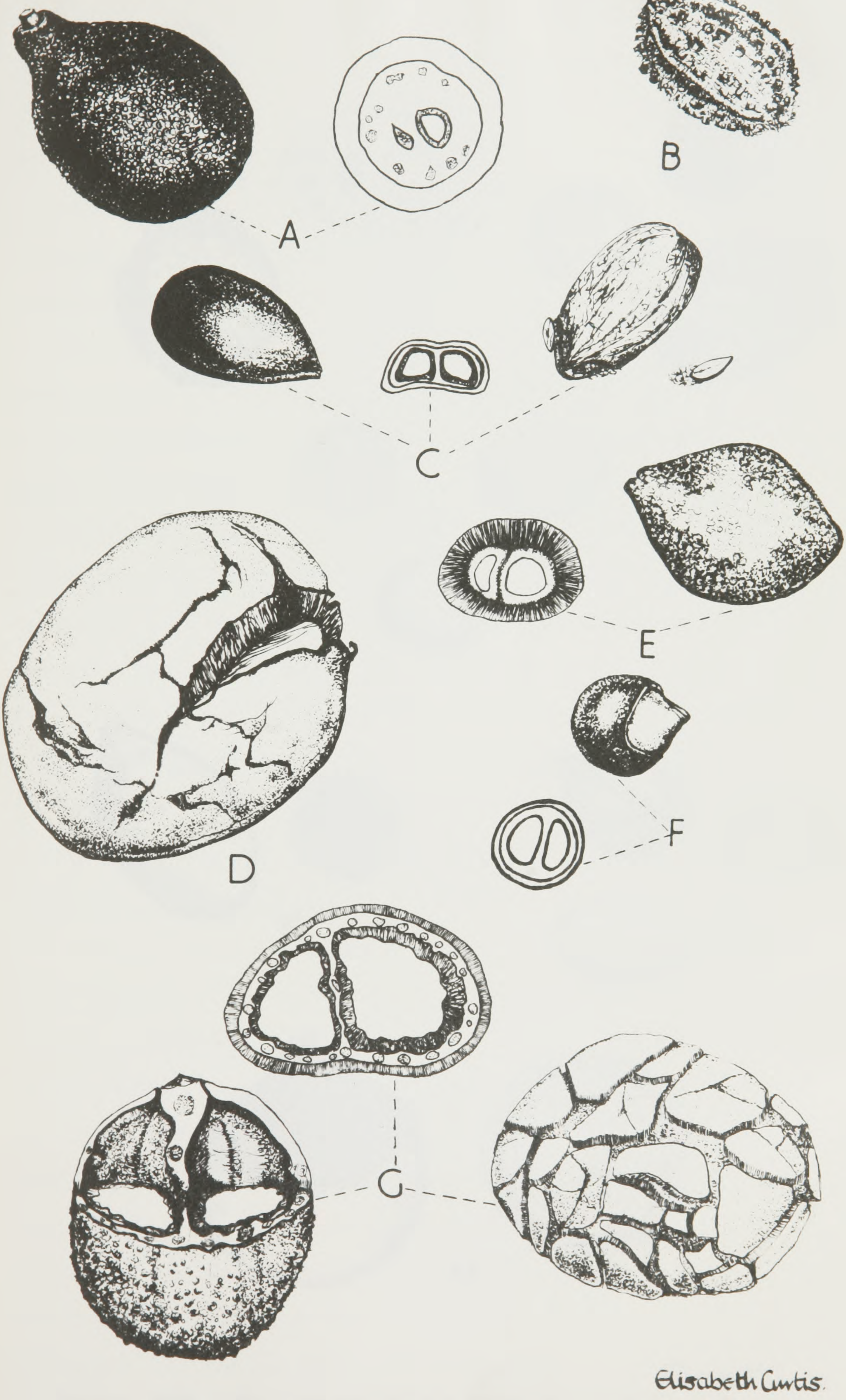
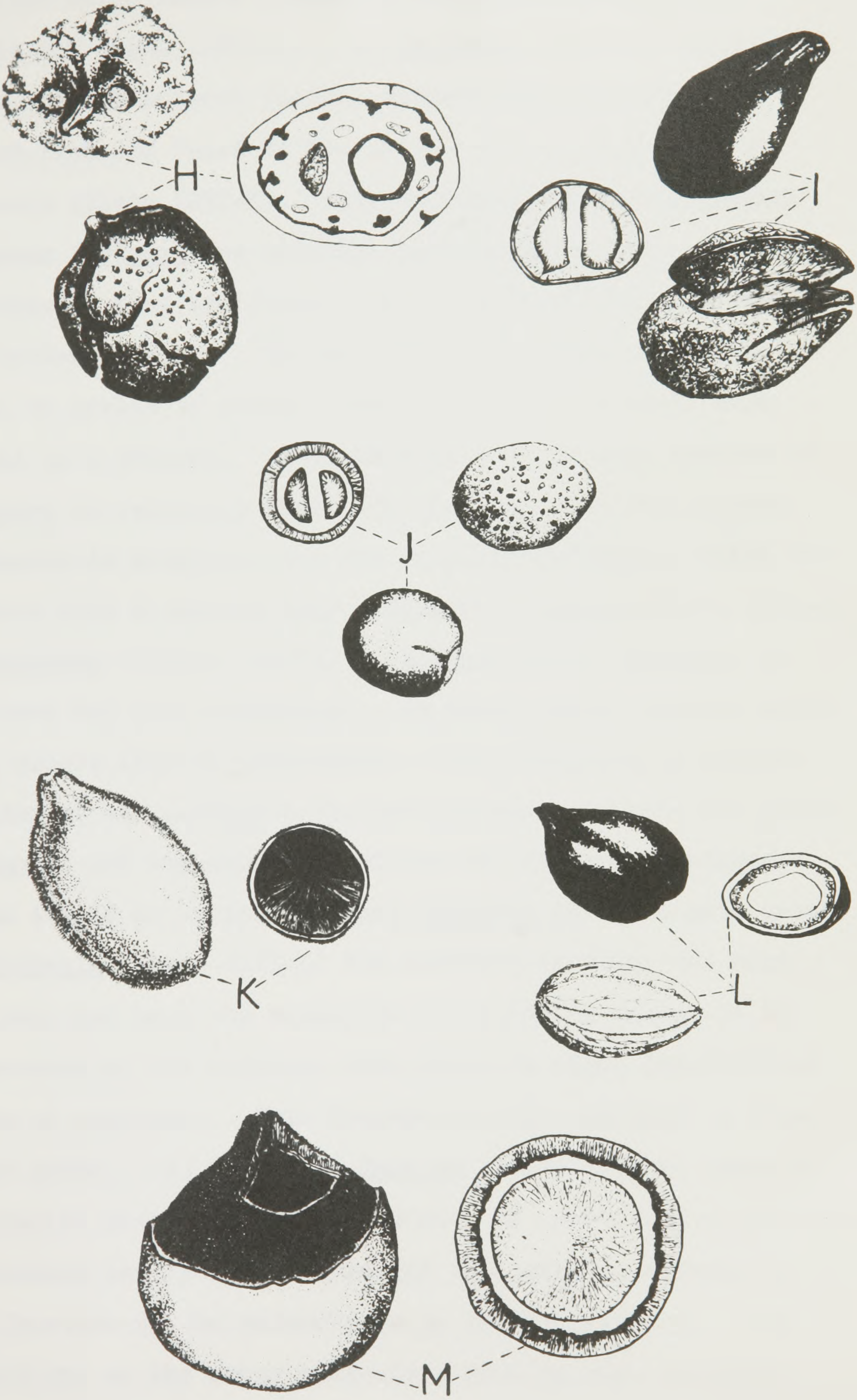


Plate XXV.- The fruit of the Hirtelleae 1.

A and B, Parinari excelsa Sabine; C, Parinari congolana Th.& H. Dur.; D, Cyclandrophora glaberrima Hasskl.; E, Kostermansia myriandra (Merr.)Prance; F, Duckea coriacea(Benth.)Prance; G, Magnistipula tessmannii (Engl.)Prance (all x 1).



Elisabeth Curtis

Plate XXVI.- The fruit of the Hirtelleae 2.

H, Neocarya macrophylla (Sabine)Prance; I, Maranthes robusta (Oliv.)Prance; J, Bafodeya benna (Sc. Elliot)Prance; K, Magnistipula bangweolensis (R.E.Fr.)R.Graham; L, Hirtella americana L.; M, Couepia canomensis (Mart.)Benth. (all x 1).

Parinari and Neocarya. In these subgenera the endocarp has two plugs or stoppers at its base. These are forced out like corks from a bottle by the germinating embryo (Plate XXV-C and XXVI-H). In Parinari subgenus Sarcostegia there are two lateral plates, rather than stoppers which detach from one third to two thirds of the length of the endocarp (Plate XXVI-I). This difference between Parinari subgenus Parinari and subgenus Sarcostegia is not surprising considering that the former has hypogeal germination, and the latter epigeal. In the latter the large cotyledons would be unable to escape from the relatively small hole filled by a stopper. The endocarp wall of some species of Parinari is extremely thick and hard, so that some special mechanism is essential for the seedling to escape, while the species with a thinner bony endocarp, P. benna (Plate XXVI-J), P. coriacea (Plate XXV-F), P. cordata and P. barbata, do not have any such mechanism. In these latter species there is a single line of dehiscence. The diversity in specialization of the mechanism of seedling escape within the genus Parinari, yet the constancy within the different subgenera is in itself an indication that Parinari is not a good genus. In Hirtella (Plate XXVI-L) the endocarp is thin, but hard and bony and here the mechanism for seedling escape is by dehiscence of the endocarp down three to eight longitudinal lines of weakness. This feature is very constant in this large genus. In the genus Couepia (Plate XXVI-M) there is no special mechanism. The endocarp is usually of a granular appearance and rather brittle and the seedling escapes by the fracture of the endocarp to no special pattern. All except one of the other characters used in this analysis are vegetative (characters 4, 8-10, 14, 15). Character four expresses the way in which the bracteoles enclose the flowers in small groups as in all species of Parinari subgenus

Parinari except one. This is a very striking feature in that subgenus. Character eight, whether the stipules are enlarged or not is taken to represent species with persistent stipules at least one centimetre long and half a centimetre broad as in some species of both *Magnistipula* and *Parinari*.

Character fourteen expressed the type of leaf indumentum. The leaves may be glabrous in some species of most genera, but this does not detract from the value of the indumentum as a taxonomic character, as when present, it is of a constant type within any one genus. The most striking type of leaf-undersurface is that found in *Parinari* subgenera *Parinari* and *Neocarya*, and in *P. benna*. The venation is reticulate and the leaf-surface is riddled with small cavities which contain the stomata (Plate XXVII-E). These cavities are filled at the mouth with woolly hairs. I have termed them 'stomatal cavities' which is a translation of the French term 'cryptes stomatiques' used by Hauman (1951) and by Duvigneaud *et al*. (1951). The latter authors have described and illustrated more fully the anatomy of these cavities, although they were not concerned with them as a taxonomic character. It is interesting that this is a constant feature of nearly all species of *Parinari* subgenus *Parinari* throughout its geographical range. The genus *Couepia* is characterized by a dense arachnoid tomentum (2) (Plate XXVII-D), which also occurs in some species of *Parinari* subgenus *Sarcostegia*. In the genus *Hirtella* neither of these latter types of indumentum occurs, the species of this genus that are not glabrous have a rust coloured, stiff, strigose or hirsute tomentum (4). (Plate XXVII-C).

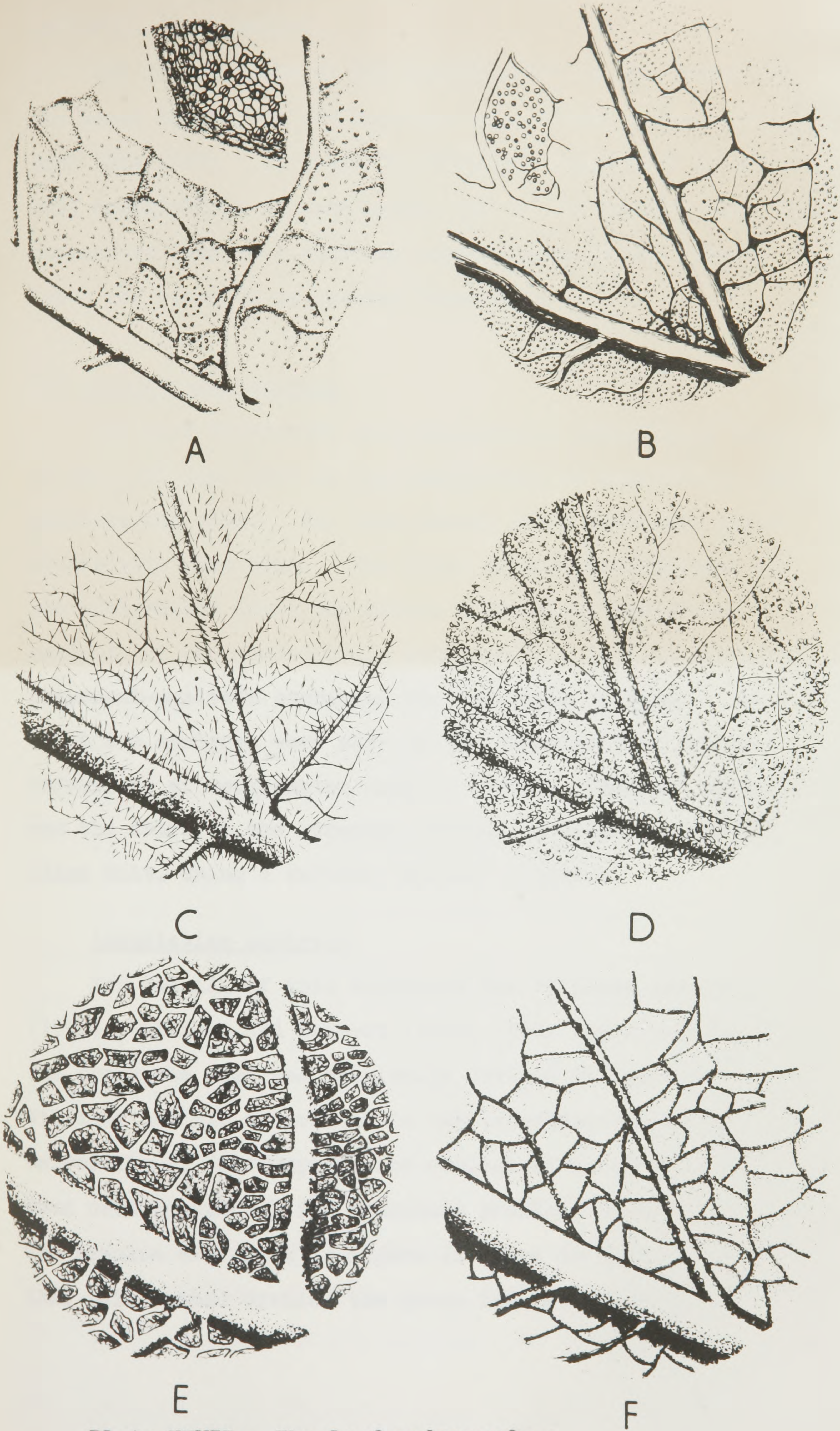


Plate XXVII.- The leaf undersurface

A, Hunga gerontogea; B, Licania (Geobalanus)sp.; C, Hirtella americana; D, Couepia uiti; E, Parinari borneensis; F, Cyclandrophora asperula. (all x 35).

The remaining characters given in the list need no further explanation.

The descriptions of the genera given in the Conspectus are based largely on the eighteen significant characters from this list. It would be extremely repetitive to give full descriptions of each genus, and so for brevity only the characters that vary with any significance at the generic level are given in my generic diagnoses.

(2) Statistical Analysis

The main difficulty in a statistical analysis of data of the sort used here is the combination of qualitative and quantitative data. For this reason three different types of analysis were used. The first association-analysis of the qualitative data, the second a principle component-analysis of the quantitative data, and the third a principle component-analysis combining the two types of data. The first two analyses were made in the Department of Botany, University of Southampton using a Feranti 'Pegasus' computer and the third at the Forestry Commission Research Station, Alice Holt, using a Feranti 'Sirius' computer.

Association-analysis

For details of this technique see Williams and Lance (1958), Williams and Lambert (1959, 1960, 1961a and 1961b). The programme used was originally devised by Professor W.T. Williams and his associates in the Department of Botany, University of Southampton, for ecological data and had not been used previously for taxonomic problems of this nature. The results are given in figure II where it can be seen that this method divided the group into seven divisions.

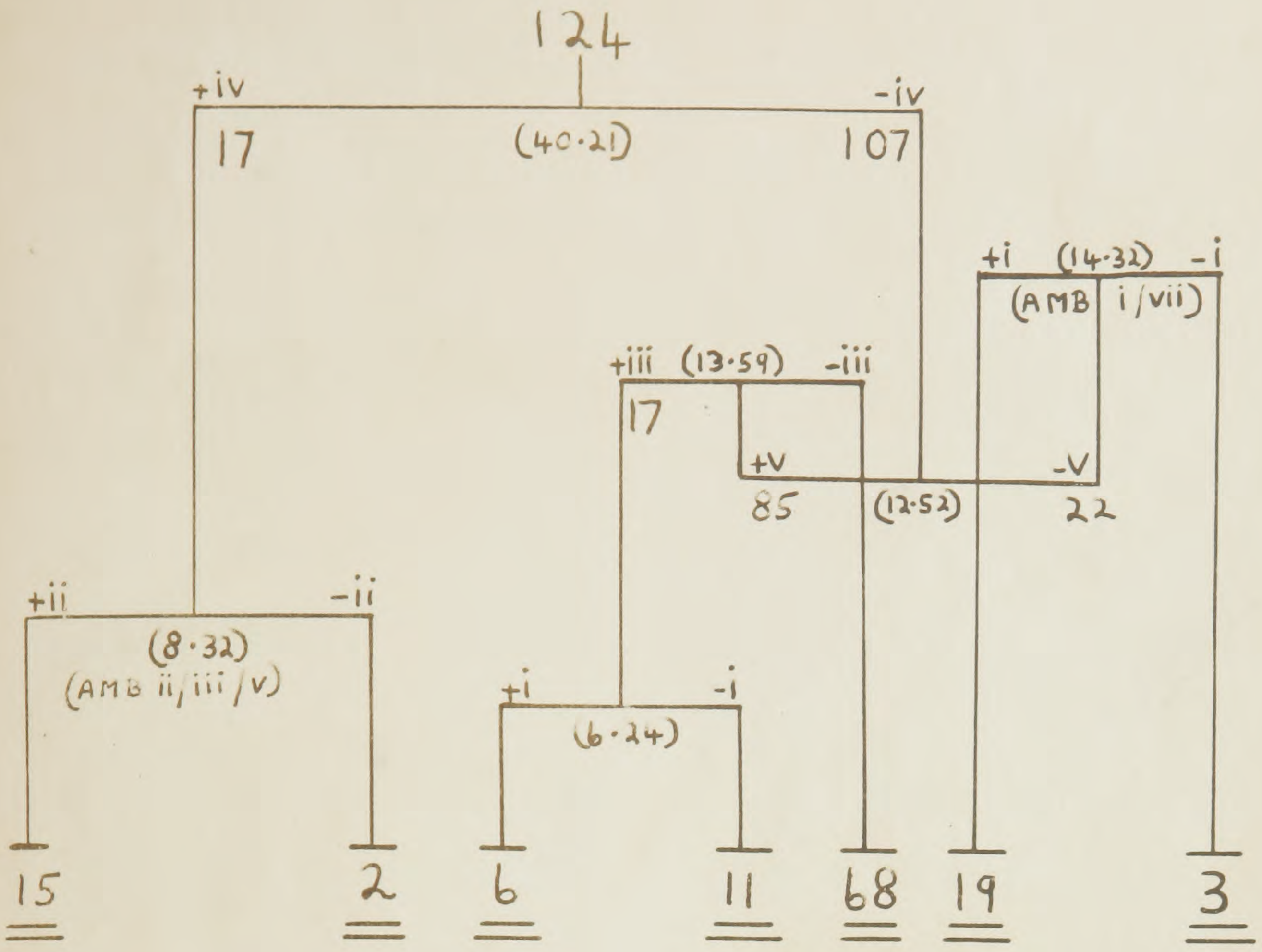


Fig. II - Results of Association-analysis

ii = character selected

(40.21) = Max χ^2 value

85 = number of species to be divided.

In Fig. II the bottom row of figures represents the number of the original species in each of the seven final groups. The contents of these groups is summarized below. Appendix 4c gives a more detailed list of the individual species contained in each of these groups.

15 - Parinari subgenus Parinari including P. sericeo-argentea

2 - Couepia bracteosa and Couepia subcordata

6 - Parinari subg. Cyclandrophora, P. macrophylla

11 - Parinari subg. Sarcostegia, Hirtella carbonaria

68 - Hirtella (35 species), Couepia (32 species), Parinari myriandra

19 - Parinari subg. Pellegriniella, P. benna, P. tessmannii, P. canarioides, all Magnistipula.

3 - all Grangeria

With this and the second method used it must be pointed out that only half the possible characters are utilized. This means that there are several disadvantages; correlated characters may be in the two different groups, and the number of characters used is reduced. Because of this a careful comparison between the two results must be made. Obviously some groups may be largely separated on either the characters represented by the quantitative or the qualitative data. For example Hirtella and Couepia come together in the association-analysis, but they are clearly separable by the component analysis. The reverse of this may also happen. Two species of Couepia (C. bracteosa and C. subcordata) are separated from the rest of Couepia by the association-analysis. This is because of the selection of character four at the first division. These two species of Couepia are similar to other Couepia in all other respects. The fact that they can be divided from Parinari by three characters (two, three and five) indicated that they are not closely related to this group. The association-analysis and component analysis do, however, divide the tribe in a similar way. Where these two essentially different methods are used using different sets of characters a good knowledge of the group being analysed is required, especially to account for discrepancies. Without such knowledge the results could be misleading. The association-analysis furnishes several examples in which a knowledge of the group is essential for interpretation. (1) The case of the two species of Couepia already quoted above. (2) Hirtella carbonaria is placed with Parinari subgenus Sarcostegia because they share character three selected for the division of the eighty-five species and (3) Parinari myriandra is placed with Hirtella and Couepia through the selection of character five at the division of the hundred and seven species. However, with these cautionary points one is now able to interpret the results of the association-analysis. These are better interpreted together with the component analysis in Section 3 of the present chapter.

Principle-Component Analysis of Quantitative data

For an account of this method of analysis see G. Thomson (1951), Williams and Lambert (1961b), Kendall (1952) and Jeffers (1962). Here the coefficients of correlation between all variables are first found, and from this the principle-components. In this case it was found that only the first two principle-components were significant enough to be computed, (i.e. they account for a large percentage of the original variation). This is fortunate since it enables one to plot the final results on an ordinary two dimensional graph. The proportional weightings for each component are given in table 2 below.

Character	Component I	Component II
12	- 0.0724	+ 0.1424
13	+ 0.5657	- 0.2605
14	+ 0.4563	+ 0.7925
15	- 0.6617	- 0.3773
16	+ 0.2283	+ 0.7040
17	+ 0.6776	+ 0.0906
18	- 0.1272	+ 0.5348
19	- 0.0966	+ 0.4583
20	- 0.7927	+ 0.2189
21	- 0.8028	+ 0.3328

Table 2. Weighting for original characters in computed component.

Taking note of those weightings greater than 0.50 it is possible to identify the components.

Component I (+13, -15, +17, -20, -21)

The position of the stamens and the type of endocarp, contrasted with the nature of the glands of the bracts and bracteoles, the number of stamens and the flower size.

Component II (+14, +16, +18)

The type of leaf-undersurface, the type of epicarp and the method of seedling escape.

Using these weightings and the original data normalized by calculating $\frac{x-\bar{x}}{\sigma}$, the value of each component for all the original 108 species was computed. (x = number of original data, $\bar{x}$ = mean x for that character, and σ = standard deviation). The results obtained were then plotted graphically, see Fig. III, the two components being the axes.

Since the fruit characters were missing on sixteen of the species used in the association-analysis a further component-analysis was made using seven characters only. The proportional weightings for each component were:-

Character	Component I	Component II
12	- 0.1492	- 0.1358
13	- 0.6622	- 0.3357
14	- 0.4012	+ 0.7792
15	+ 0.6219	- 0.5407
19	+ 0.1967	+ 0.6428
20	+ 0.8469	+ 0.1711
21	+ 0.7947	+ 0.1700

Table 3. Weighting for 7 original characters in computed component.

This shows the components to be:-

Component I (-13, +15, +20, +21)

The nature of the glands of the bracts, the number of stamens and the flower size contrasted with the position of the stamens.

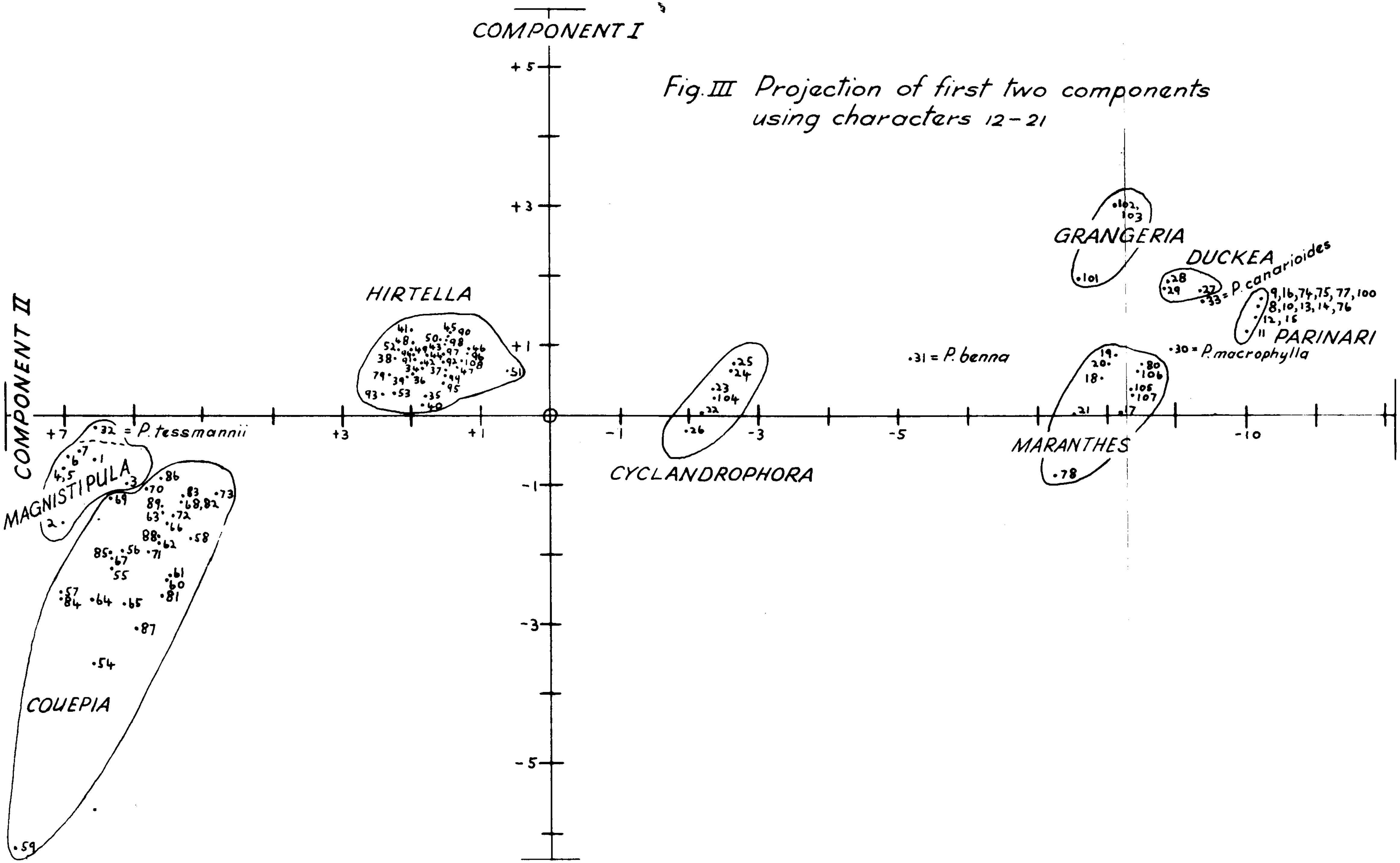


Fig. III Projection of first two components using characters 12–21

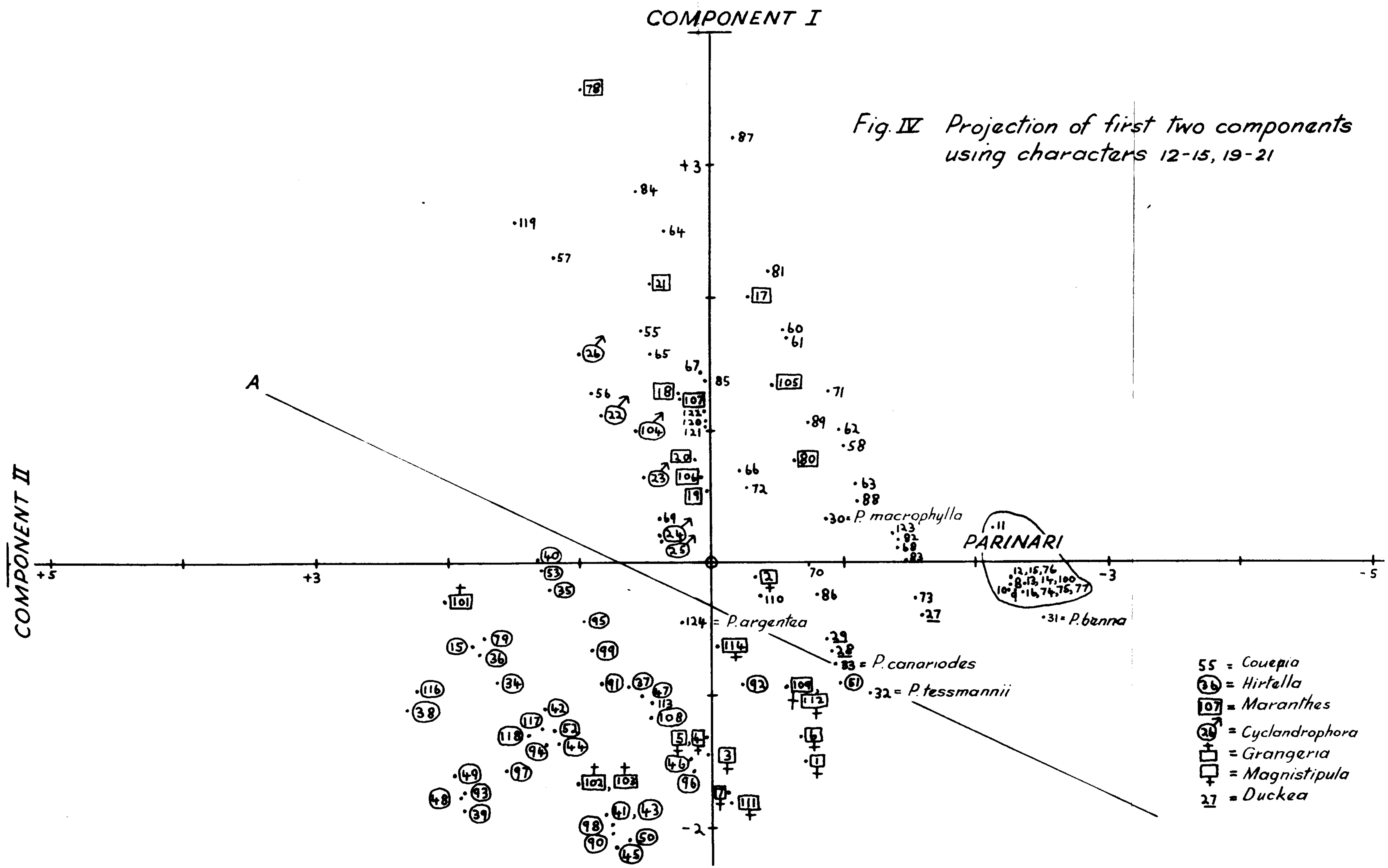


Fig. IV Projection of first two components using characters 12-15, 19-21

Component II (+14, +19)

The type of leaf-undersurface and the type of inflorescence.

The results were obtained in the same way as in the previous analysis and were plotted, see Fig. IV.

As three characters were missing, and one has changed its axis, it is hardly surprising that the results are rather different. Whereas the method using all the ten characters indicates about eight groups, that using only seven characters does not give any clear-cut grouping. This is a very fine demonstration of the value of the fruit characters in the taxonomy of this group. In the past little or no weight has been given to them because of the lack of fruiting specimens in herbaria. As indicated by my initial researches the fruit yields important taxonomic characters which help to define the genera. All three fruit characters used occur as part of the significant components in the first analysis (characters seventeen in component I and characters sixteen and eighteen in component II).

Principle-component analysis of both types of data

Two separate analyses were made, the first using only the species included in the last two analyses and the second with sixteen additional species including members of the genus Acioa. The first of these is now described. It was found necessary to consider the first five components and the proportional weightings for these are given in Table 4.

Proportional weighting for component:-

Character	I	II	III	IV	V
1	+ 0.0280	- 0.0597	+ 0.0204	- 0.0134	+ 0.0634
2	+ 0.0879	- 0.0109	+ 0.0201	+ 0.0259	+ 0.0688
3	+ 0.0929	+ 0.0169	+ 0.0197	+ 0.0494	- 0.0134
4	+ 0.1000	- 0.0074	- 0.0311	- 0.0209	+ 0.0154
5	- 0.0818	+ 0.0343	- 0.0380	+ 0.0218	+ 0.0148
6	+ 0.0128	+ 0.0221	+ 0.7404	- 0.0081	- 0.0794
7	+ 0.0221	+ 0.0484	+ 0.0254	- 0.0528	+ 0.0775
8	+ 0.0292	- 0.0042	- 0.0129	- 0.0087	+ 0.0169
9	+ 0.0858	+ 0.0319	- 0.0136	+ 0.0161	- 0.0470
10	- 0.0771	- 0.0053	- 0.0081	+ 0.0133	- 0.0164
11	- 0.0049	+ 0.0037	+ 0.0192	+ 0.0581	+ 0.1000
12	+ 0.0063	+ 0.0114	+ 0.1000	- 0.0138	- 0.0555
13	+ 0.0377	- 0.0719	+ 0.0452	+ 0.0046	+ 0.0274
14	- 0.0874	- 0.0459	+ 0.0273	+ 0.0202	- 0.0095
15	+ 0.0492	+ 0.0829	- 0.0012	+ 0.0015	+ 0.0497
16	- 0.0517	- 0.0193	+ 0.0729	+ 0.0537	+ 0.0499
17	+ 0.0046	+ 0.0808	+ 0.0591	- 0.0198	+ 0.0096
18	- 0.0812	+ 0.0131	+ 0.0063	- 0.0799	+ 0.0486
19	- 0.0440	+ 0.0103	- 0.0153	+ 0.1000	- 0.0113
20	- 0.0202	+ 0.0956	- 0.0181	+ 0.0195	+ 0.0061
21	- 0.0229	+ 0.1000	+ 0.0147	+ 0.0186	+ 0.0062
Percentage of variation accounted for by components	24.3%	15.2%	9.4%	7.4%	6.7%

Table 4. Weighting for original characters in computed component.

It is possible to identify the components (as those underlined numbers in table 4) by taking note of these weightings.

Component I

+2 - hairs on inside of the receptacle or not.

+3 - bilocular or unilocular ovary.

+4 - bracts enclosing the flower buds or not.

+9 - glanding of the petiole.

+10 - prominent lenticels on young stem or not.

-5 - stamens exserted or included.

-18 - dehiscence of the endocarp.

Component II

+15 - nature of the glands of the bracts.

+17 - type of endocarp.

+20 - number of stamens.

+21 - flower size.

Component III

+12 - shape of receptacle.

Component IV

+19 - type of inflorescence.

-18 - dehiscence of endocarp.

Component V

+7 - level of ovary insertion.

+11 - staminal ligule or not.

-6 - staminodes united or free.

Seventeen of the original twenty-one characters are given significant weightings in these five components, which account for 68.2% of the total variation. Table 4 shows that the first component accounts for 24.3% of the variation. That one component only accounts for such a comparatively small percentage and that the first five components only for 68% of the total variation indicate the complexity of the variation within the Hirtelleae. The further components account for less than 5% of each and are not worth considering. The fact that there are five significant components means that each must be plotted against the other four. Figures V-XIV represent the projections of these components using their values for each individual species calculated in the same way as in the previous component analysis.

(2) Taxonomic Conclusions

The association-analysis gives definite groups which are illustrated in a single diagram. These correspond appreciably to the genera recognized by visual inspection. The component analysis of the quantitative data also gives definite groups which are illustrated in a single diagram, and in this case the genera are much more definitely circumscribed, all but two being quite isolated from the others. The third method of analysis, using both qualitative and quantitative data, confirms the objective nature of the genera but as more characters are used more figures are required to demonstrate this, because a component-analysis using so many qualitative characters will tend to yield components representing a lower percentage of the total variation of the group being studied. Because more characters are used truer relationships are expressed by this analysis.

Table 5 is a list that compares the main groups suggested by the first two methods of analysis.

The results obtained show surprising similarity considering the comparatively small number of characters used, especially in the association analysis. Most of the differences can be easily accounted for by knowing the diagnostic characters which are missing from each type of analysis. The most obvious conclusion from these results is that the genus *Parinari* must be split into a number of genera if the *Hirtelleae* is to be subdivided at all. The separation between other genera is often less than that between groups of species formerly all included in *Parinari*. This in fact

Fig. V - Projection of first and second components - Hirtelleae.

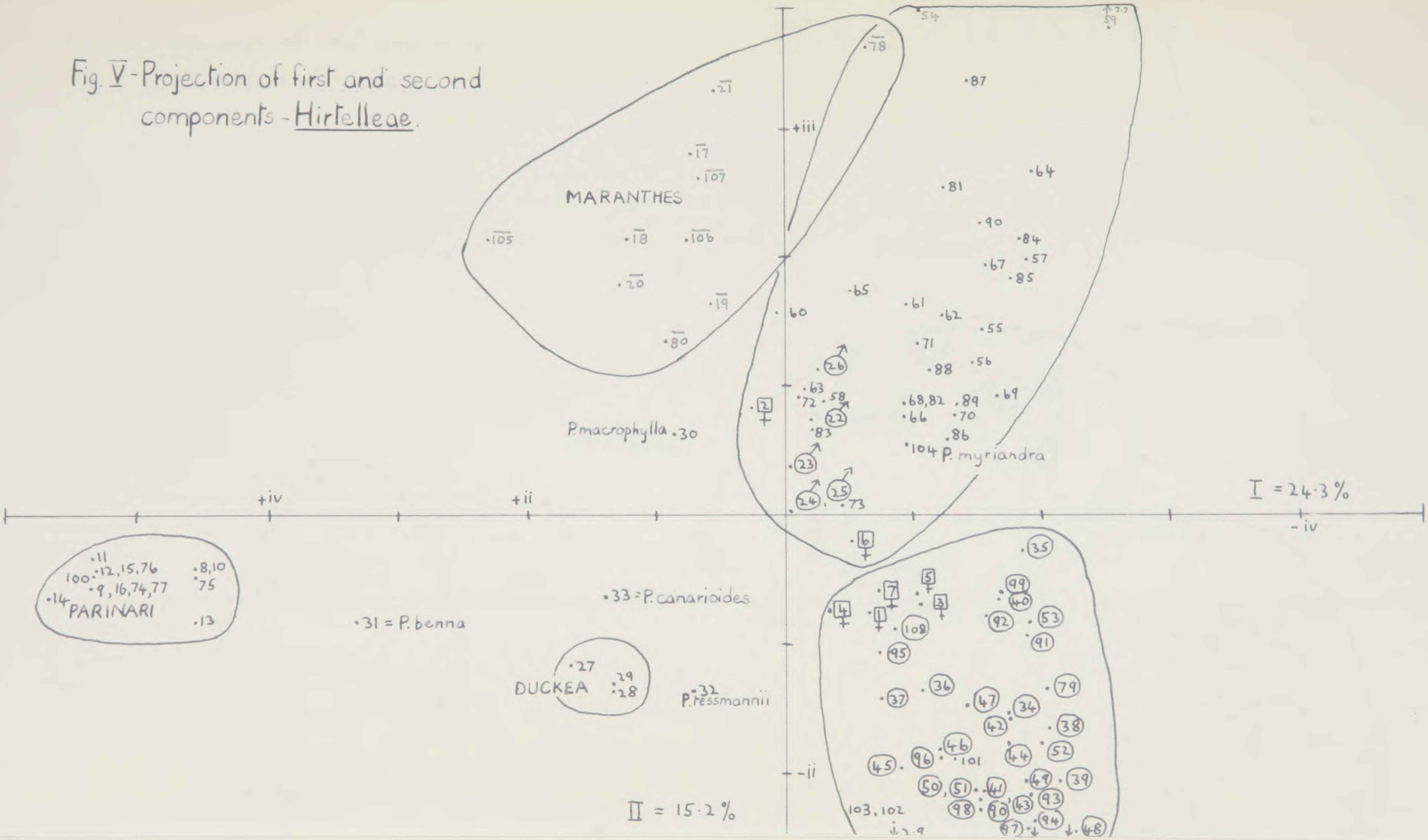


Fig. VI - Projection of first and third components - Hirtelleae.

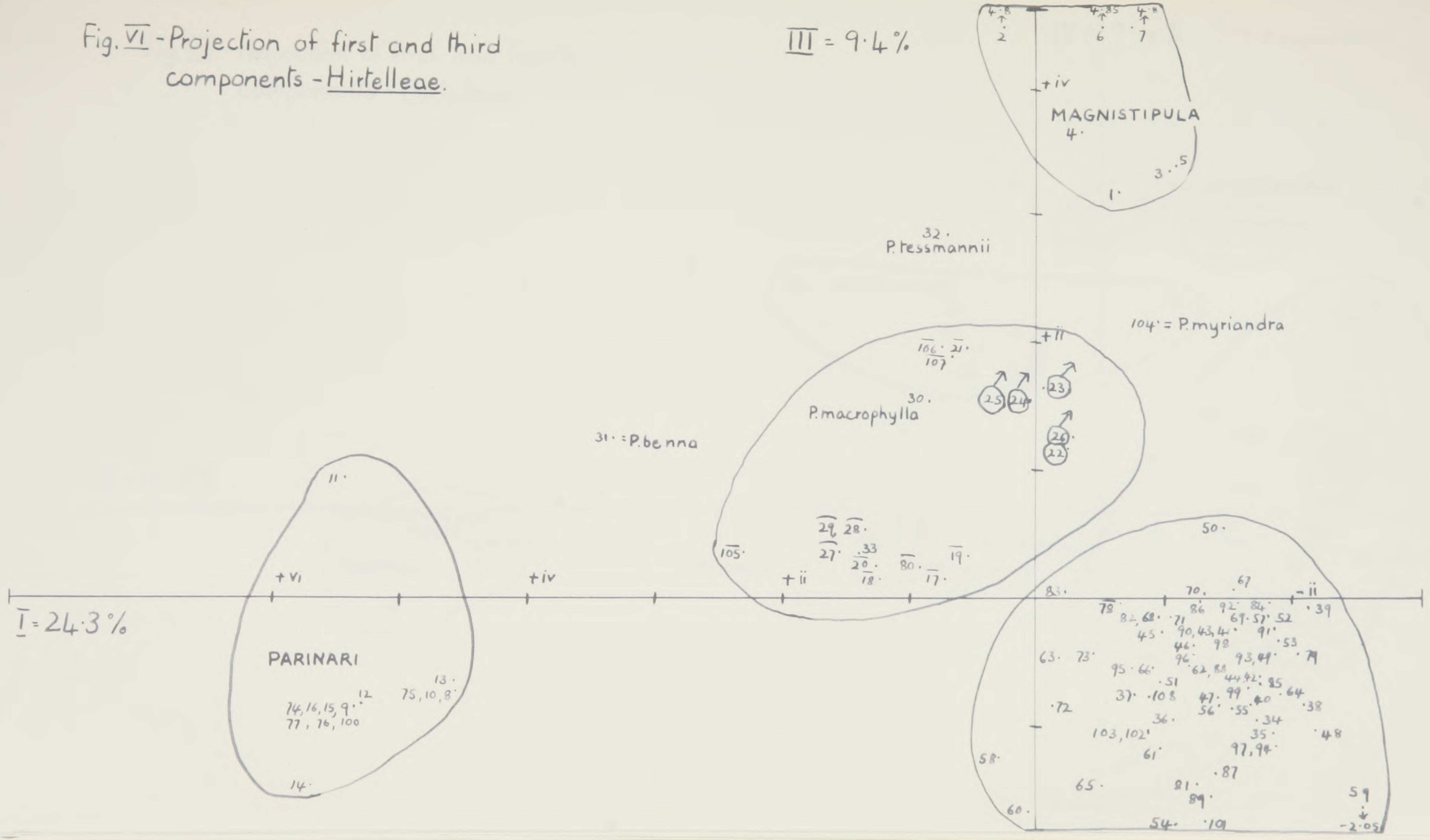


Fig. VII - Projection of first and fourth components - Hirtelleae.

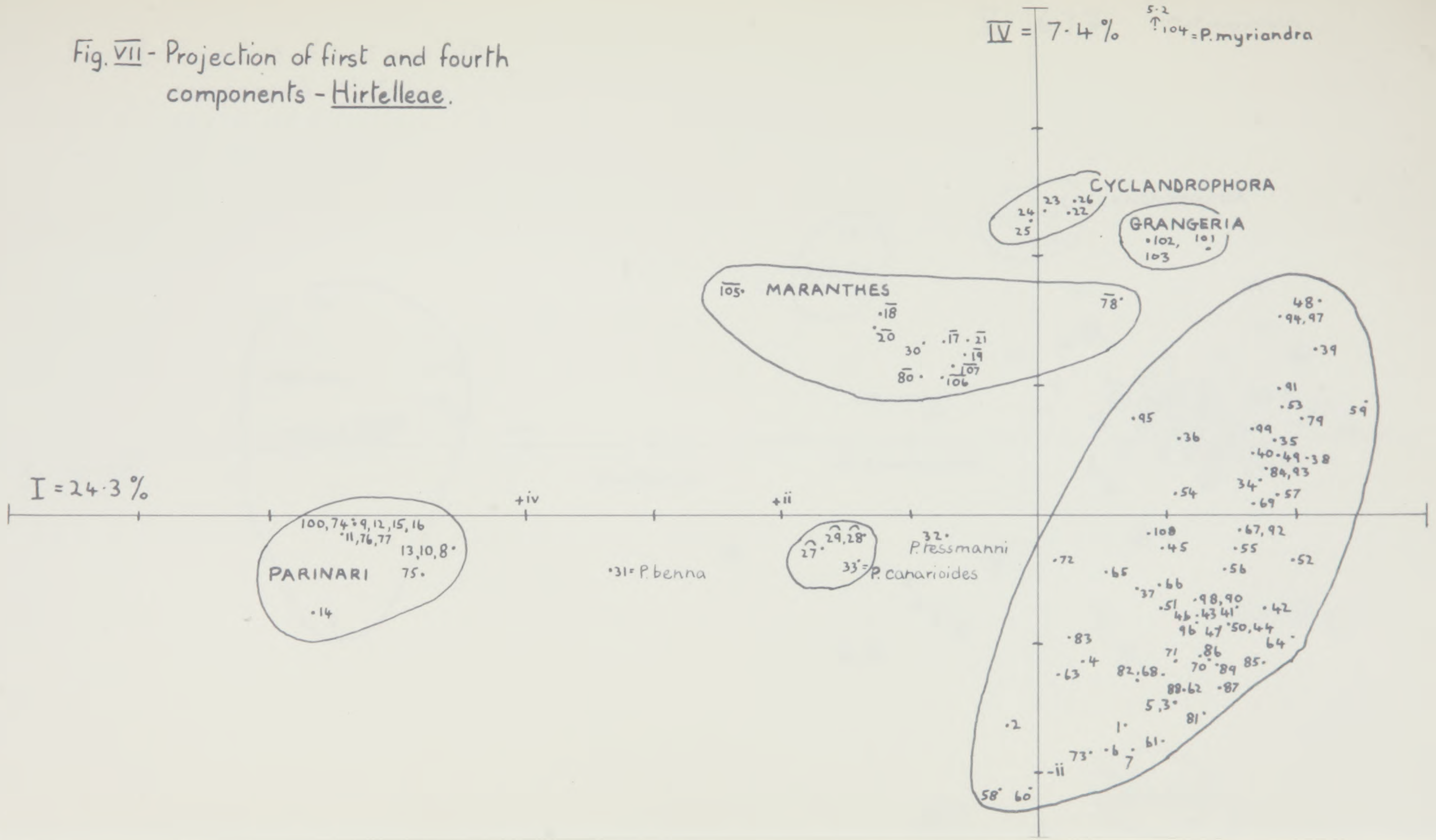


Fig. VIII - Projection of first and fifth components - Hirtelleae.

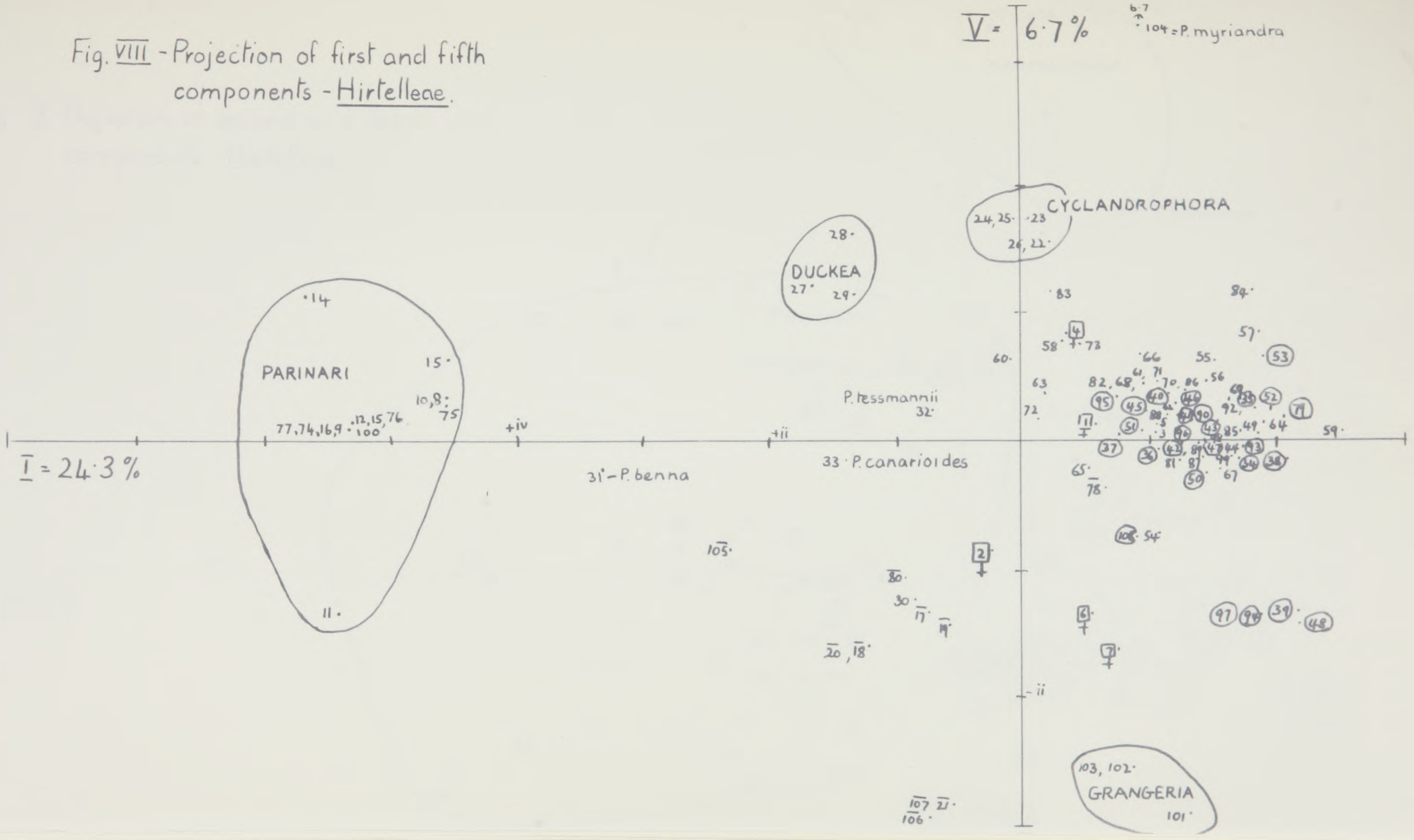


Fig. IX - Projection of second and third components - Hirtelleae.

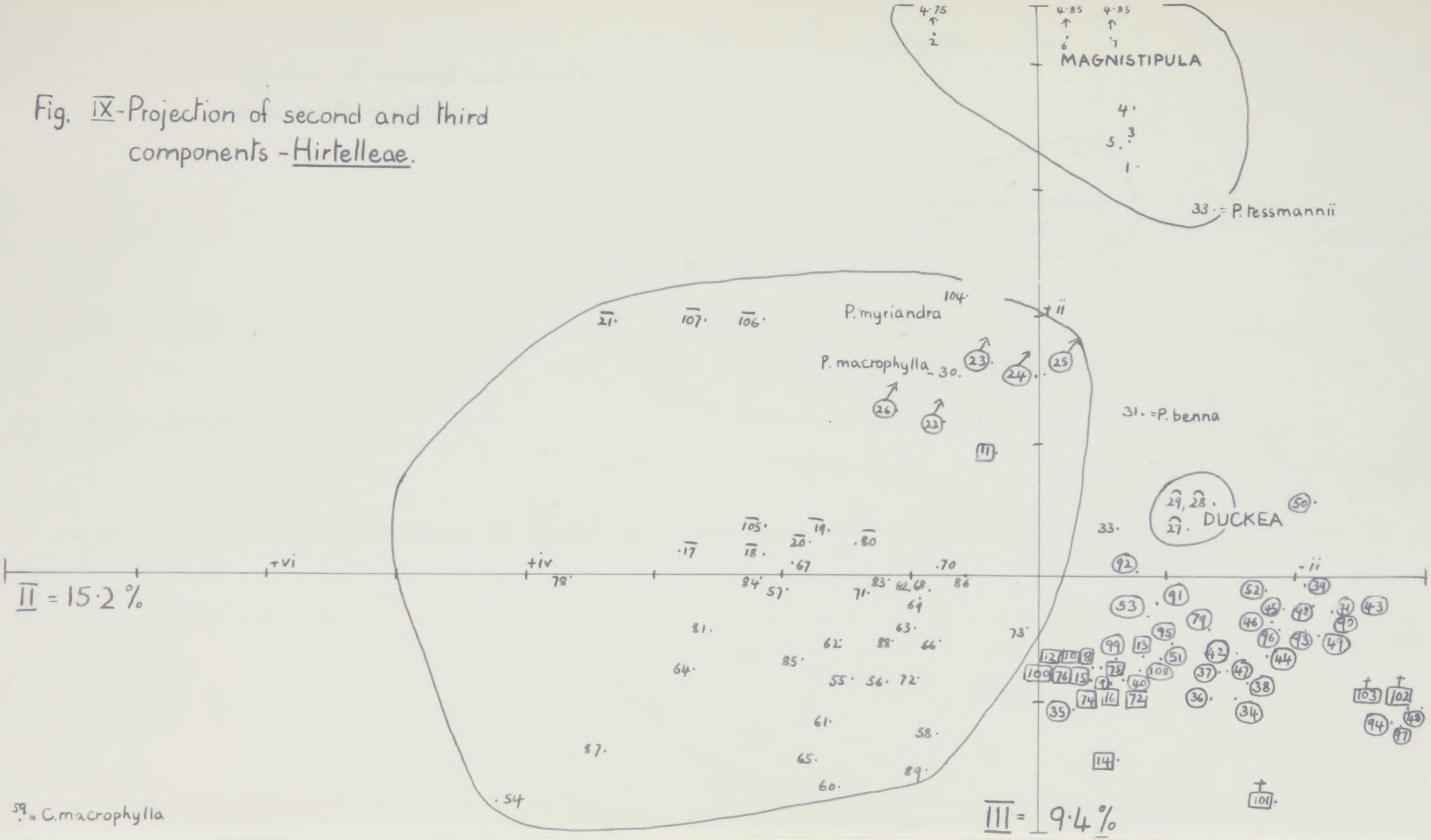


Fig. X - Projection of second and fourth components - Hirtelleae.

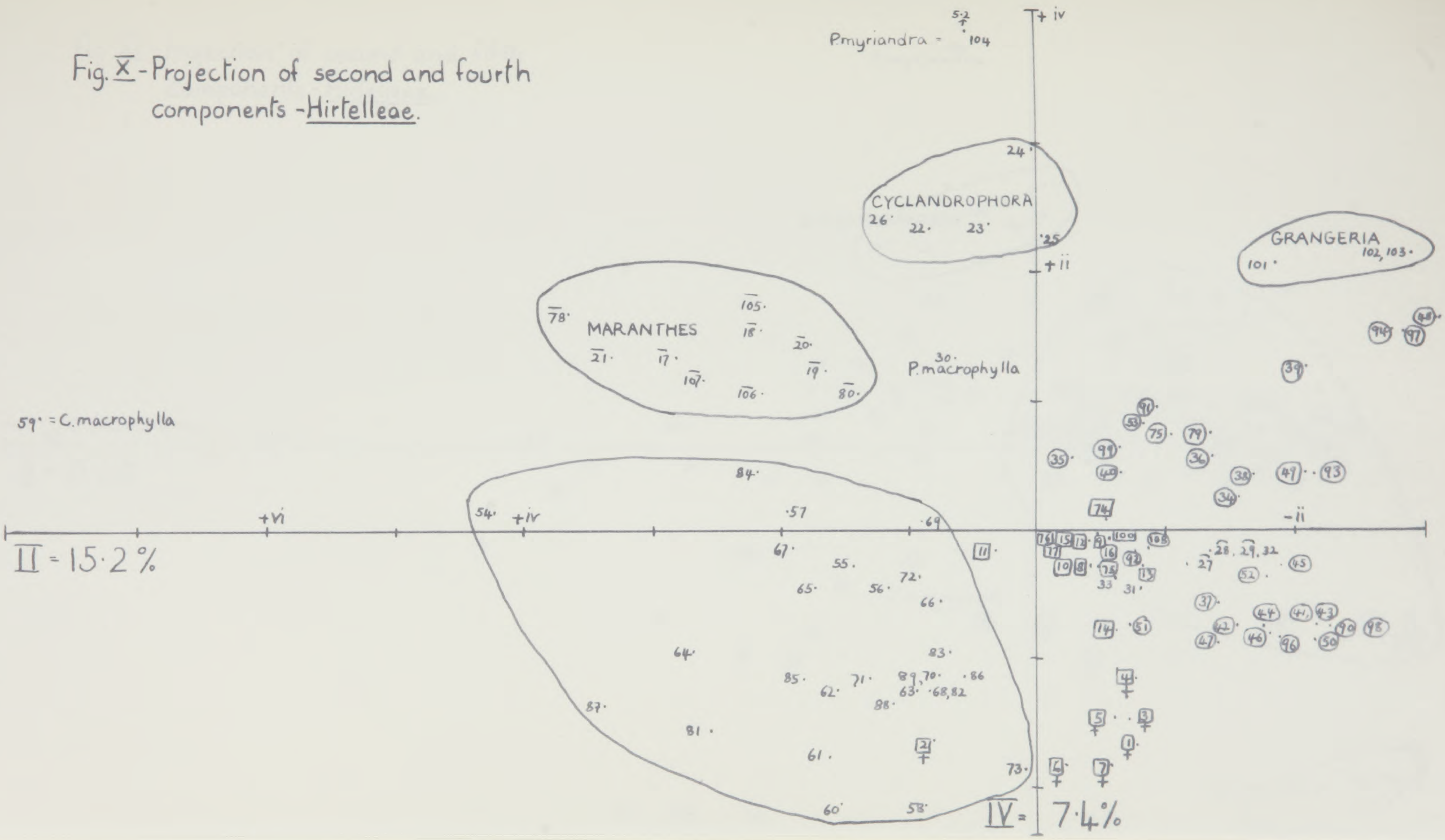


Fig. XI - Projection of second and fifth components - Hirtelleae.

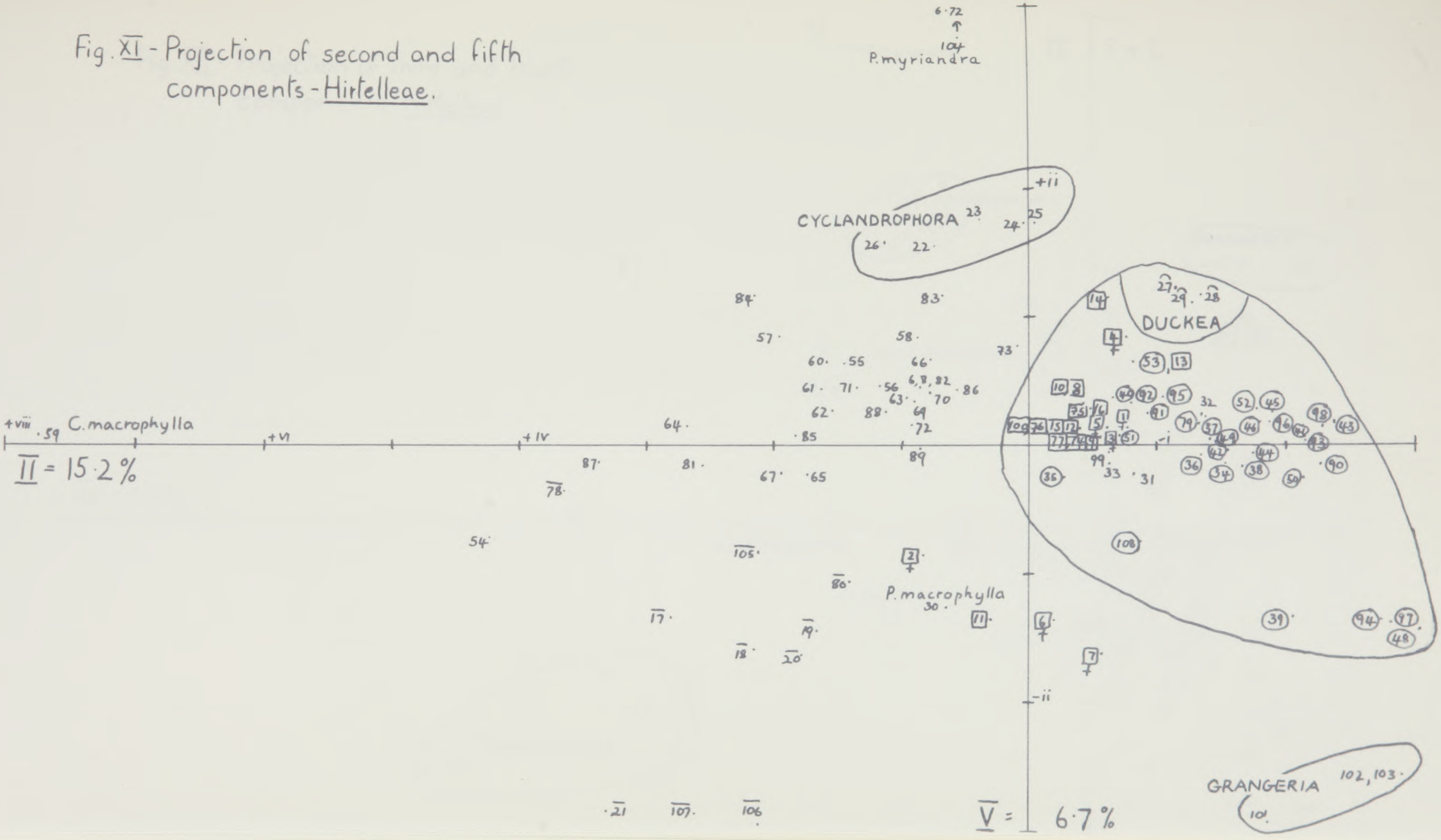


Fig. XII - Projection of third and fourth components - *Hirtelleae*.

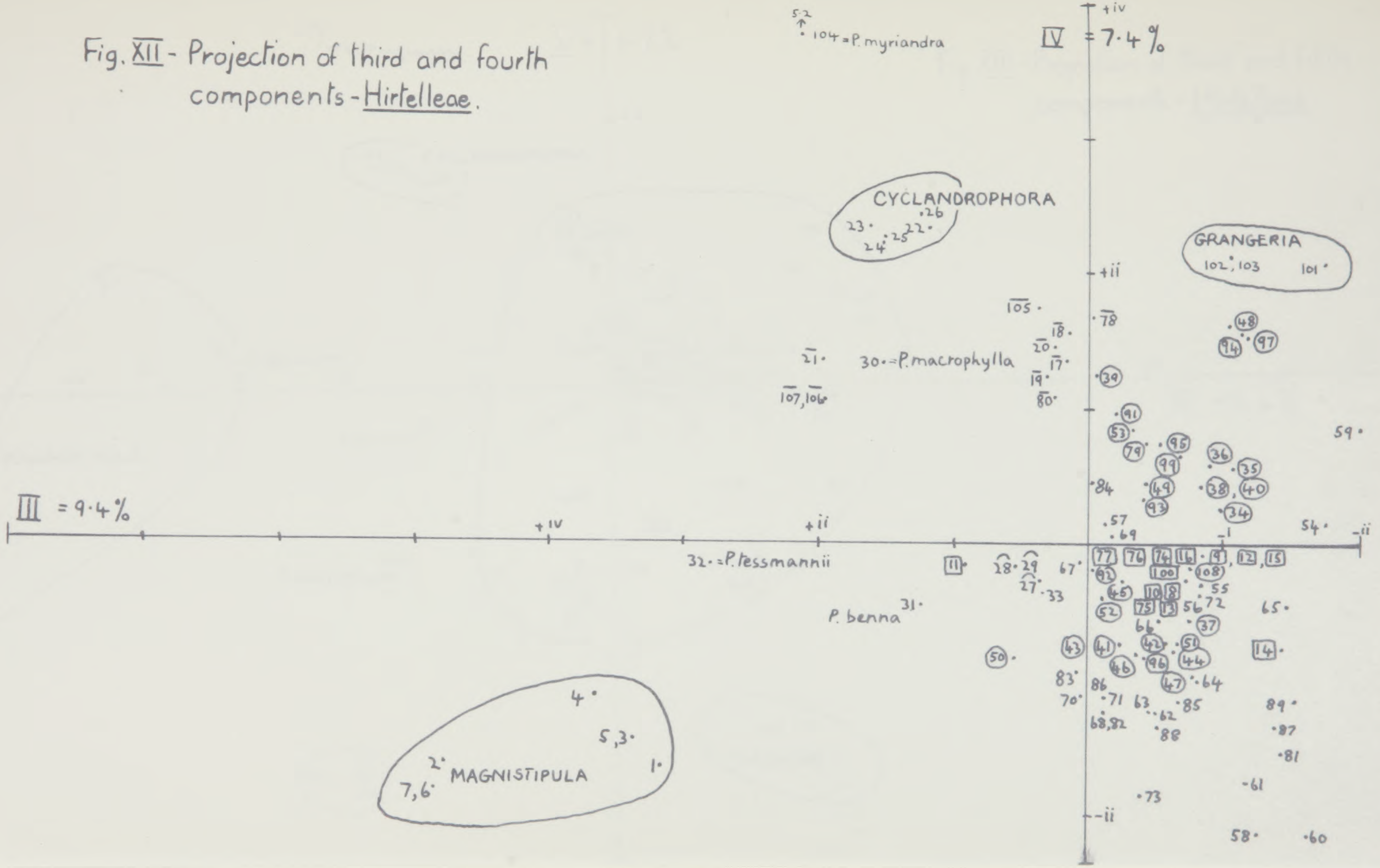
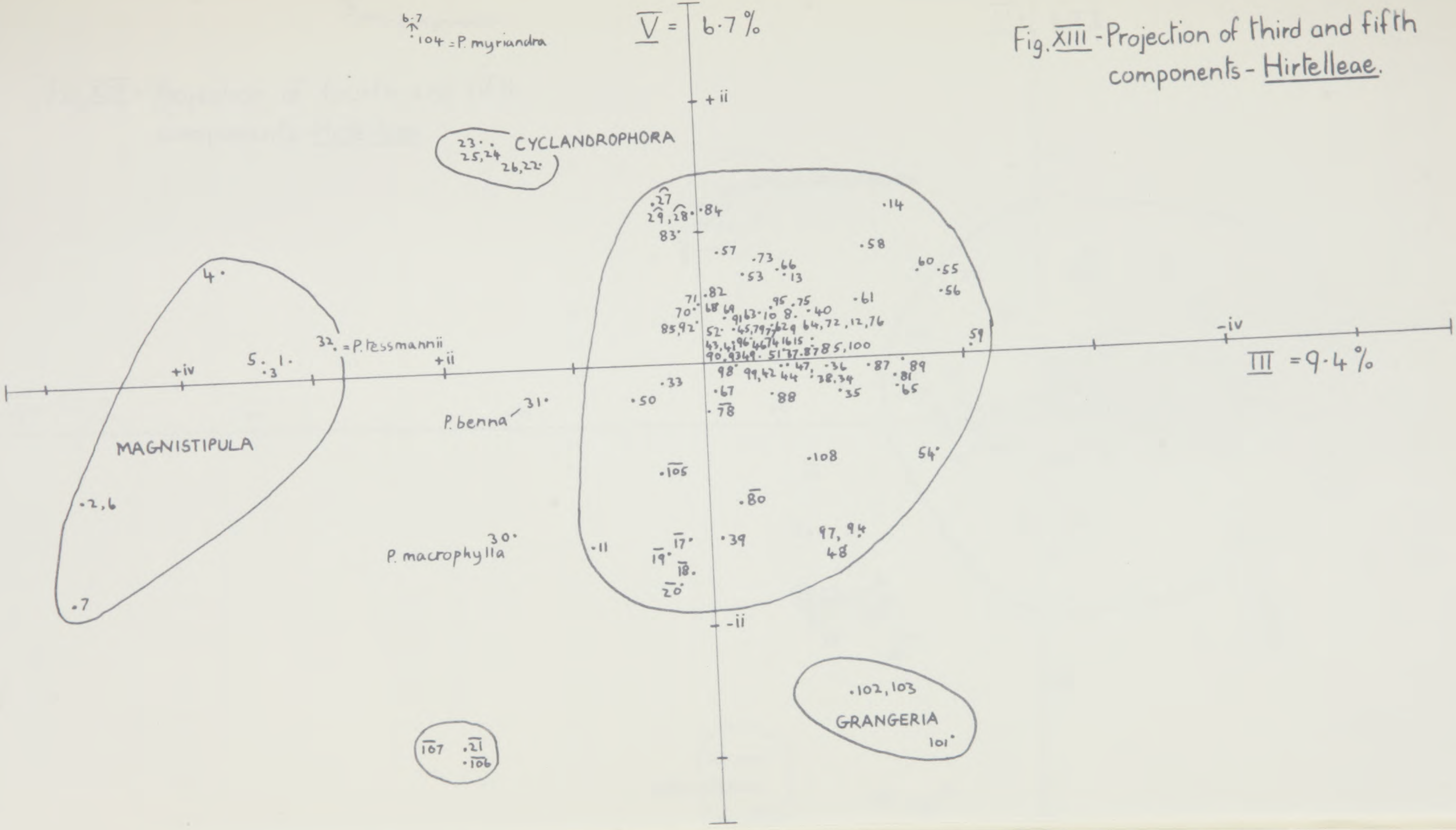


Fig. XIII - Projection of third and fifth components - *Hirtelleae*.



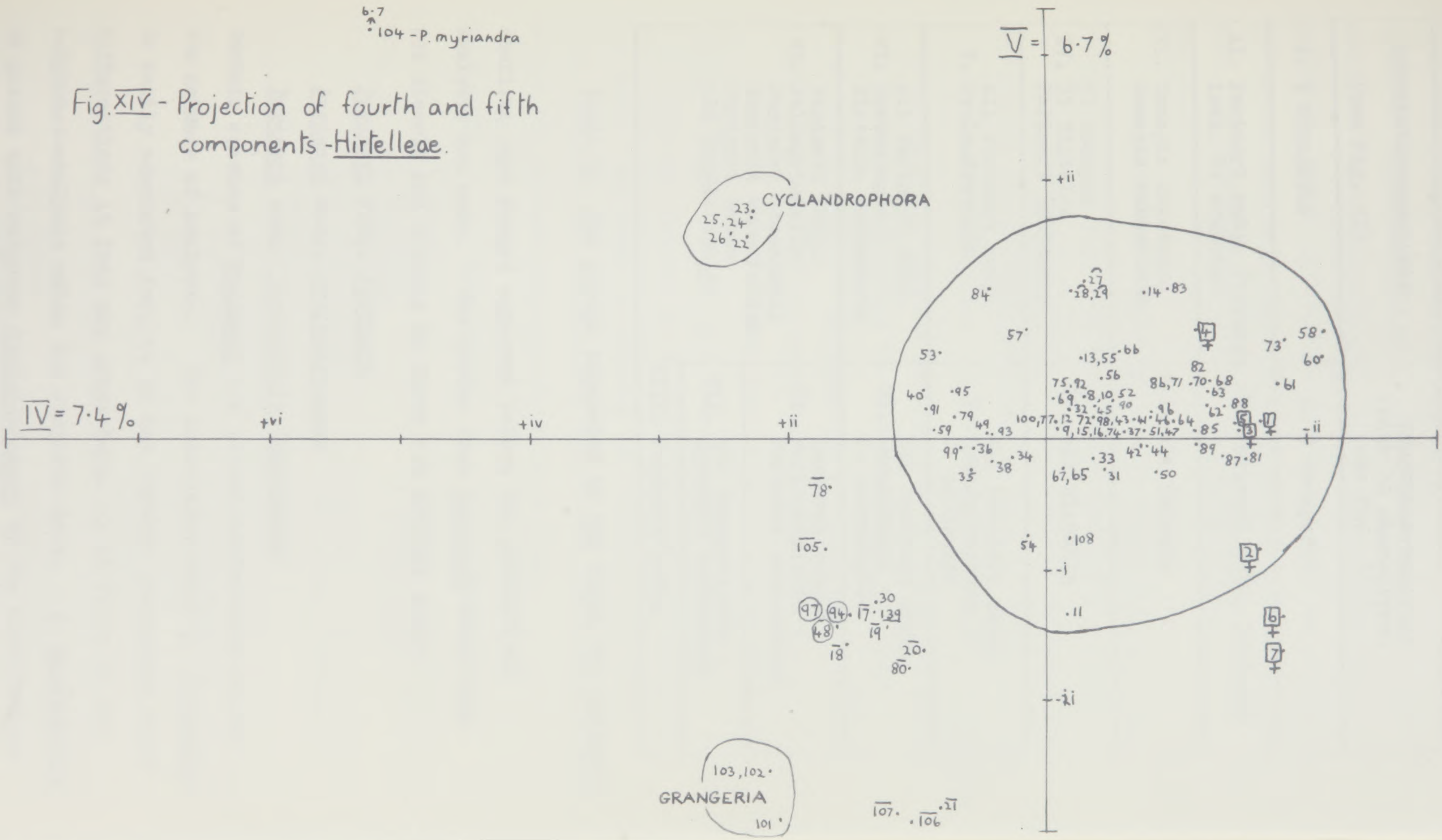


Fig. XIV - Projection of fourth and fifth components - Hirtelleae.

Association-analysis (see Fig. II)	Component-analysis (with 10 characters) (see Fig. III)
I. 3 Grangeria	I. 3 Grangeria
II. Parinari subg. Parinari incl. P. argentea	II. Parinari subg. Parinari
III. Couepia bracteosa Couepia subcordata	III. all Couepia
IV. 32 Couepia 35 Hirtella Parinari myriandra	IV. all Hirtella
V. all Parinari subg. Cyclandrophora	V. all Parinari subg. Cyclandrophora + P. myriandra
VI. all Parinari subg. Sarcostegia + Hirtella carbonaria	VI. all Parinari subg. Sarcostegia + P. macrophylla
VI. Parinari subg. Pellegriniella Parinari tessmannii Parinari canarioides Parinari benna all Magnistipula	VI. Parinari subg. Pellegriniella + Parinari canarioides
	VII. all Magnistipula + Parinari tessmannii
	VIII. Parinari benna

Table 5. The groups suggested by the first two analyses

confirms what seemed apparent before the statistical analysis was made. The groups from Parinari which come out clearly and cleanly by these two methods are:-

Parinari subg. *Parinari*

Parinari subg. *Cyclandrophora*

Parinari subg. *Sarcostegia* (*Maranthes*)

Certain species of *Parinari* are placed differently by the two methods of analysis. The indecision about *P. myriandra* is easily accounted for, as it has further characters which differentiate it from any group here, as is shown by the component-analysis using the complete data. *P. macrophylla* is placed with subgenus *Cyclandrophora* by the association-analysis, and with subgenus Sarcostegia by the component analysis. Parinari benna is placed with a rather mixed group containing Magnistipula, Parinari subgenus Pellegriniella, and P. canarioides by the association-analysis but in the component-analysis it is placed entirely on its own. P. tessmannii is placed with Magnistipula in both analyses.

Few taxonomic conclusions can be drawn from the component-analysis that excludes fruit characters, as can be seen from figure IV. However, two points of interest (in addition to the demonstration of the value of fruit characters) arise from this analysis. First is the uniformity of Parinari subgenus Parinari which is the only group really isolated by this analysis, and second is that the line A on figure IV shows that Couepia and Hirtella can still be kept apart without the use of fruit characters.

With the definite groupings indicated by the first two analyses in mind, it is now easier to interpret figures V-XIV which show the results of the component analysis using all the data. In order to simplify the findings from these projections of the components a list of the groups which are sorted out by each pair of components is given.

Components	Pure groups	Mixed groups
I/II (Fig. V)	1 PARINARI 2 P. BENNA 3 MARANTHES 4 P. MACROPHYLLA 5 P. CANARIOIDES 6 P. TESSMANNII 7 DUCKEA	1 Couepia + Cyclandrophora + Magnistipula pro parte + P, myriandra 2 Hirtella + Magnistipula pro parte + Grangeria
I/III (FIG. VI)	1 MAGNISTIPULA + P. TESSMANNII 2 PARINARI 3 P. BENNA 4 P. MYRIANDRA	1 Maranthes + P. macrophylla + Cyclandrophora + P. canarioides 2 Hirtella + Couepia + Grangeria
I/IV (Fig. VII)	1 PARINARI 2 P. BENNA 3 DUCKEA + P. CANARIOIDES 4 P. MYRIANDRA	1 Maranthes + Grangeria + Cyclandrophora 2 Hirtella + Couepia + Grangeria + Magnistipula

Components	Pure groups	Mixed groups
I/V (Fig. VIII)	1. PARINARI 2. P. BENNA 3. P. MYRIANDRA 4. DUCKEA 5. CYCLANDROPHORA	1. Hirtella + Couepia + P. canarioides + P. tessmannii + Magnistipula + Grangeria
II/III (Fig. IX)	1. MAGNISTIPULA + P. TESSMANNII 2. COUEPIA MACROPHYLLA 3. P. BENNA	1. Cyclandrophora + Maranthes + Couepia + P. macrophylla + P. myriandra 2. Duckea + Parinari + P. canarioides + Grangeria + Hirtella
II/IV (Fig. X)	1. P. MYRIANDRA 2. COUEPIA MACROPHYLLA 3. CYCLANDROPHORA 4. MARANTHES 5. GRANGERIA 6. P. MACROPHYLLA	1. Couepia + Magnistipula pro parte 2. Hirtella + Parinari + P. canarioides + Duckea + Magnistipula pro parte + P. tessmannii + P. benna
II/V (Fig. XI)	1. CYCLANDROPHORA 2. GRANGERIA 3. P. MYRIANDRA	1. Couepia + Maranthes + Magnistipula pro parte + P. macrophylla 2. Hirtella + Parinari + Duckea + P. canarioides + P. tessmannii + P. benna + Magnistipula pro parte
III/IV (Fig. XII)	1. P. MYRIANDRA 2. CYCLANDROPHORA 3. MAGNISTIPULA 4. P. TESSMANNII 5. MARANTHES + P. MACROPHYLLA	1. Couepia + Hirtella + P. benna + Parinari + P. canarioides + Duckea
III/V (Fig.XIII)	1. P. MYRIANDRA 2. MAGNISTIPULA + P. TESSMANNII 3. CYCLANDROPHORA 4. P. BENNA 5. P. MACROPHYLLA 6. MARANTHES pro parte 7. GRANGERIA	1. Couepia + Hirtella + Parinari + Maranthes pro parte + P. canarioides + Duckea
IV/V (Fig. XIV)	1. P. MYRIANDRA 2. CYCLANDROPHORA 3. GRANGERIA 4. MARANTHES pro parte	1. Maranthes pro parte + Hirtella pro parte + P. macrophylla 2. Couepia = Hirtella pro parte + Parinari + Duckea + P. canarioides + Magnistipula

Table 6. Grouping obtained from analysis of complete data

In this list and in the figures, the subgenera of Parinari are represented solely by their subgeneric names, and individual species, which are separated from any other group by their specific name preceded by the first letter of the generic name.

From these results, and with the knowledge of the group accumulated in the course of this work, it is now possible to discuss the best way to classify the genera of this group.

The most obvious conclusion is that _Parinari_ subgenus _Parinari_ is distinct from the other genera. This is indicated by all three types of statistical analysis. Similarly the two subgenera of _Parinari_ - _Sarcostegia_ and _Cyclandrophora_ are distinct as genera. (As an older generic name exists for _Sarcostegia_ it is referred to as _Maranthes_ in the Conspectus where the necessary explanation is given.)

The classification of the remainder of the genus _Parinari_ requires more careful consideration. _P. benna_ is isolated by both component analyses. It does not fit into any of the other genera and certainly does not belong within the very uniform _Parinari_ sens. strict., as both the fruit structure and the shape of the receptacle are very different. For these reasons it seems best to regard _P. benna_ as a unispecific genus on its own. Similarly _P. macrophylla_ (= _Parinari_ subgenus _Neocarya_) is isolated by the second component-analysis and where it is not isolated it is grouped with different genera by the various pairs of components. The shape of the receptacle of this species is very distinct not only from _Parinari_ but also from the rest of the Chrysobalanaceae. Thus, it is proposed to elevate the subgenus _Neocarya_ to generic status.

Parinari subgenus _Pellegriniella_ is an interesting case. The type species of this subgenus, _P. tessmannii_, occupies a position always far from the other species (_P. coriacea_ , _P. barbata_ and _P. gardneri_). At the outset of the statistical work I was sure that _P. tessmannii_ could not be placed within _Parinari_ sens. strict., but was not convinced that a new genus need be created for this species, because of its similarity with the genus Magnistipula. The decision whether to transfer this species to Magnistipula was a difficult one to make, but in light of the statistical work the answer is clear. In all three types of analysis this species is grouped with Magnistipula, but in some cases rather apart from the other species. It seems best to treat P. tessmannii as a subgenus (Pellegriniella) of Magnistipula.

The other three species of Parinari subgenus Pellegriniella were not apparently studied in detail by Hauman (1951) when he established the subgenus and clearly do not belong to it. The three species are separated by the component-analysis and must be considered as a separate genus. Their fruit structure is quite unlike that found in any other species of Parinari. This new genus has been named Duckea, and appears under this name in the figures representing the statistical work.

Parinari myriandra is also isolated by the third component-analysis and placed differently by the first two. This species must certainly be regarded as a separate genus. In fact it does not even have a bilocular ovary, the one character which formerly held the species of Parinari together. Apart from this, its stamens are ligulately connate as in the genus Acioa. The new genus Kostermansia is described to accommodate this species, and also Parinari heteropetala, a species not included in the statistical analyses.

The only remaining species of Parinari to be discussed is P. canarioides, which is isolated by the first component of the analysis using the complete data, but variously positioned by the other analyses. Although this species is isolated and differs from Parinari in a few characters I propose that it remain in Parinari sens. strict.

There is a small group of species of Parinari from the

Malaysian region that differs from the rest in not having the characteristic type of leaf-undersurface, but both the floral and fruit structure are typical of the genus. These species are _P. canarioides_, _P. sericeo-argentea_ and an undescribed species. They certainly do not merit recognition as a separate genus. _P. sericeo-argentea_ has bracts which enclose the young flowers in small groups whilst _P. canarioides_ does not. The latter species differs in this and the leaf character and has been rather isolated by the statistical analysis since both these characters are constituents of the component that isolated it. These are important characters and this group is clearly borderline but in my opinion the differences between _P. canarioides_ and its relatives and _Parinari_ sens. strict. are not sufficient to justify the recognition of the former as a genus. This is further discussed in the Conspectus in a note following _Parinari_. A summary of the new classification of _Parinari_ as concluded here is now given.

Parinari sens. strict.	(_Parinari_ subg. _Parinari_)
Cyclandrophora Hasskl.	(_Parinari_ subg. _Cyclandrophora_)
Maranthes Blume	(_Parinari_ subg. _Sarcostegia_)
Neocarya gen. nov.	(_Parinari_ subg. _Neocarya_)
Kostermansia gen. nov.	(_Parinari myriandra_ and _P. heteropetala_)
Duckea gen. nov.	(_Parinari coriacea_, _P. barbata_ etc.)
Bafodeya gen. nov.	(_Parinari benna_)
Magnistipula subgenus _Pellegriniella_	(_Parinari tessmannii_)

The statistical analyses show that _Magnistipula_ should be defined in the way that Graham (1957) suggested. The species of _Hirtella_ subgenus _Afrohirtella_ (Hauman, 1951) clearly belong with the other species of _Magnistipula_. This is indicated by all three statistical methods.

Magnistipula defined in this way is clearly separable from Hirtella. This leaves only two African species in Hirtella sens. strict. (H. zanzibarica and H. megacarpa). These two species certainly belong with their South American congeners.

This now leaves Hirtella and Couepia to discuss. In the association-analysis they are grouped together, but in the first component-analysis they are clearly separated from each other. The third component-analysis indicates that these two genera are closely related but separable. The conclusion drawn is that it is possible to maintain these two closely related genera. Many species are separated by a long distance by the component-analysis, but certain species of the one genus come close to certain species of the other. The component-analysis of the quantitative data indicates that even the borderline species fall clearly into one genus or the other, for example Couepia dodecandra and C. polyandra are placed with the other species of Couepia. As a result of this analysis, and in the light of the fruit structure it is possible to state more definitely that these species belong to Couepia. No change in the definition of either Couepia or Hirtella is necessary and the distinctions between these genera made by Zuccarini (1832b) seem the best. In the projections of several of the components in both component-analyses the species Couepia macrophylla (59) is isolated from the rest of the genus. This is because of the much larger size of the flowers and the vast number of stamens (two hundred more than in any other species of Couepia). This species is only placed away from other species of Couepia by the component including flower size and staminal number. I do not consider that differences in these characters merit the creation of any new taxon for C. macrophylla, which in every other respect is a typical member of Couepia.

In addition to the component-analyses already described a further analysis using the complete set of data was made of this group, but including species of the genus _Acioa_. As the resulting groups were similar to those of the analysis already described the full details are not given here. However, in order to show that results are the same five of the projections of the components are given in figures XV-XIX. From these it can be seen that, in addition to the groups already suggested, _Acioa_ is separated. The details of the components are also summed up in the figures.

As a result of this work it is proposed to divide the tribe _Hirtelleae_ into the following genera.

Acioa

Hirtella

Magnistipula (including _Hirtella_ subgenus _Afrohirtella_ Hauman and _Parinari tessmannii_)

Couepia

Grangeria

The 7 genera from _Parinari_ already listed.

Hunga.

The latter is a new genus from New Caledonia which is now placed in this tribe (see Chapter 7), but consists of species formerly included in both _Licania_ (_Chrysobalaneae_) and _Parinari_ (_Hirtelleae_). This genus is more fully discussed in the next section under the tribe _Chrysobalaneae_ because it mainly includes species formerly considered as members of the genus _Licania_.

The statistical evidence for the recognition of these genera can be summarized as follows:-

Parinari sens. strict. is indicated as the most distinct group in the tribe by all component-analyses, where it is always separated by the first component. It is also separated by the association-analysis.

Fig. XV - Projection of first and third components - Hirtelleae. (Increased data.)

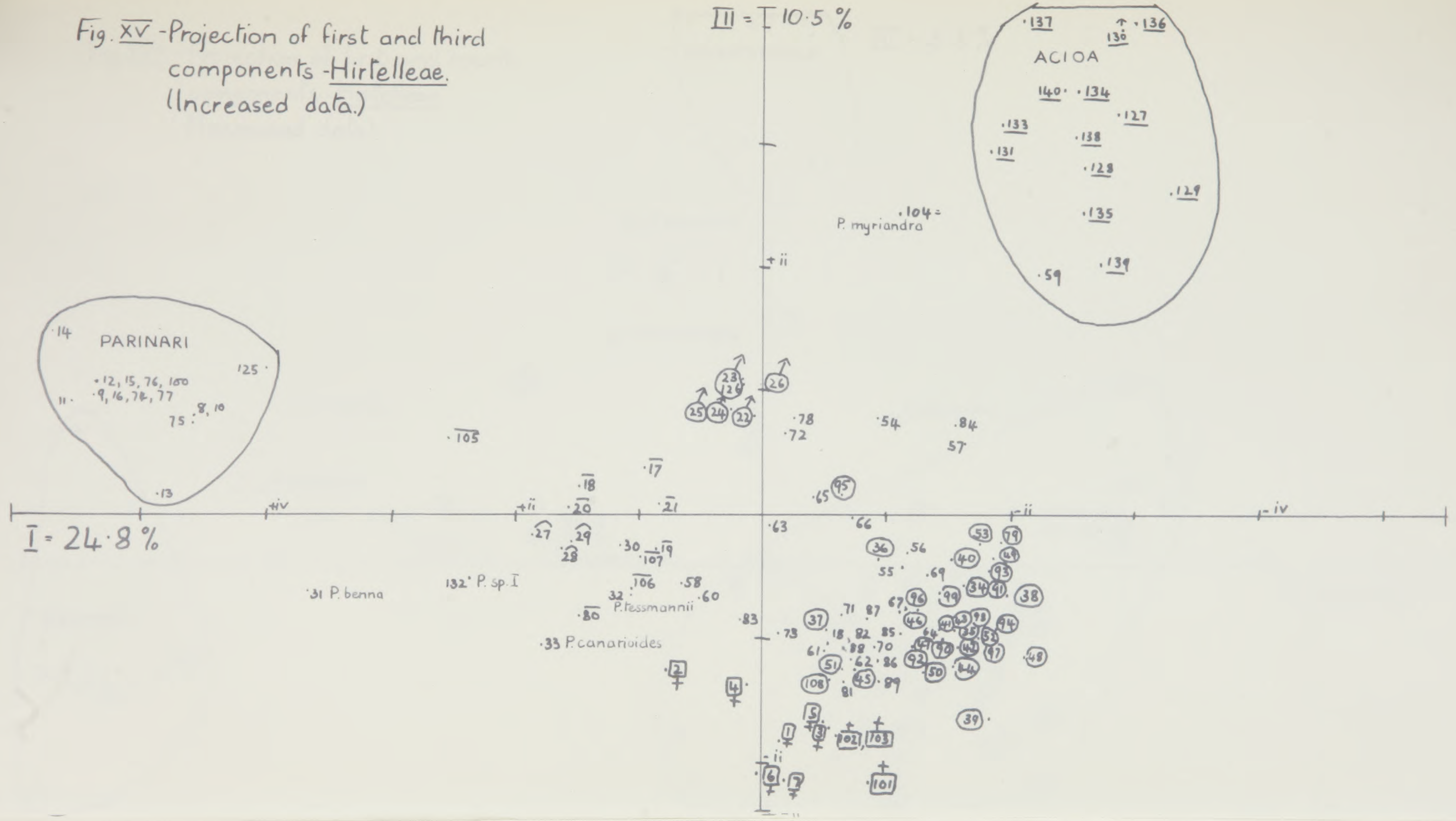


Fig. XVI - Projection of first and fourth components - Hirtelleae. (Increased data.)

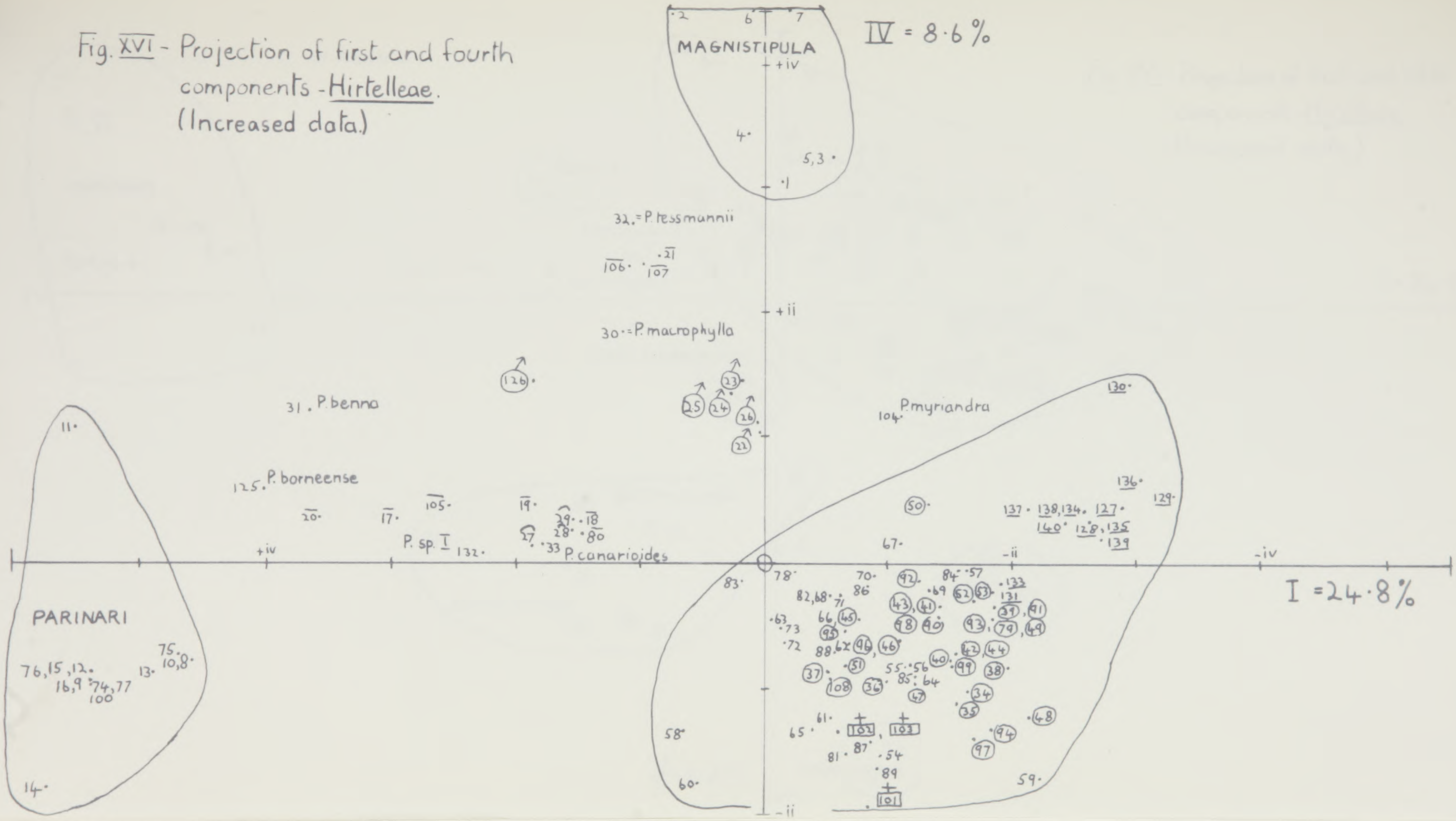
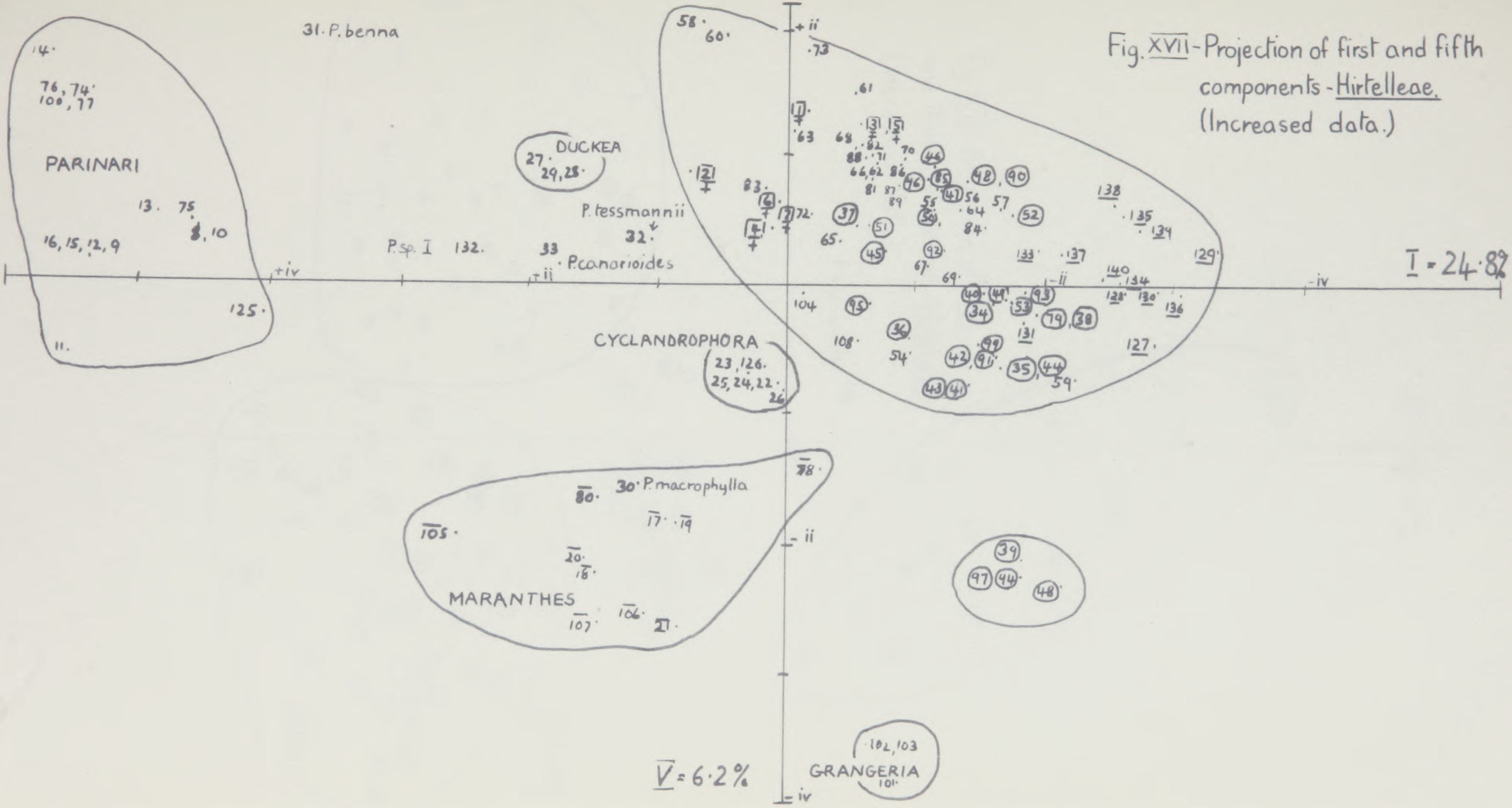


Fig. XVII - Projection of first and fifth components - Hirtelleae. (Increased data.)



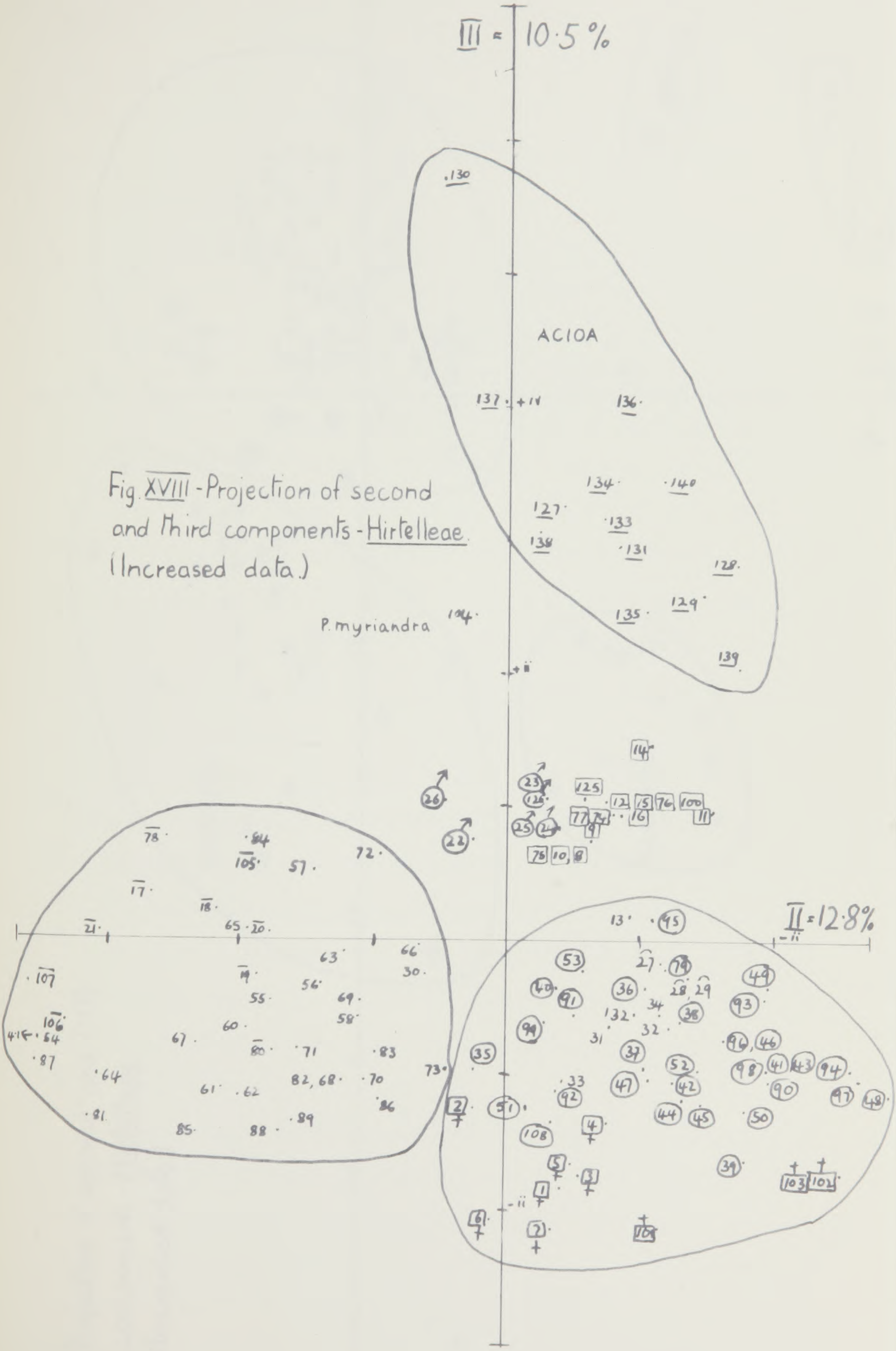
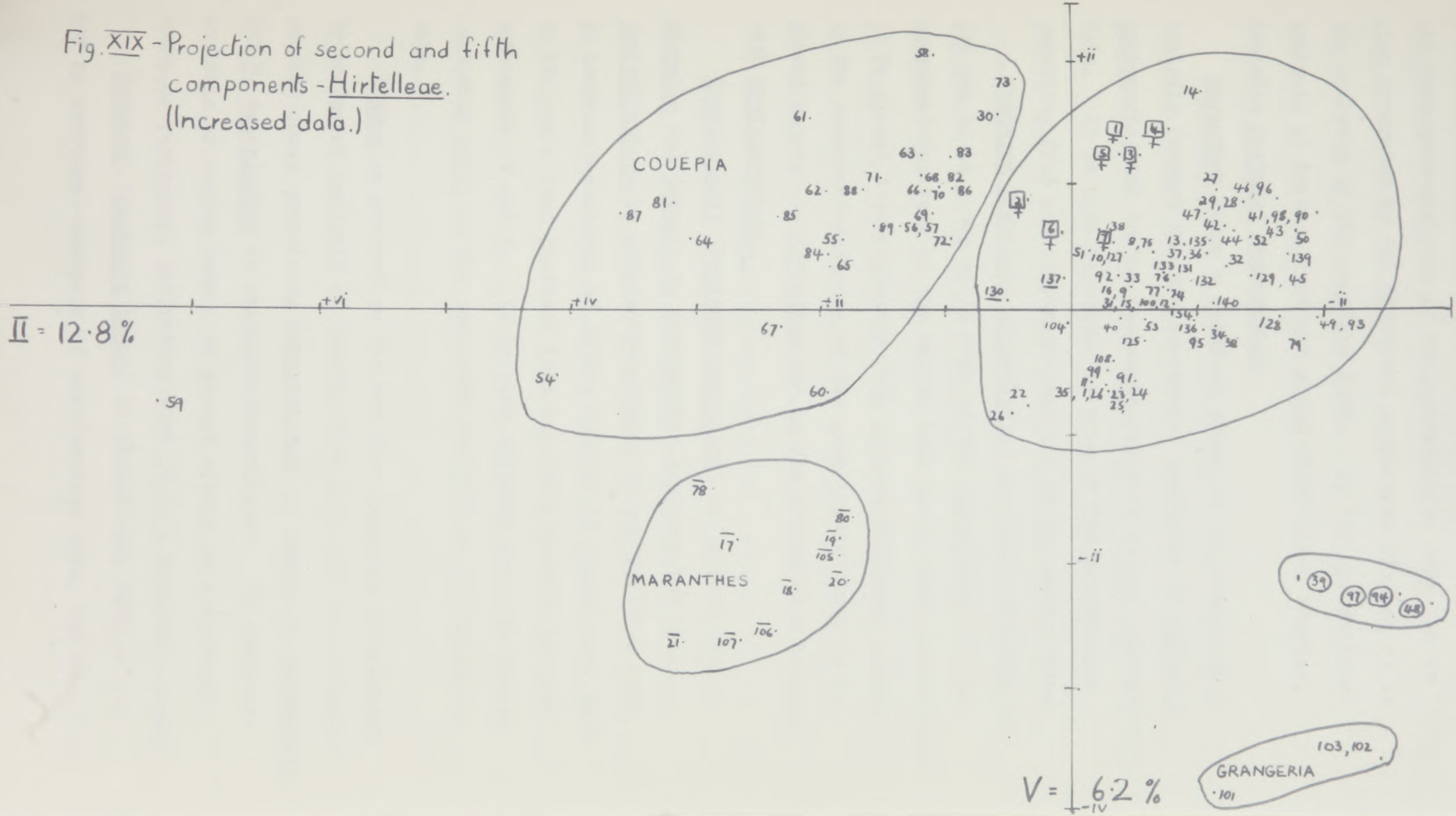


Fig. XVIII - Projection of second and third components - Hirtelleae. (Increased data.)

Fig. XIX - Projection of second and fifth components - Hirtelleae. (Increased data.)



Cyclandrophora is grouped very much on its own by the component-analysis of the quantitative data and is also separated by two different components (IV and V) in the analysis of the complete data. In the association-analysis it forms a distinct group which also, however, includes *Parinari macrophylla*.

Maranthes forms a distinct group in the association-analysis (except for the accidental inclusion of *Hirtella carbonaria*) and in the component-analysis of the quantitative data. It is also separated by some of the projections resulting from the component-analysis of the entire data.

Neocarya (Parinari macrophylla) is either situated on its own in no group as in some of the projections of the component-analysis of the entire data or in other projections it is placed inconsistently with various different groups. In the component-analysis of the quantitative data it is placed nearest to *Maranthes* and in the association analysis with *Cyclandrophora*.

Kostermansia (*Parinari myriandra*) is placed with *Hirtella* and *Couepia* by association-analysis but with *Cyclandrophora* by component-analysis of quantitative data. In component-analysis of entire data it is placed very much on its own a long distance from any other species by both components IV and V. It is also distinct from all genera including *Acioa* on the component analysis of the increased data.

Duckea is grouped on its own with *Parinari canarioides* by component analysis of quantitative data but in a heterogeneous group containing *Magnistipula*, *P. benna*, *P. tessmannii* and *P. canarioides* by association-analysis. In component analysis of entire data is placed either as a distinct group or variously, indicating that it is a separable genus.

Bafodeya (*Parinari benna*) is placed very much on its own by component-analysis of quantitative data, not close to any other group. By association-analysis it is placed in the heterogeneous group already listed under the previous genus. In the component-analysis of entire data it is separated on its own by six out of the ten projections of the components, which demonstrates that it is certainly a distinct group.

Magnistipula is placed very close to and not really separable from Couepia by component-analysis of quantitative data, this group also contains Parinari tessmannii. It forms part of the heterogeneous group listed under Duckea in the association-analysis. The component-analysis of entire data separates it as a distinct group on the basis of component II. Parinari tessmannii is again near to and often inside this group.

Grangeria is grouped on its own by association-analysis, component-analysis of quantitative data and in several of the projections resulting from component-analysis of entire data and so is unquestionably shown as a distinct genus.

Hirtella and Couepia. These two genera fall apart from all the other genera discussed above but are clearly very closely related to one another. Statistically they are only definitely separated by component-analysis of quantitative data where they are in separate groups but these groups are near to each other. By association-analysis they are placed together in a single group. By component-analysis of entire data they are not separated into pure groups by any of the projections of the components. They are, however, separated from each other in many cases both in this analysis and component-analysis of increased data. The statistical analysis indicates the proximity of these two genera and that it is possible to separate them if desirable to do so. The relationship of these two genera is discussed further in Part 2 of the present work.

Acioa was only examined statistically by component-analysis of increased data, which indicates that it is the most distinct group other than Parinari.

b) The Chrysobalaneae

In this group Focke, in Engler and Prantl's "Die Natürlichen Pflanzenfamilien," recognized the following genera - Chrysobalanus, Licania, Moquilea, Angelesia, and Parastemon, although his groupings differ appreciably from mine. Afrolicania and Geobalanus were described subsequently. Few botanists other than Focke have regarded Moquilea as distinct from Licania. During the early stages of this work it appeared that Angelesia could not be kept satisfactorily apart from Licania, and that the difference separating the other genera were in most cases less than those in the tribe Hirtelleae. Furthermore four species of Licania and three of Parinari from New Caledonia, and one species of Angelesia from Papua appeared to be congeneric and distinct from the other genera. To anticipate, this was confirmed by the analysis and in the following account this group will be referred to as "Hunga".

Because of this it was decided to use a computer to analyse the variation in a way similar to that done for the Hirtelleae. A single principle component-analysis was made.

(1) The characters

The data was scored numerically as in the case of the Hirtelleae. It consisted of two quantitative and thirteen qualitative characters a list of which is now given:-

1. Number of stamens.
2. Ovary unilocular (1) or bilocular (0).
3. Ovary inserted at the base (1) or the middle (0) of the receptacle.
4. Stigma distinctly 3-lobed (1) or very indistinctly lobed (0).

5. Staminal filaments hairy (1) or glabrous (0).
6. Stamens exserted (1) or included (0).
7. Endocarp prominently ridged (1) or smooth (0).
8. Endocarp with two lateral plates (0) or without (1).
9. Petioles glandular (1) or eglandular (0).
10. Flowers androdioecious (1) or hermaphrodite (0).
11. Receptacle flattened (1) or cupuliform (0).
12. Fruit-interior hairy (1) or glabrous (0).
13. Stamens in a complete circle (1) or part circle (0).
14. Prominent stomata on leaf-undersurface (1) or not (0).
15. Inflorescence a raceme or recemoid (1), cymose (2), a panicle (3).

This list is in the main part self-explanatory and consists of all the important characters previously used to delimit the genera of this group. There are nine flower, three fruit, two leaf and one inflorescence characters. The fruit in this group does not yield such clear-cut characters as that of the Hirtelleae. Plate XXVIII shows the diversity of fruit within the single genus Licania and Plate XXIX shows the fruit of the other genera. Although the fruit of Licania varies greatly in the type of experior and the thickness of the various layers of its wall, it does not have any special mechanism for seedling escape comparable to those found in the Hirtelleae. The genus Parastemon is the only one to have any such mechanism. Here two plates detach from the side of the endocarp wall in an exactly similar manner as in the genus Grangeria. The fruit of Licania is still only known in about half the species of the genus, but is of little value as a generic character.

The type of leaf-undersurface is not used as a generic character for this group, because of the diversity within the genus Licania. Licania is the only other genus of the Chrysobalanaceae besides Parinari in which stomatal cavities occur on the leaf-undersurface. These occur in species of

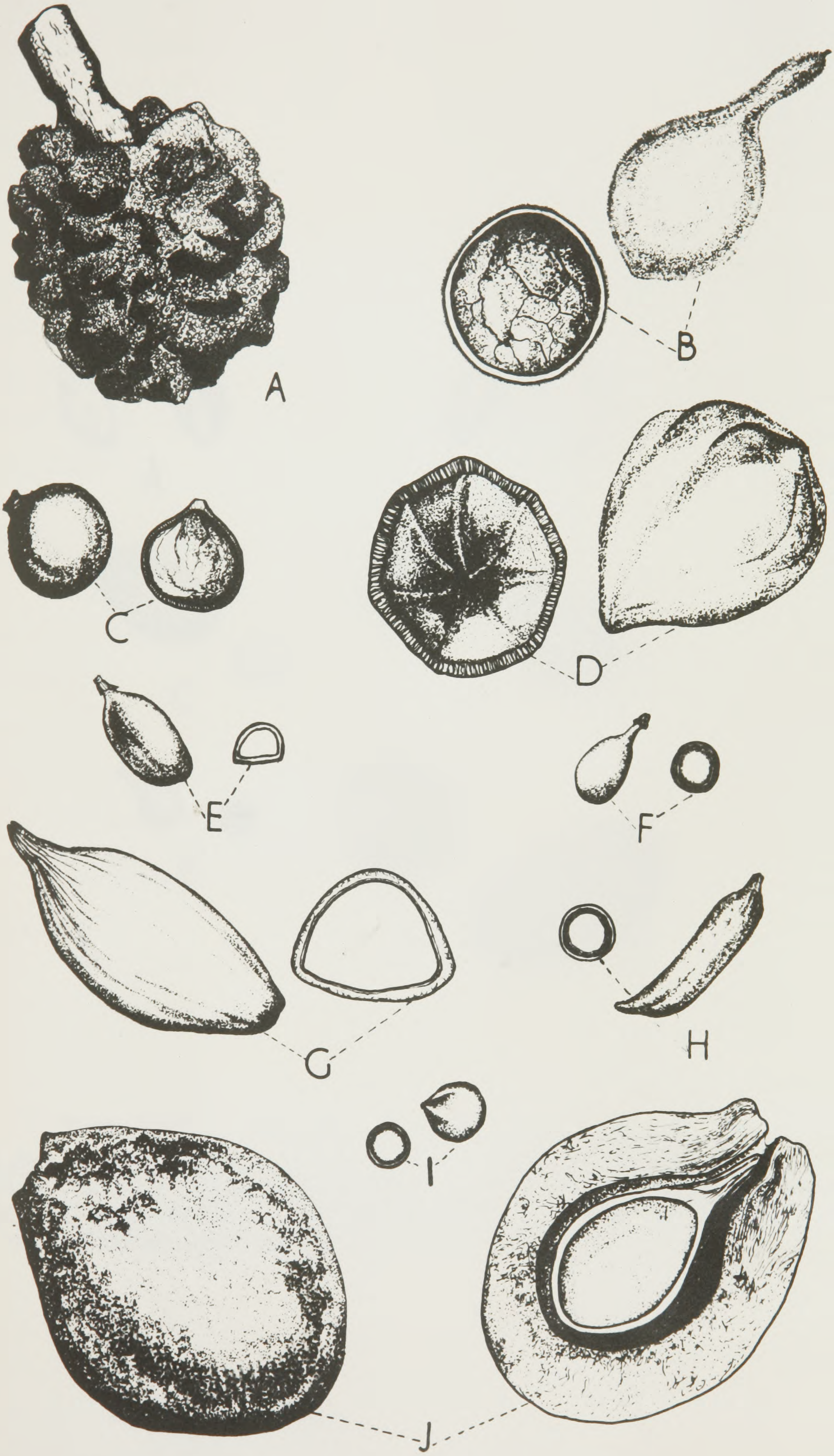


Plate XXIII.- The fruit of Licania

A,L.octandra; B,L.cuprea; C,L.sparsipilis; D,L.majuscula; E,L.arborea; F,L.hypoleuca; G,L.rigida; H,L.turuiva; I,L.grisea; J,L.pallida. (all x 1).

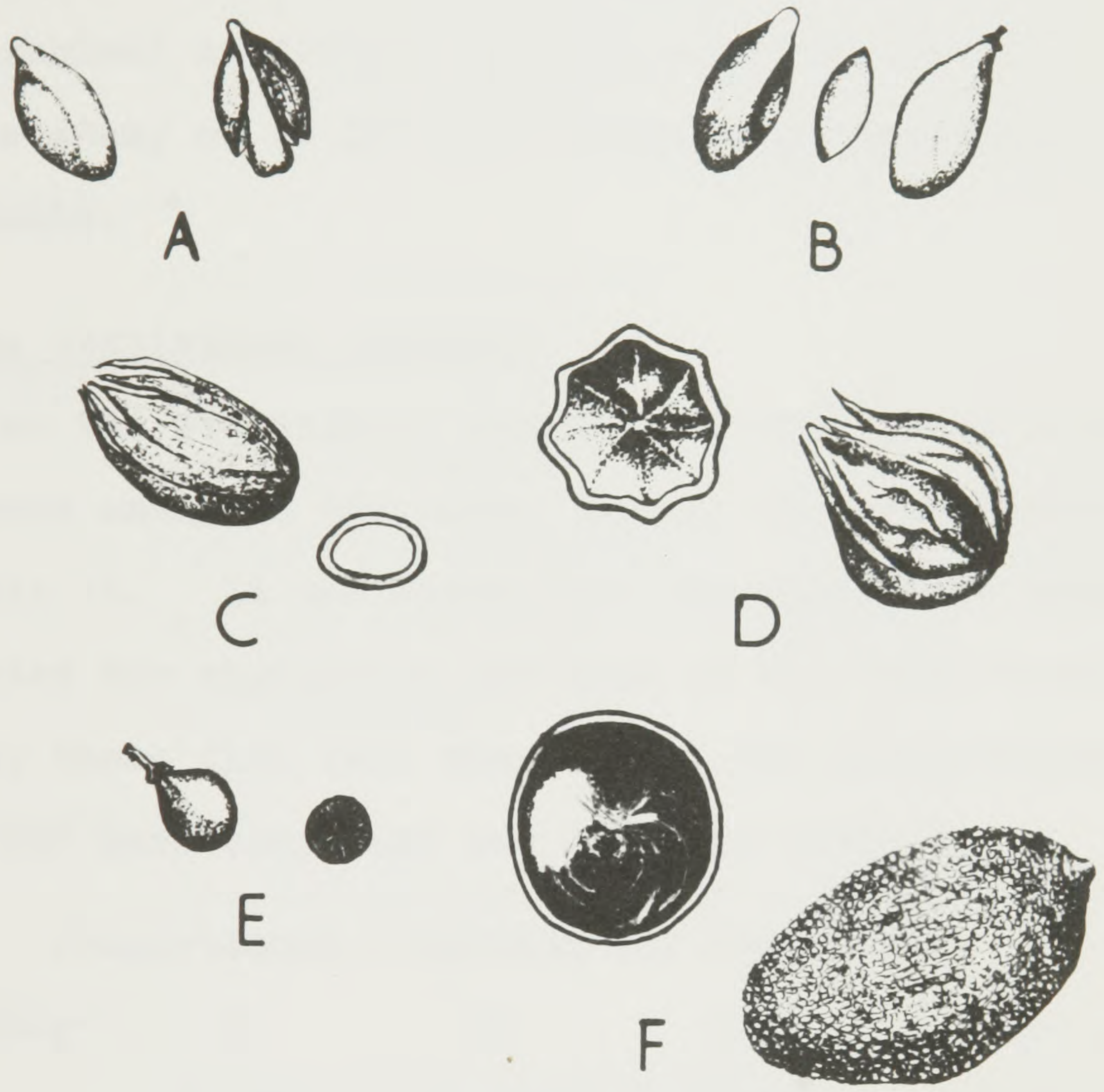


Plate XXIX.- The fruit of the Chrysobalaneae

A, Grangeria porosa Boiv.ex Baill.; B, Parastemon urophyllus (A.DC.)A.DC.; C, Licania (Geobalanus)sp.; D, Chrysobalanus orbicularis Schum.; E, Licania splendens (Korth.)Prance; F, Afrolicania elaeosperma Mildbr. (all x 1).

both the sections Licania and Moquilea. However, other species of Licania may have a lanate or strigose indumentum, or the leaves may be glabrous. In the other genera of the Chrysobalaneae the leaves are mostly glabrous except for some species of Hunga and one of Geobalanus, thus leaf indumentum would not be a valuable generic character. The species of Hunga have extremely prominent stomata as is shown in Plate XXVII-A. The nature of the cuticle has not been examined in detail, but this work indicates that a further study of it for this group would probably be profitable.

(2) The Statistical Analysis

For the statistical analysis of this group a principle-component analysis was used, for all the data listed in Appendix 1B. It was found that the first five components accounted for eighty-two per cent of the total variation, and so only these five were computed. The proportional weightings for each component are given in table 7.

	Proportional weighting for Component:-				
Character	I	II	III	IV	V
1	+ 0.0570	- 0.0267	+ 0.0881	+ 0.0225	- 0.0698
2	+ 0.0956	- 0.0082	- 0.0811	- 0.0187	- 0.0086
3	+ 0.1000	+ 0.0131	- 0.0428	+ 0.0123	+ 0.0140
4	+ 0.0907	+ 0.0432	- 0.0130	+ 0.0126	+ 0.0513
5	+ 0.0471	- 0.0349	+ 0.0874	- 0.0369	+ 0.1000
6	+ 0.0616	- 0.0170	+ 0.0816	- 0.0117	- 0.0896
7	+ 0.0459	- 0.0445	+ 0.1000	- 0.0345	+ 0.0741
8	+ 0.0284	+ 0.0809	+ 0.0985	+ 0.0335	+ 0.0233
9	- 0.0230	- 0.0569	+ 0.0945	+ 0.0433	- 0.0247
10	+ 0.0094	- 0.0216	- 0.0211	+ 0.1000	+ 0.0441
11	- 0.0057	- 0.0757	- 0.0819	+ 0.0575	+ 0.0294
12	- 0.0591	+ 0.0591	- 0.0309	- 0.0345	+ 0.0042
13	+ 0.0909	+ 0.0191	- 0.0094	+ 0.0124	- 0.0532
14	- 0.0937	+ 0.0064	+ 0.0806	+ 0.0181	+ 0.0032
15	+ 0.0034	+ 0.1000	+ 0.0395	+ 0.0468	+ 0.0157
Percentage variation accounted for	31.5%	18.6%	16%	10%	6.5%

Table 7. Weighting for original characters in computed component.

Taking note of the weightings it is possible to identify the components in table 7 where they are underlined. The components are:-

Component I

+2 - Ovary unilocular or bilocular

+3 - Insertion of the ovary

+4 - Type of stigma

+13 - Insertion of the stamens

+14 - The type of stomata

Component II

+15 - Type of inflorescence

Component III

+1 - Number of stamens

+7 - Fruit ridged or smooth

+8 - Endocarp with plate of dehiscence

+9 - Leaf glanding.

Component IV

+10 - Flowers hermaphrodite or androdioecious

Component V

+5 - Stamens hairy or glabrous

-6 - Stamens exserted or included.

From this it can be seen that only two of the original fifteen characters are not included in the first five components. These are number 12; whether the interior of the fruit is hairy or glabrous, and number 11; whether the receptacle is flat or cupuliform. The grouping obtained is not affected by either of these characters, and neither of these are diagnostic of one genus, and so are comparatively insignificant as this analysis indicates.

Figures XX-XXIX represent the projection of the value of each component against each other component, obtained by computing the weighting of table 7 and the basic data of appendix 1B normalized in the same way as in the previous

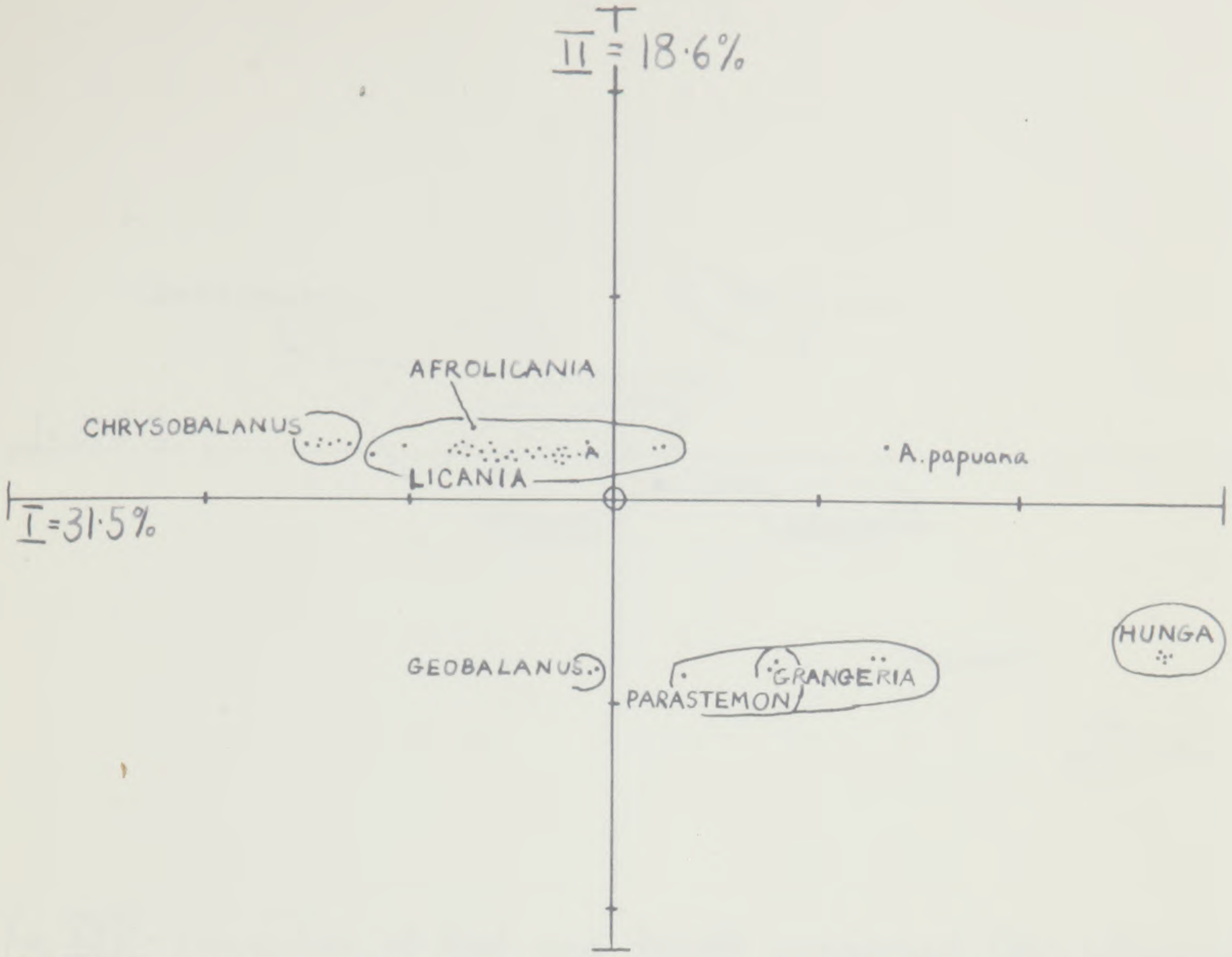


Fig. XX - Projection of first and second components - Chrysobalaneae.

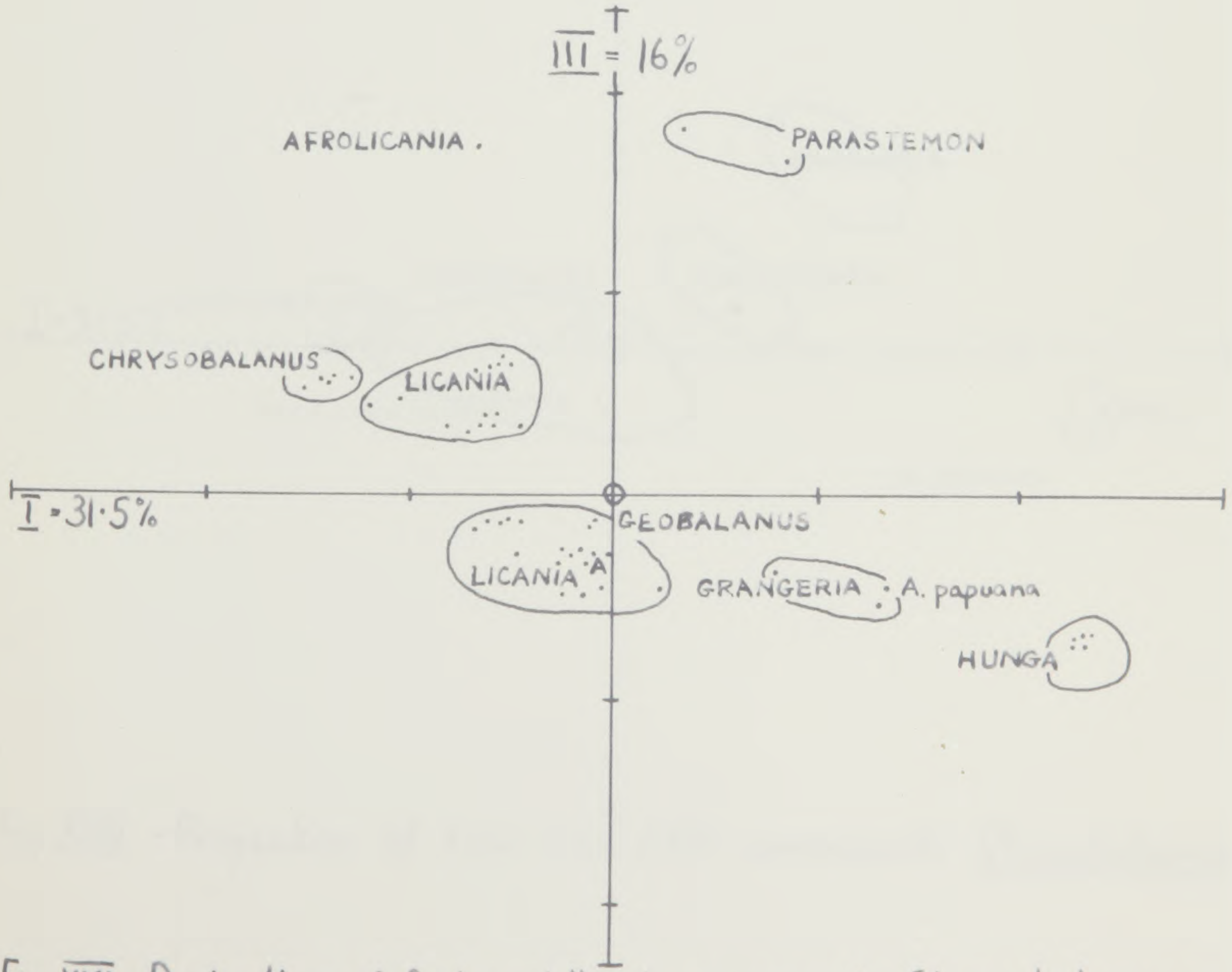


Fig. XXI - Projection of first and third components - Chrysobalaneae.

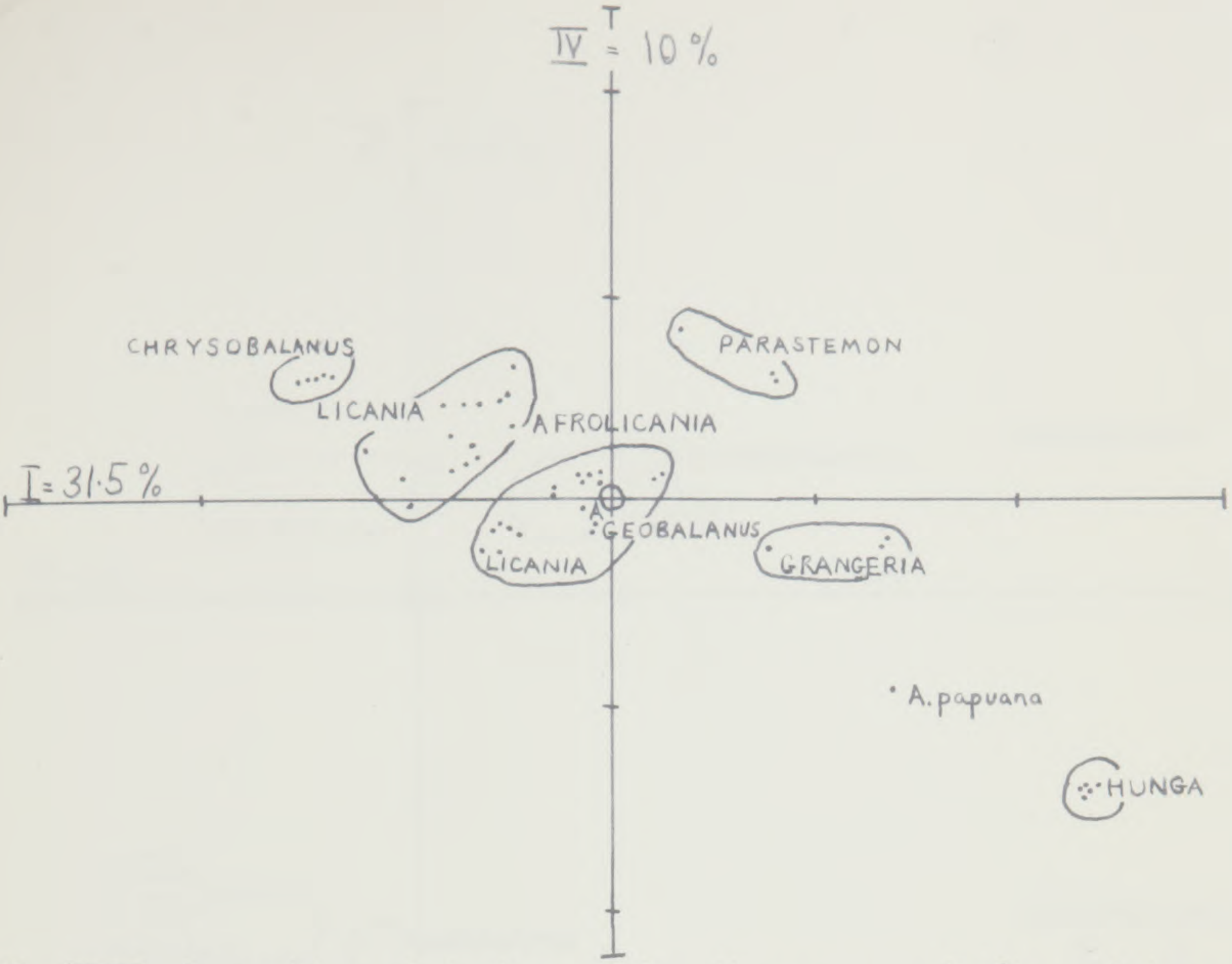


Fig. XXII - Projection of first and fourth components - Chrysobalaneae

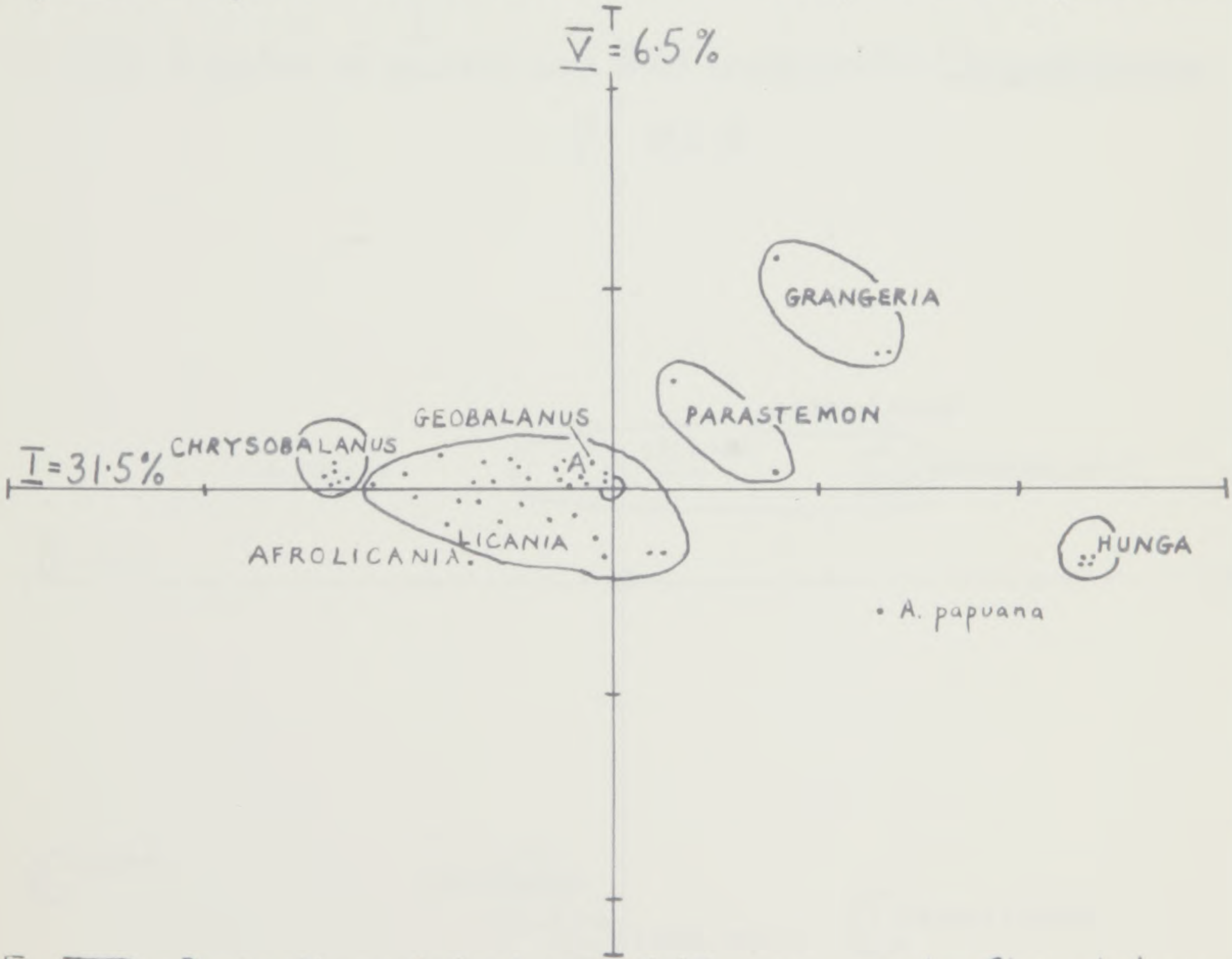


Fig. XXIII - Projection of first and fifth components - Chrysobalaneae

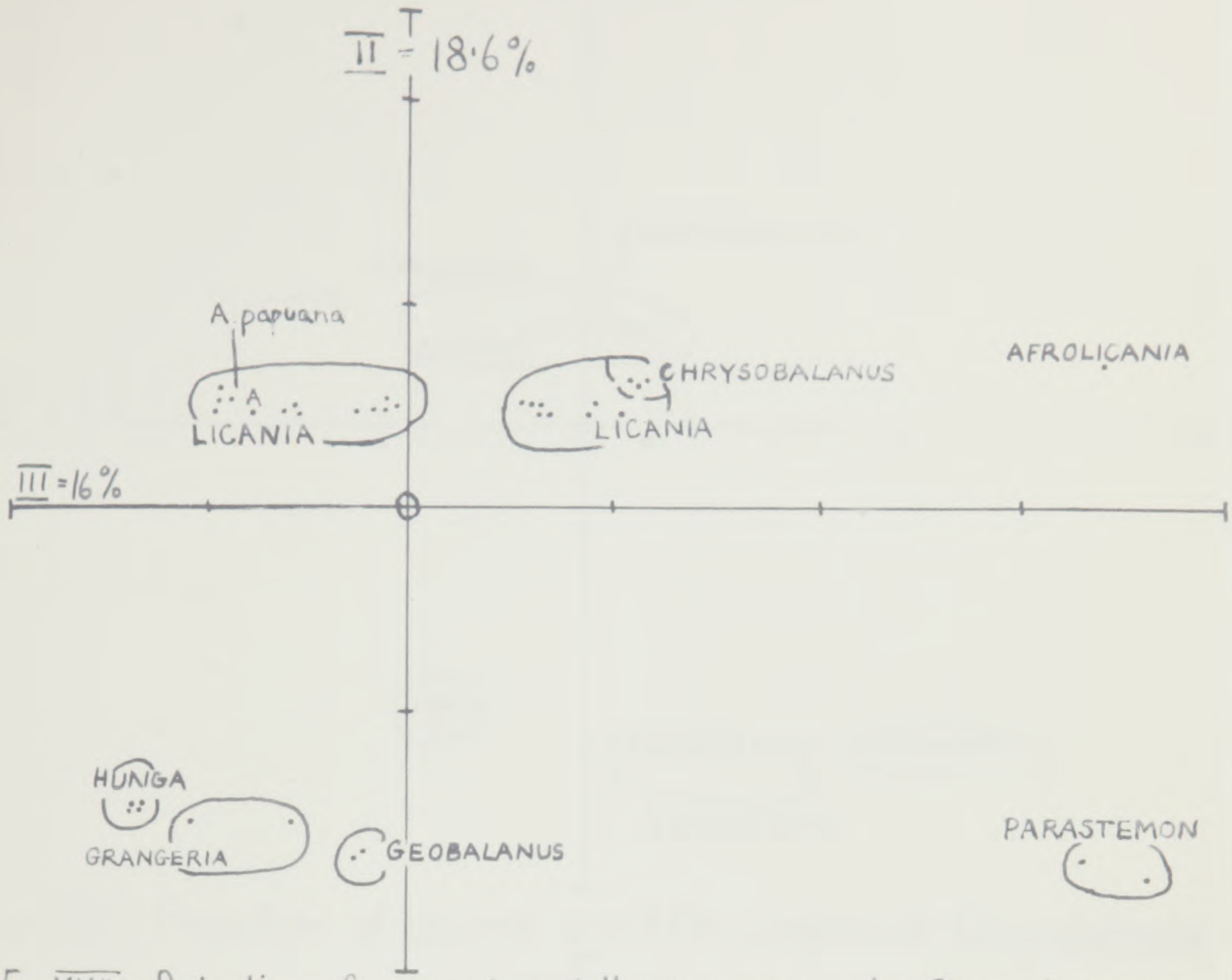


Fig. XXIV - Projection of second and third components - Chrysobalaneae.

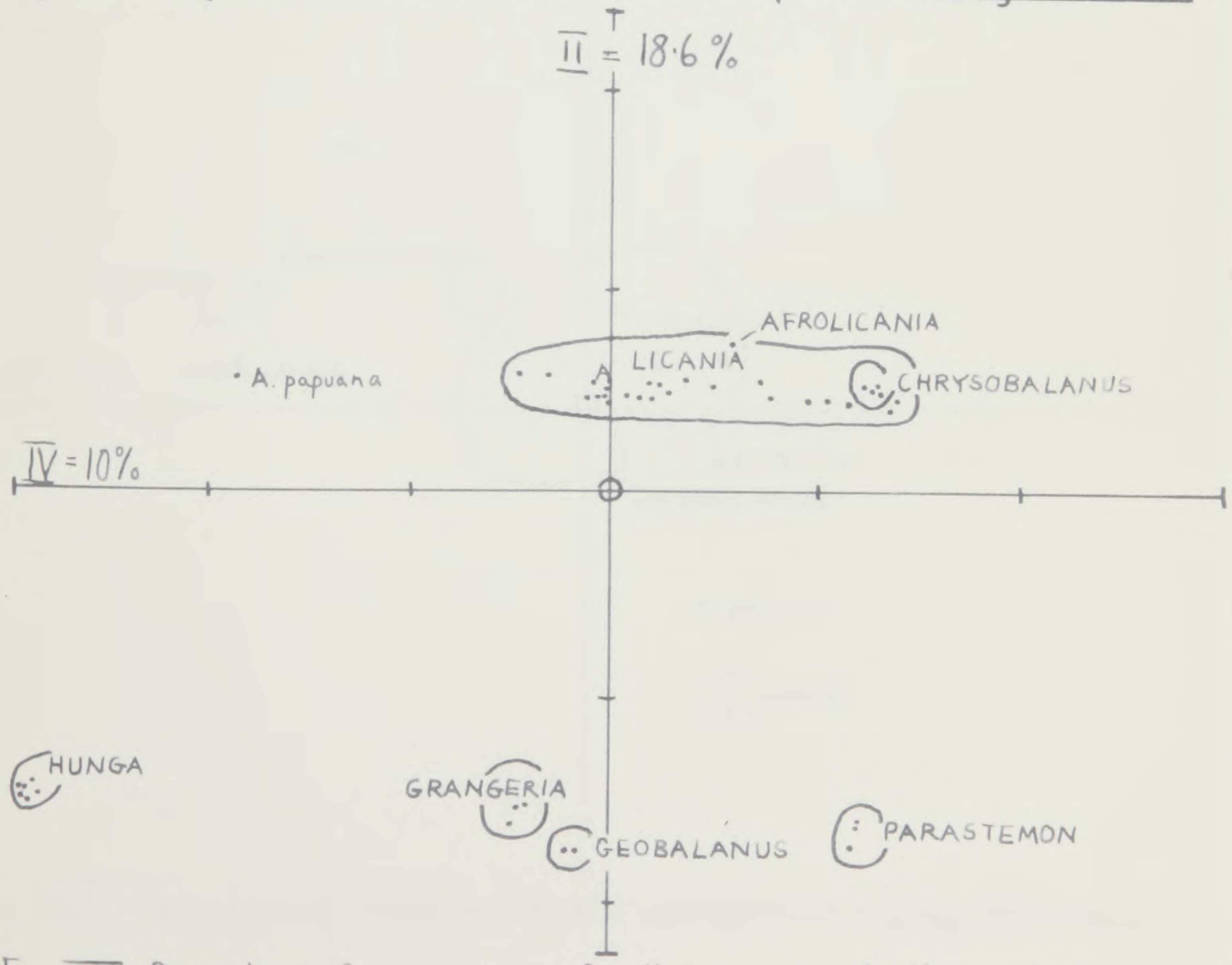


Fig. XXV - Projection of second and fourth components - Chrysobalaneae.

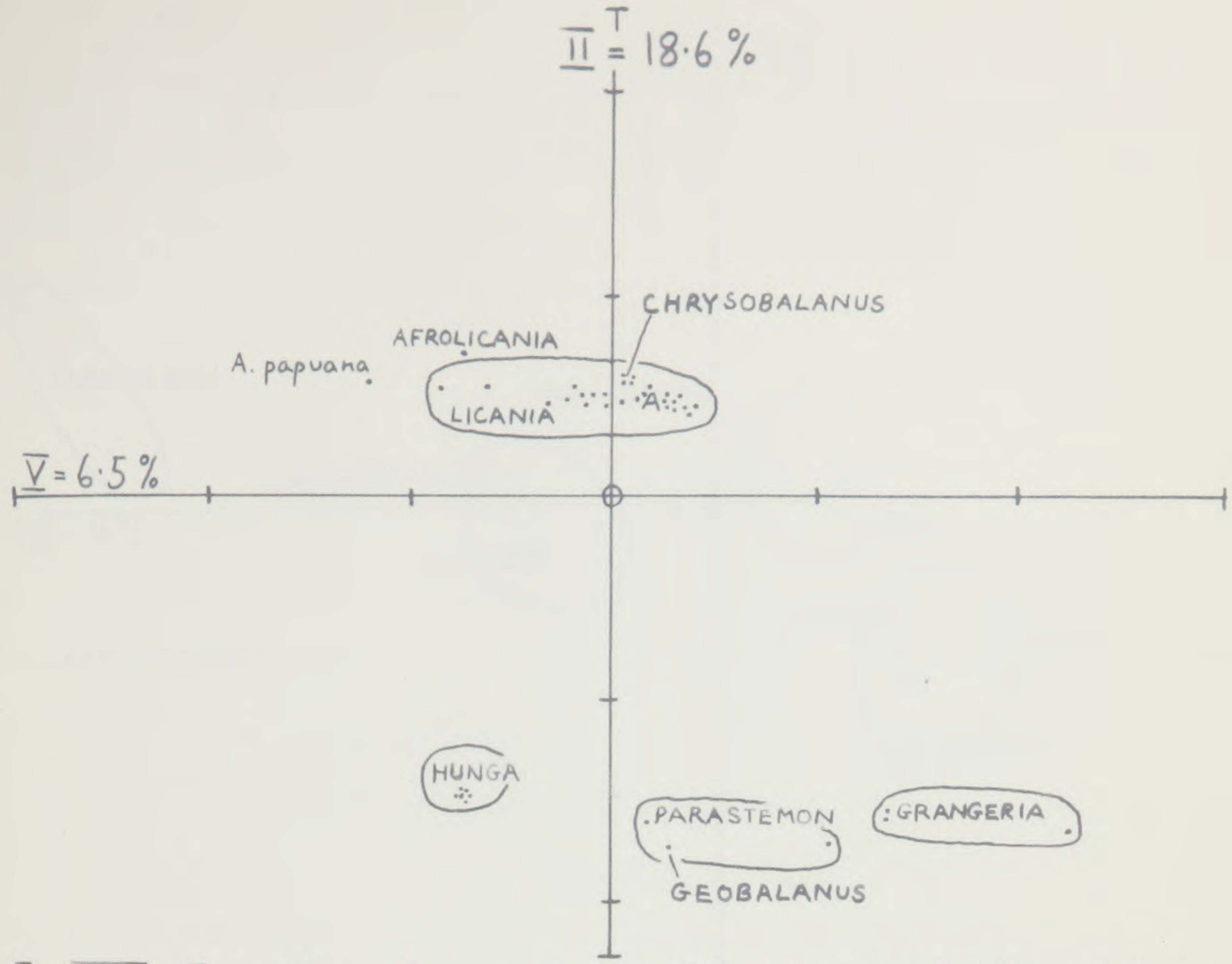


Fig. XXVI - Projection of second and fifth components - *Chrysobalaneae*.

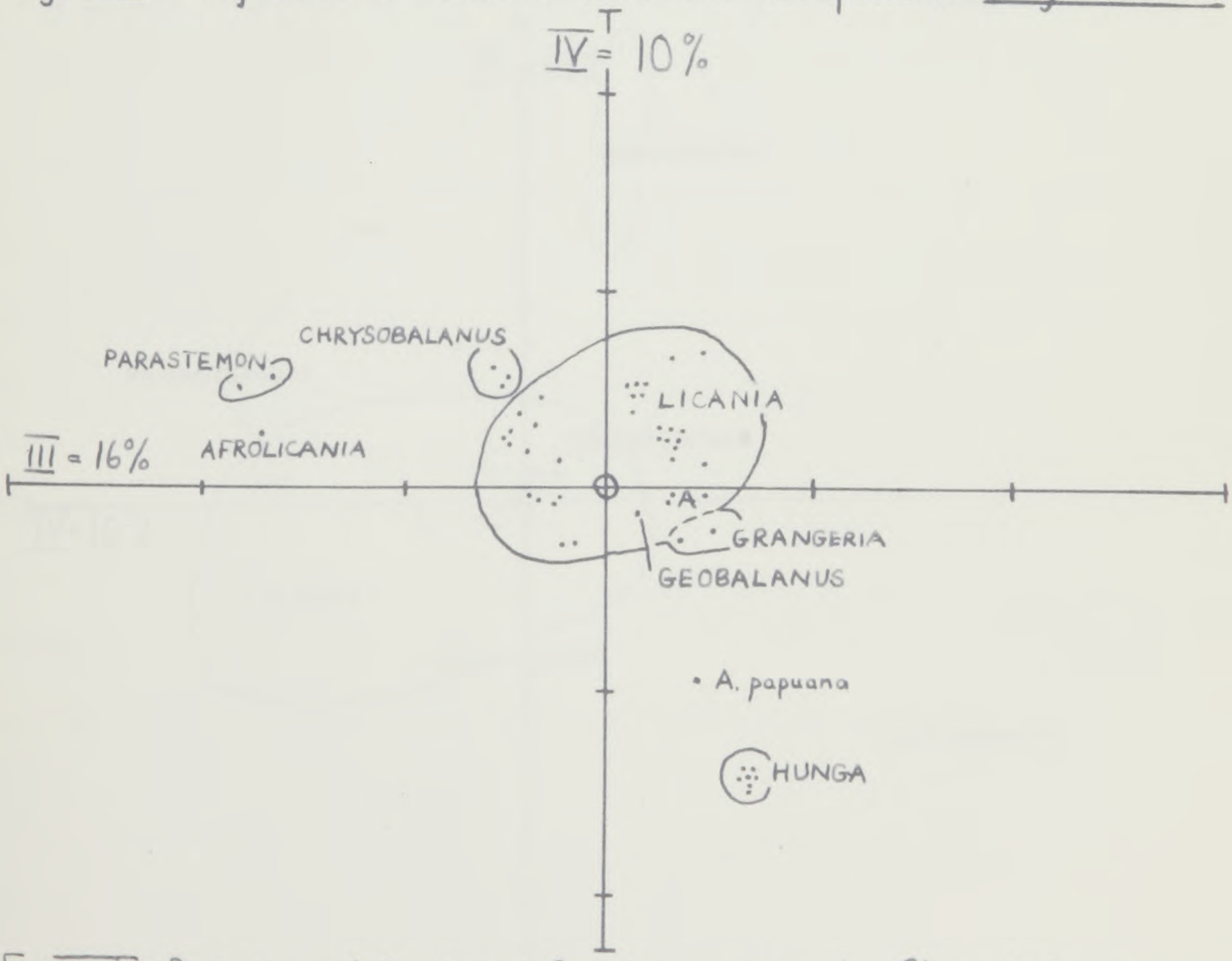


Fig. XXVII - Projection of third and fourth components - *Chrysobalaneae*.

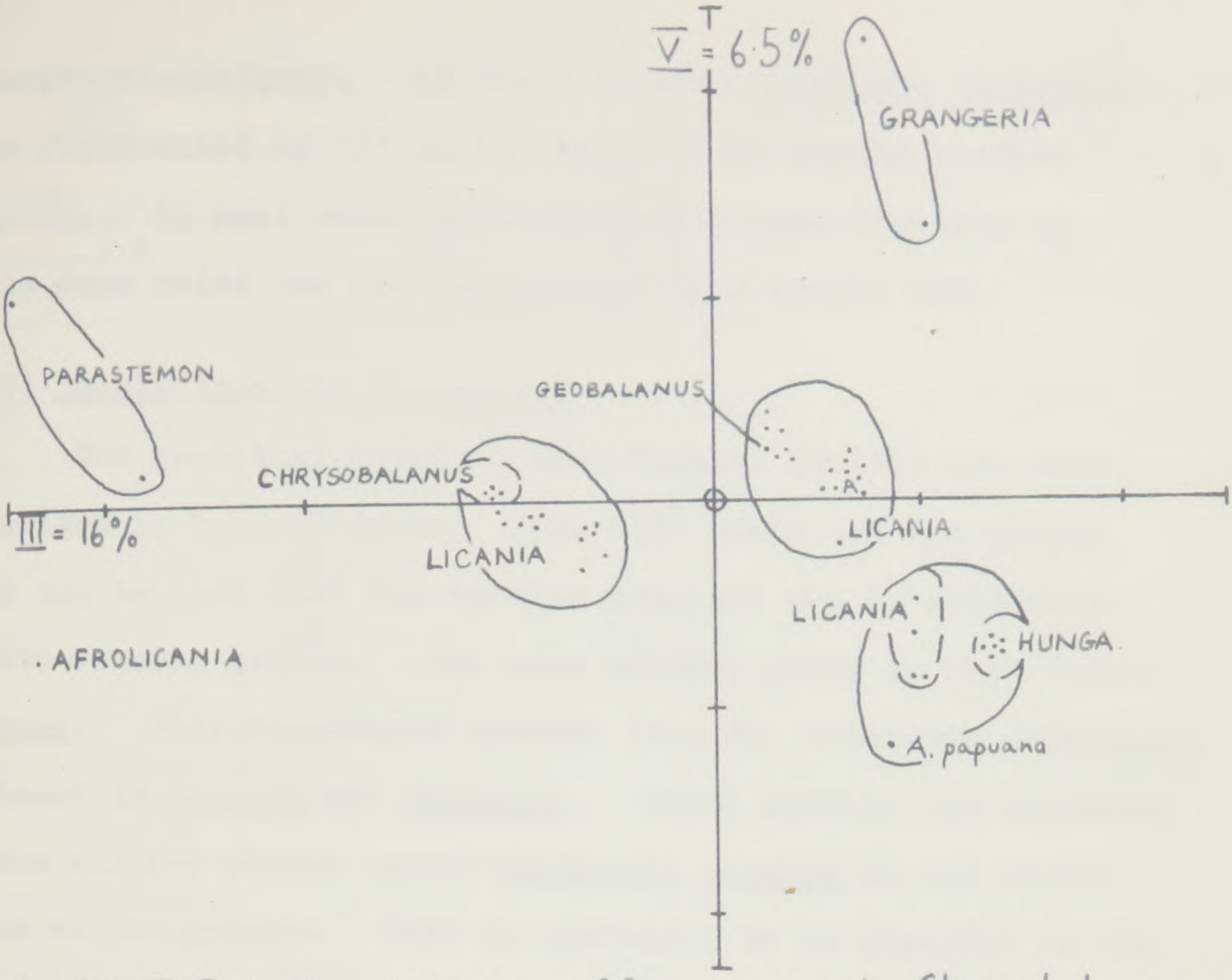


Fig. XXVIII - Projection of third and fifth components - Chrysobalaneae.

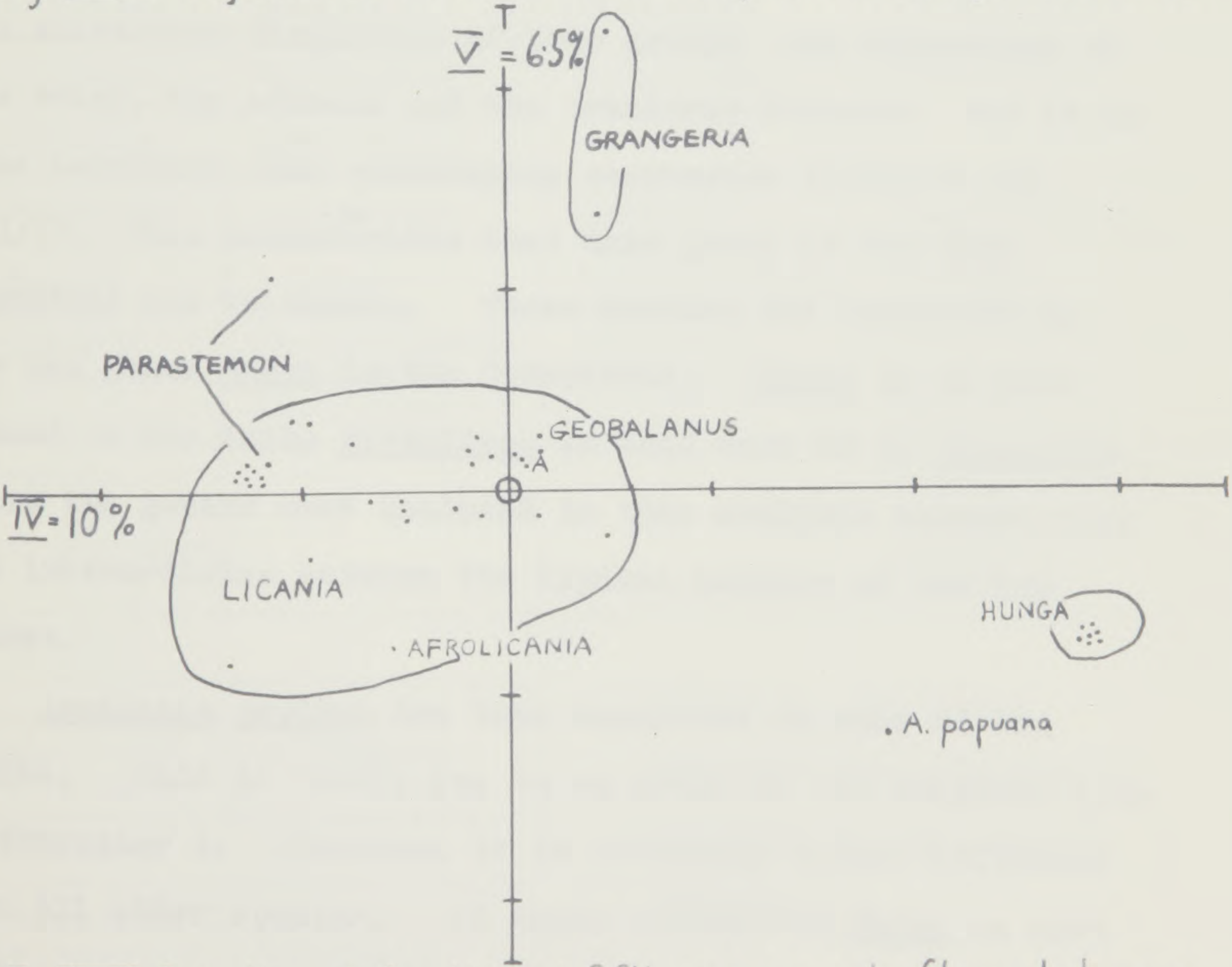


Fig. XXIX - Projection of fourth and fifth components - Chrysobalaneae.

component-analysis. In these figures _Angelesia splendens_ is represented by 'A' as it always falls inside another group. In most cases several species come together on the same point and are represented by a single dot.

(3) Conclusions and Discussion

The groupings obtained from figures XX-XXIX are summarized in table 8 below. From this table and the graphs it can be seen that the species analysed can be subdivided into several genera. The most obvious group is that termed _Hunga_. This represents species from New Caledonia previously placed in _Licania_ and _Parinari_. These species are separated from all the others except _Angelesia papuana_ in all except one of the graphs. This is certainly to be expected in the graphs containing component I, as this component consists of the characters diagnostic of this group; the characters of the ovary, the stamens and the prominent stomata; but it is also separated when considering components II/III-V and III/IV. This demonstrates that this group is the most important one to remove. These species are described as the new genus _Hunga_ in the Conspectus. _Hunga_ is in fact placed in the tribe _Hirtelleae_ in this work as is _Grangeria_. These two genera were included in this analysis because they are intermediates between the typical members of the two tribes.

Angelesia papuana has been separated on many of the graphs. This is partly due to an error in the original data of character 4. However, it is obviously rather different from all other species. It comes nearest to _Hunga_ on most of the graphs, and with _Hunga_ in two. After a careful consideration of all its features I have decided to include it in _Hunga_.

The two species of _Grangeria_ are also clearly separated by this analysis as they stand apart from all other species on six of the graphs, and are placed near to various species

I/II	I/III	I/IV	I/IV
Hunga	Hunga	Hunga	Hunga
Grangeria Parastemon	Grangeria A. papuana	Grangeria	Grangeria
		Parastemon	
Geobalanus	Afrolicania	A. papuana	A. papuana
A. papuana	Parastemon	Licania- Moquilea i + Afrolicania	Afrolicania
Licania Moquilea Afrolicania Angelesia	Licania- Moquilea I	Licania- Moquilea ii Angelesia Geobalanus	Licania- Moquilea a Angelesia Geobalanus
	Licania- Moquilea II Geobalanus Angelesia		Licania- Moquilea b
Chrysobalanus	Chrysobalanus	Chrysobalanus	+ Chrysobalanus

II/III	II/IV	II/V	III/IV
Hunga	Hunga	Hunga	Hunga
Grangeria	Grangeria	Grangeria	A. papuana
Geobalanus	Geobalanus	Geobalanus Parastemon	Parastemon
Parastemon	Parastemon		
Afrolicania	A. papuana	Licania- Moquilea Chrysobalanus Afrolicania Angelesia A. papuana	Chrysobalanus
Licania- Moquilea A Angelesia A. papuana	Licania- Moquilea Chrysobalanus Afrolicania Angelesia		Licania- Moquilea (1)
			Licania- Moquilea (2)
Licania- Moquilea B Chrysobalanus			Licania- Moquilea (3) Grangeria Geobalanus

III/IV	IV/V
Hunga Licania (1) A. papuana	Hunga A. papuana
Parastemon	Parastemon
Afrolicania	Afrolicania Grangeria
Grangeria	Licania- Moquilea Angelesia Geobalanus Chrysobalanus Afrolicania Parastemon
Licania- Moquilea (2) Chrysobalanus	
Licania- Moquilea (3) Geobalanus	

Table 8. Groupings obtained from Component Analysis of the _Chrysobalaneae_

of other genera in others. G. porosa is always at some distance from G. borbonica but its relationship is clearly to the latter species. The same pattern is found in Parastemon where P. versteeghii is always situated some distance from the other two species. The genus Parastemon is also separated on six of the graphs. The other genus that is clearly distinct is Afrolicania, represented by a single species.

The component-analysis indicates that all the groups discussed so far unquestionably belong in the separate genera Hunga (incl. Angelesia papuana), Grangeria, Parastemon Afrolicania. The remaining species needed more careful consideration as they are obviously more closely related, and consist of species from the genera Licania, Moquilea, Chrysobalanus, Geobalanus, and Angelesia.

The species of Chrysobalanus form a distinct group in the figures of components I/IV, III/IV and I/V. In II/V they are at the centre of the Licania-Moquilea cluster and in the remainder they are at the extreme edge. The indication is that they are closely related to, but separable from, Licania-Moquilea. They are separated by component I, the component that accounts for the largest percentage of the total variation.

The two species of Geobalanus are only clearly separated in two of the projections of component II. In projections of all other components they are inside the Licania-Moquilea cluster. It is interesting that Geobalanus is well apart from Chrysobalanus even judged by component II, although they have a similar type of inflorescence. The indication is that these species do not belong to Chrysobalanus as is generally accepted. There are in fact absolutely no good characters to separate Geobalanus from Licania and so it must be merged with that genus rather than with Chrysobalanus.

Angelesia splendens falls within the Licania-Moquilea cluster on the basis of all five components. This is useful supporting evidence for the merging of Angelesia (excl. A. papuana) with Licania.

The species of Licania and Moquilea have a very interesting distribution on the graphs. These species form one diverse group in the projections of components I/II, II/IV, II/V and IV/V. They are divided into three groups by III/IV and III/V, and into two groups in the other four projections. The contents of these groups were studied and it was found that no two projections divided the group in the same way, furthermore, none of the groups separate all species of Licania from those of Moquilea. The fact that these groups are all different indicates that they are of no taxonomic value, but that the genus covers a large range of variation. The only conclusion it is possible to draw from the analysis is that these species belong to one large genus, as was originally suggested by morphological evidence alone.

It would not be possible to subdivide Licania without taking it to excess because of the lack of correlations between characters. This is discussed further in the Conspectus in a note under Licania. Although only thirty-five species of the genus Licania were used for the statistical analysis many more (about 110 in all) have been studied before coming to these conclusions.

The proposed classification of the tribe Chrysobalaneae may be summarized as follows:-

Chrysobalanus, Licania (incl. Moquilea, Angelesia and Geobalanus), Parastemon and Afrolicania.

The taxonomic information resulting from the conclusions drawn in this chapter and the descriptions and definitions of the genera are presented separately in Part II, which is a conspectus of the Chrysobalanaceae. The generic descriptions are based on those characters found to be significant in this chapter.

PART II

A CONSPECTUS OF THE CHRYSOBALANACEAE R.BR.

PART II. A CONSPECTUS OF THE CHRYSOBALANACEAE R.BR.

Pre-Jussieu references to the family

Aublet, Pl. Guiane 1:119,514-22; 2:698 (1775); Schreb., Gen. Pl. ed. 8:153, 160, 245, 336, 458 (1789).

ROSACEAE tribe Prockieae pro parte and tribe Amygdaleae pro parte - Jussieu, Gen. Pl.L 340-42 (1789).

Post-Jussieu references to the family

ROSACEAE - Chrysobalaneae - De Candolle, Prodr. 2:525-29 (1825); Meisner, Pl. Vasc. Gen. 1:101-3 (1836); Benth. in Benth. & Hook., Gen. Pl. 1(2):607-9 (1865); Hook. in Mart., Fl. Bras. 14(2):5-56 (1867); Hallier in Abh. Naturw. Hamburg 18:1-98 (1903).

Rosaceae - Chrysobalanoideae Focke in Engl. & Prantl, Nat. Pflanzenfam. 3(3):53 (1894); Hauman in Bull. Jard. Bot. Brux. 21: 167-98 (1951).

CHRYSOBALANEAE (fam.) R.Br. in Tuckey, Narrat. Exp. Zaire Congo:433 (1818); Bartling, Ord. Nat. Pl.:405-6 (1830); Endl., Gen. Pl.:1251 (1840); Suppl.2:95 (1942). Zuccarini in Mart. & Zucc. in Abh. Maths.-Phys. Bayer. Akad. Wissensch. 1:372-91 (1832), in Flora 1832 beibl.:78-93 (1832); C. Muell in Walp., Ann. Bot. Syst. 4:640-49 (1857).

CHRYSOBALANACEAE - Lindley, Nat. Syst. Bot. ed. 2:158 (1836); Benth. in Hook., Journ. of Bot. 2:210-23 (1840); Fritsch in Verh. Zool.-Bot. Ges. Wien 38:93 (1888); Warming & Mobius, Handb. Syst. Bot. ed. 3: (1911); Wettstein, Handb. Syst. Bot. ed. 4, 1:771 (1933); Gundersen, Fam. Dicot.: 109 (1950).

Flowers actinomorphic to zygomorphic, hermaphrodite or rarely polygamous, markedly perigynous. Receptacle of varied shape and size, short to elongate, often gibbous at the base; lobes 5, imbricate, often unequal, erect or reflexed. Disc always present, forming a lining to the receptacle. Petals (4) 5 sometimes absent, inserted on the margin of the disc, commonly unequal, imbricate, deciduous, rarely distinctly unguiculate. Stamens indefinite, from 2-100 (or to 300 in one species of Couepia), inserted on the margin of the disc, in a complete circle or unilateral, all fertile or some without anthers and often reduced to small staminodes; filaments filiform, free, connate or ligulately connate, very short to elongate, included to far exserted; anthers small, 2-locular, longitudinally dehiscent, glabrous or rarely slightly hairy. Ovary basically of three carpels but usually with only one developed, attached to the base, middle or mouth of the receptacle, sessile or with a short gynophore, pubescent or villous, each carpel unilocular with 2 ovules or bilocular (owing to a false partition) with one ovule in each compartment. Style filiform, basally attached, stigma 3 lobed or truncate. Ovules 2 (in each carpel), erect, with micropyle at the base. Fruit a dry or fleshy drupe of varied size, interior often densely hairy; endocarp extremely varied, thick or thin, fibrous or bony, often with a special mechanism for seedling escape. Seed erect, exalbuminous, testa membranaceous; cotyledons amygdaloid, plano-convex, fleshy, sometimes ruminate. Germination hypogeal or epigeal with opposite or alternate first leaves.

Trees shrubs or suffrutices. Leaves simple entire, alternate, often coriaceous, undersurface glabrous or with an indumentum; petioles often with 2 glands. Stipules 2, small and caducous to large and persistent, of varied shape.

Inflorescence of racemes, panicles or cymes; flowers bracteate and usually 2-bracteolate.

A family containing about 450 species distributed throughout the tropical regions of both hemispheres.

Works of regional importance only have been, for the most part, omitted from the references to the family given above. An additional list of regional floras and other important works of regional significance, including information on members of the Chrysobalanaceae, is given below.

Guill. & Per., Fl. Seneg.: 272-5, t.61, 62 (1833); Benth., Niger Fl.:333-6 (1849); Miq., Fl. Ind. Bat. 1:351-59, 1084 (1853); Grisebach, Fl. Brit. W. Ind.:229-31 (1864); Benth., Fl. Austral.:425-6 (1864); Oliv. Fl. Trop. Afr. 2:364-74 (1871); Baker, J.G., Fl. Maurit. & Seychel.:94-5 (1877); Hooker, Fl. Brit. Ind. 2:307-12 (1879); Hemsley, Biol. Central-amer. 1:365 (1880); Pobéguin, Fl. Guín. Franç.: 308 (1906); Fawcett & Rendle, Fl. Jamaica 3:253-7 (1914); Standley, Trees & shrubs of Mexico: 343-45 (1920); Merrill, Bibl. Enum. Borneo Pl.: 290 (1921); Ridley, Fl. Mal. Penins.: 665-72 (1922); Merrill, Enum. Philipp. Fl. Pl. 2:235-37 (1923); Hutch. & Dalz., Fl. W. Trop. Afr. 1(2):313-21 (1928); Standley & Record, For. & Fl. Brit. Honduras: 147-150 (1936); Macbride, Fl. Peru: 1070-83 (1938); Kleinhoonte in Pulle, Fl. Surinam 2(1):426-56 (1939); Guillaumin, Fl. Nouv. Caled.: 143 (1948); Aubréville, Fl. Forest Soud-Guin.:201-208 (1950); Hauman in Fl. Congo Belge et Ruanda Urundi 3:1-69 (1952); Andrews, Fl. Pl. A.E. Sudan 2:104-106 (1952); Keay, Fl. W. Trop. Afr. ed. 2,1(2):432-33 (1958); Aubréville, Fl. Forest. Côte d'Ivoire: 171-92 (1959); Graham in Fl. Trop. E. Afr. - Rosaceae: 47-58 (1960); White, For. Fl. N. Rhod.:67-70 (1962).

Artificial key to genera

In the following key the characters are briefly expressed. Floral and fruit characters are clearly illustrated elsewhere in this work and the other characters are more fully described with the relevant genera.

I. Ovary inserted at or near the base of the receptacle ...

Tribe 1. Chrysobalaneae

1a Endocarp with distinct longitudinal ridges ....

1. Chrysobalanus

1b Endocarp not distinctly ridged:

2a Endocarp without lateral plates to allow the seedling to escape:

3a Receptacle not flattened, flowers hermaphrodite .... 2. Licania

3b Receptacle flattened-turbinate, flowers androdioecious .... 3. Afrolicania

2b Endocarp dehiscing on germination by means of a pair of large lateral plates.....4. Parastemon

II. Ovary inserted laterally or at the mouth of the receptacle .... Tribe 2. Hirtelleae

1a Endocarp with two basal "plugs" or stoppers:

2a Receptacle turbinate-campanulate, fertile stamens 6-8 .... 11. Parinari

2b Receptacle saccate, fertile stamens 12-17 ....

13. Neocarya

1b Endocarp without two basal "plugs" but sometimes dehiscing at germination by means of two large lateral plates:

3a Endocarp with two lateral plates:

4a Ovary inserted at mouth of receptacle, carpels bilocular, inflorescence of corymbose panicles ....

16. Maranthes

4b Ovary inserted laterally, carpels unilocular, inflorescence of racemes..5..Grangeria

3b Endocarp without lateral plates:

5a Endocarp opening by longitudinal lines of weakness which allow the seedling to escape:

6a Stamens far exerted, ovary unilocular ..... 8. Hirtella

6b Stamens included, ovary bilocular ...

6. Hunga

5b Endocarp without lines of weakness:

7a Stamens ligulately connate:

8a Two anterior petals unguiculate, enclosing staminal ligule in the bud, epicarp densely verrucose .... 17. Kostermansia

8b Two anterior petals not unguiculate, epicarp not densely verrucose ....

10. Acioa

7b Stamens not ligulately connate:

9a Receptacle oblique, ventricose:

10a Leaf undersurface with stomatal cavities, endocarp hard, beaked, with a smooth surface, epicarp weakly verrucose .. 12. Bafodeya

10b Leaf undersurface without stomatal cavities, endocarp with a rough surface or soft, epicarp not verrucose ...... 9. Magnistipula

9b Receptacle campanulate to cylindrical, not oblique:

11a Endocarp beaked, with a smooth surface, stamens 6-8 ..... 14. Duckea

11b Endocarp not beaked, with a rough surface, stamens 10-300:

12a Endocarp clearly differentiated from the mesocarp, with a granular surface, fragile, crumbling on germination, carpels unilocular ....

7. Couepia

12b Endocarp not easily detached from mesocarp, hard, not crumbling but breaking up irregularly on germination, carpels bilocular .....

15. Cyclandrophora.

1. CHRYSOBALANUS

Linn., Gen. Pl., ed. 1:365 (1737); Sp. Pl.:514 (1753) & Gen. Pl., ed. 5:229 (1854).

Small trees or shrubs with hermaphrodite flowers. Leaf-undersurface glabrous or with a few stiff appressed hairs; stomata visible at X 25 magnification in all species. Lamina with two glands (sometimes obscure) at base. Bracts small, eglandular. Inflorescence of terminal or axillary cymules; Receptacle cupuliform, interior and exterior puberulous; calyx-lobes 5, acute. Petals 5, longer than the calyx-lobes. Stamens 12-26 some sometimes shorter than the others forming a complete or nearly complete circle, filaments hairy, often united at the base for a short part of their length, about twice as long as the calyx-lobes. Ovary inserted at base of the receptacle, covered with a dense mass of hairs; carpel unilocular; ovules 2. Style pubescent; stigma capitate. Fruit a small fleshy drupe, epicarp smooth, black, ridged; endocarp thin, hard, interior glabrous, exterior smooth, with 4-8 prominent longitudinal ridges which correspond to the lines of fracture that allow the seedlings to escape. (Plate XXX).

Distribution: tropical America and Africa, mainly in coastal regions.

Type species: C. icaco L.

Notes - (1) Chrysobalanus is so closely related to Licania that one would be justified in regarding them as congeneric. But if this is done the 135 or so species of Licania would have to be transferred to Chrysobalanus which has, at most, only 5 species. However, all serious workers on the group have previously kept them apart, and the overwhelming majority of species of Licania can be distinguished from Chrysobalanus on the basis of a small number of well correlated characters. The only worker who has united Licania with Chrysobalanus is O. Kuntze (Rev. Gen. 3 (2):76 (1891).

In Chrysobalanus the inflorescence is a very short raceme of cymules; the filaments are exserted and hairy and the endocarp is always ridged.

In the great majority of species of Licania the inflorescence is a branched raceme of characteristic appearance, the filaments are either exserted and glabrous or, if hairy, are then included; the endocarp is never ridged. Two anomalous species of Chrysobalanus, C. oblongifolius Michx. and C. incanus Raf., which have been placed in Geobalanus by Small, differ from the rest of the genus in having glabrous filaments and a smooth endocarp. They are best placed in Licania although differing from typical Licania in having a cymose inflorescence. Atypical inflorescences occur in Licania in about four species (e.g. L. emarginata Spruce) which have sparsely branched panicles of cymules and in Licania (Angelesia) splendens (Korth.) Prance in which the inflorescence is either a panicle of cymules or cymose throughout. As these species are typical for Licania in other respects, it seems best to place most reliance on the fruit character as a generic criterion.

The statistical work shows that Chrysobalanus is only just separable from Licania.

(2) Except for C. atacorensis, which is widespread in the Congo Basin, the genus has a mainly coastal distribution,

and is abundant and widespread along the coasts of West Africa and eastern South America and the West Indies. A few specimens of Chrysobalanus have been collected outside this range. Archer 154 (fl., fr., K) from the Seychelles is C. ellipticus. Osborne Day 58 (fl., BM), Meebold 21388 (fl., CM) and Greenwood 1027A (fl., K) from Fiji are C. icaco. The Seychelles plant is naturalized (Jeffery, verbal communication) and the Fijian probably so. Chrysobalanus does not occur naturally in the Malaysian region, but is cultivated in the Botanical Garden at Kuala Lumpur (Hamid S.F.2343, fl., fr., K). The Malayan plant named Chrysobalanus racemosus by Roxburgh belongs to Cyclandrophora and an examination of the type at the British Museum (Roxburgh 2651) shows that it is Cyclandrophora glaberrima Hasskl., and bears no resemblance to the genus Chrysobalanus.

(3) For the time being I have kept C. orbicularis and C. ellipticus separate from C. icaco. The species of this genus are extremely variable as regards leaf shape and size, and fruit size. Many authors have considered these species as belonging to one very variable and polymorphic species, C. icaco. Hauman (1951) gives reasons for regarding C. orbicularis as a separate species, and his paper indicates that there are certain differences between the American and African elements, but judging by the material examined from both continents I very much doubt whether these merit the specific recognition of C. orbicularis or C. ellipticus. In South America C. icaco may have elliptical, slightly acuminate leaves especially in some material from British Guiana. J.D. Hooker regarded this variant as being the same as the African species C. ellipticus, which he treated as a variety of C. icaco. Further investigation, both in

the field and herbarium, is required to determine whether _C. orbicularis_, _C. ellipticus_ and _C. pellocarpus_ should be maintained as species or reduced to subspecific or varietal rank or merged completely. The evidence already accumulated indicates that it would be difficult to maintain the African material of _C. ellipticus_ and _C. orbicularis_ as species separate from _C. icaco_, but that they merit recognition at a lower level. It is hoped at a future date to critically revise _Chrysobalanus_. Until then it would be unwise to make any changes at specific level.

1. _Chrysobalanus icaco_ L., Sp. Pl.: 513 (1753).

Type: _Linn. Herb._ 641, W. Indies, fl. (LINN).

C. purpurea Mill., Gard. Dict., ed. 8, 2 (1768).

C. pellocarpus G.F.W. Mey., Prim. Fl. Esseq.: 193 (1818) (= _C. icaco_ L. var. _pellocarpus_ (G.F.W. Mey.) Hook. f. in Mart., Fl. Bras. 14(2):7 (1867).

C. guianensis Kl. in Schomb., Faun. et Fl. Brit. Guiana: 1024 (1848) nom. nud. (= _C. icaco_ L. var. _ellipticus_ (Soland.) Hook. f., loc. cit., pro parte quoad cit. Amer. tantum).

C. savannarum Britton in Bull. Torr. Bot. Cl. 48:331 (1922) (= _C. icaco_ L. var. _pellocarpus_ (G.F.W. Mey.) Hook. f., loc. cit.)

Distribution: Florida, Central and South America and West Indies.

2. _Chrysobalanus atacorensis_ A. Chev. in Bull. Soc. Bot. France 58, Mém.: 169 (1912).

Type: _Chevalier_ 24175, Dahomey, fl. (K:P).

C. chariensis A. Chev., Étud. Fl. Afr. Centr. Franç. 1:117 (1913) nom. nud.

Distribution: Dahomey, Nigeria, Cameroun, Cameroons, Congo, Northern Rhodesia and Angola.

This species appears to be quite distinct from C. icaco. It is the only species that extends far inland in central Africa.

3. Chrysobalanus cuspidatus [Griseb., Fl. Brit. W. Ind.: 711 (1864), nom. nud.] ex Duss, Fl. Ant. franç.: 258 (1897); Urban, Symb. Antill. 5:351 (1907).

Type: Imray s.n., Dominica, fr. (K).

Distribution: West Indies.

4. Chrysobalanus ellipticus Soland. ex Sabine in Trans. Hort. Soc. 5:423 (1824).

Type: Don 897, Sierra Leone, fl. (K).

Distribution: Portuguese Guinea and Sierra Leone to Angola.

5. Chrysobalanus orbicularis Schum. & Thonn., Beskr. Guin. Pl.: 232 (1827); Hauman in Bull. Jard. Bot. Brux. 21:172-3 (1951).

Type specimens: Vogel 34, Liberia, fl. (K); Sieber 31, Liberia, fl. (K).

Distribution: West Africa from Guinea to Angola.

Species dubiae

1. Chrysobalanus luteus Sabine in Trans. Hort. Soc. 5:453 (1824).

This species is obscure since only the fruit was described from information supplied by a correspondent. Brignoli (1862) suggests that the fruit in question belonged to the Icacinaceae or Olacaceae.

2. Chrysobalanus stuhlmannii Engl., Pflanzenw. Ost. Afr. C: 191 (1895).

The holotype (Stuhlmann 430) was destroyed in Berlin during the last war. Engler himself in the type description questions whether this species belongs to Chrysobalanus as does Graham (Fl. Trop. E. Afr. - Rosaceae: 48 (1960)).

Species exclusae

1. C. americanus (L.) Morales in An. Acad. Cienc. Med. Fisic & Nat. Habana 47:391 (1887) = Hirtella americana L.

2. C. incanus Rafin., New Fl. Am. 3:26 (1836) = Licania (Geobalanus) sp.

3. C. humilis (Cham. & Schlecht.) Kuntze, Rev. Gen. 3(2):76 (1891) = Licania humilis Cham. & Schlecht.

4. C. incanus (Aubl.) Gomez de la Maza, Fl. Cuba: 39 (1887) nom. illegit. = Licania incana Aubl.

5. C. macrophyllus Schott. in Spreng., Syst. 4, Appendix: 407 = Couepia schottii Fritsch.

6. C. montanus (Aubl.) Gomez de la Maza, loc. cit. = Parinari montana Aubl.

7. C. oblongifolius Michx., Fl. Bot. Am. 1:283 (1803) = Licania (Geobalanus) sp.

8. C. ovalifolius Schott. in Spreng., Syst. 4, Appendix: 406 (1828) = Couepia ovalifolius (Schott.) Benth.

9. C. pallidus (Small) L.B. Sm. in Rhodora 48:136 (1946) = Licania (Geobalanus) sp.

10. C. prunifolius Rafin., Loc. cit. = Licania (Geobalanus) sp.

11. C. racemosus Roxb., [Hort. Beng.: 92 (1813) nom. nud.] Fl. Ind. 2:506 (1832) = Cyclandrophora glaberrima Hasskl. (see Note 2 above).

12. C. retusus Rafin., loc. cit. = Licania (Geobalanus) sp.

13. _C._ _rugosus_ (Thuill. ex Pers.) Gomez de la Maza, Dicc. Bot. Nom. Vulg. Cub. Puerto-Riquenas: 101 (1889) = _Hirtella_ _rugosa_ Thuill. ex Pers.

14. _C._ _sublanatus_ Kuntze, Rev. Gen. 3(2):76 (1891) = _Licania_ sp.

15. _C._ _subundulatus_ Brign. in Mem. Soc. Ital. Mod. Ser. 2 (1):71 (1862) = ? _Couepia_ sp.

I have not seen material of this species, but from the description it obviously does not belong in _Chrysobalanus_, and judging by the author's comparison with _C._ _ovalifolius_ Schott and _C._ _macrophyllus_ Schott it probably belongs with them to _Couepia_. It is excluded from _Chrysobalanus_ because of its terminal panicles, glabrous stamens, and tomentose leaf-undersurface. There is nothing in the description to exclude it from _Couepia_.

16. _C._ _triandra_ (Sw.) Morales tom. cit.: 390 (1887) = _Hirtella_ _triandra_ Sw.

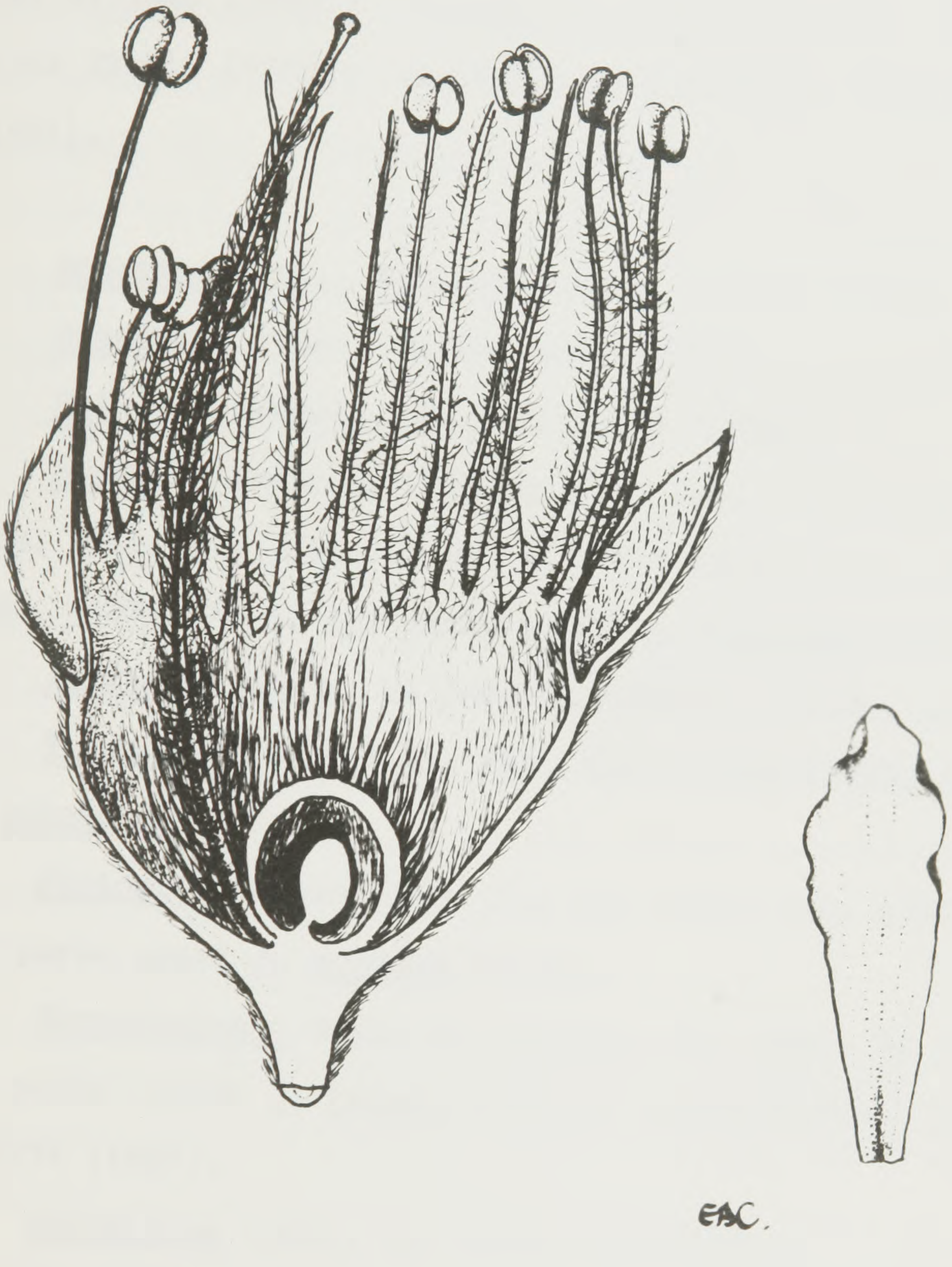


Plate XXX.- CHRYSOBALANUS ICACO L.
flower and petal (x20).

2. LICANIA

Aubl. Pl. Guian. 1:119, t.45 (1775); G. Don, Gen. Syst. 2:479 (1832), "Lincania"; Benth. in Hook. Journ. of Bot. 2:212-215, 218-222 (1840); Hook. f. in Mart., Fl. Bras. 14(2):8-26 (1867); Fritsch in Ann. natur-hist. Hofmus. Wien 4:33-60 (1889); Benoist in Bull. Mus. Nat. Hist. Nat. Paris 25:512 (1919); Sandwith in Kew Bull. 1931:369-74 (1931).

Moquilea Aubl., tom. cit.: 521, t.208 (1775)

Dahuronia Scop., Introd.:217 (1777).

Hedycrea Schreb., Gen. Pl.: 160 (1789).

Hirtella sensu E. Mey. in Nov. Act. Phys. Med. Acad. Caes. Leop. Nat. Cur. 21:803 (1825); sensu Roem. & Schult., Syst. 5:274 (1819) pro parte quoad H. octandra tantum.

Angelesia Korth. in Nederl. Kruidk. Archiv. 3:384 (1854).

Trichocarya Miq., Fl. Ind. Bot. 1:358 (1855) quoad T. splendens tantum.

Parinarium sensu Hook. f., Fl. Brit. Ind. 2:310 (1878) pro parte quoad P. nitidum tantum.

Chrysobalanus Gomez de la Maza, Fl. Cuba: 39 (1887) pro parte quoad C. incana tantum; sensu Kuntze, Rev. Gen. 3(2):76 (1891).

Geobalanus Small, Fl. Miami: 80 (1913).

Coccomelia Ridl. in Journ. As. Soc. Str. Branch 72: 183 (1920).

Large or small trees or shrubs, rarely suffrutices, with hermaphrodite flowers. Leaf-undersurface glabrous or with lanate or rarely strigose tomentum or with stomatal cavities filled with hairs; Petioles eglandular or with two glands. Inflorescence nearly always a sparsely branched panicle, very rarely a panicle of cymules or cymose throughout. Bracts and bracteoles of varying size, usually eglandular. Receptacle 2-7 mm. long, of varied shape, subglobose, campanulate or urceolate, interior hairy or glabrous; calyx-lobes 5, acute. Petals 5 or absent, short. Stamens 3-35, most often forming a complete circle round the mouth of the receptacle, less often the circle is incomplete and a few staminodes occur; filaments free to their base, extremely short and therefore included or long, filiform and exserted, glabrous or rarely hairy (only in some species with very short filaments). Ovary inserted at, or near, the base of the receptacle, pilose, carpel unilocular, ovules 2. Style filiform, of varied length, stigma truncate, not markedly three lobed. Fruit a small to large dry or fleshy drupe, exterior often densely tomentose, or smooth and glabrous, or verrucose, interior hairy or glabrous; endocarp thick and hard or fibrous, dehiscing either by no special mechanism, or by several longitudinal lines; seed large, erect, filling the loculus.

Approximately 135 species widely distributed in Tropical South and Central America and the West Indies with two species in Florida and Georgia; there is also a single widely distributed species in the Malaysian region. (Plates XXVII, XXXI, XXXII, XXXIII, XXXIV, XXXV).

Type species: Licania incana Aubl.

Type: Aublet s.n., French Guiana, st. (BM).

Notes - (1) Bentham (1840) and most later authors, for example Hooker (1867) and Fritsch (1889) wrongly interpreted L. incana Aubl. Licania incana sensu Benth. is conspecific with L. kunthiana Hook. f., and L. incana sensu Hook. f. is conspecific with L. leptostachya Benth. Sandwith (1931) has pointed out that L. crassifolia Benth. is conspecific with L. incana Aubl. A comparison of the types of these species at the British Museum unquestionably shows that Sandwith's conclusion is correct.

(2) The present study confirms the widely accepted opinion that Licania and Moquilea should be united. Fritsch (1889) following Grisebach (1857), Baillon (1869) and Eichler (1878) in his conspectus of the genus Licania gave convincing reasons for uniting them. The present study confirms that there is a complete gradation in filament length and number of stamens.

(3) As appears from the generic diagnosis given above, many morphological features within Licania are extremely variable. The following features, that are comparatively constant in other genera of the Chrysobalanaceae vary to quite a large extent in Licania:-

1. The type of leaf undersurface. For example some species have stomatal cavities similar to those found in Parinari, the only other genus of the family to possess this distinctive feature. Other species have a lanate or strigose tomentum or are glabrous.

2. The presence or absence of 2 glands on the petiole.

3. The type of inflorescence.

4. The flower size.

5. The presence or absence of petals.

6. The number of stamens.

7. The length of the staminal filaments.

8. The structure of the fruit. The range of fruit structure can be seen in Plate XXVIII. Although the fruit is extremely variable it does not vary to the extent of the fruit of the genus Parinari as previously defined. The differences are mainly in the type of exterior and the thickness of the various layers of the fruit wall. There are no special mechanisms of endocarp-dehiscence comparable with that of Parinari. There is certainly no clear-cut distinction between the fruit of Licania and Moquilea contrary to the suggestion of Miers (1879).

These eight features vary independently and do not provide a basis for subdividing Licania (incl. Moquilea) at the generic level.

Bentham (loc. cit.) divided Licania into five sections but Fritsch (loc. cit.) gives reasons for not adopting them. In the component analysis investigation (figs. XX-XXIX) Licania is frequently split into two or three groups but each time the groups have different compositions. This demonstrates that Licania is heterogeneous but that the characters used in the analysis vary independently. Whether it would be possible to base sections on other characters remains to be seen.

(4) Some species of Licania are easily recognized, but others belong to complexes of closely related species which have not yet been critically examined. I hope to revise Licania at a later date. Preliminary studies indicate that many nomenclatural as well as taxonomic changes need to be made. In view of the unsatisfactory state of knowledge, and the amount of work that would be involved in such a revision, it was not thought advisable to list the species here.

(5) Huber in Bol. Mus. Pará. 5:368 (1909) described a new species, L. parinarioides, for which he created a subgenus Parinariopsis. L. parinarioides differs from the rest of Licania chiefly in having large bracteoles which enclose the young flowers in groups and a slightly eccentric insertion of the ovary. There seems to be little merit in placing slightly aberrant species in subgenera on their own.

(6) The position of the genus Angelesia. The main reasons for the inclusion of this genus in Licania are given in Chapter 10 where it is shown that it is impossible to distinguish it from such a large and diverse genus as Licania. This has in fact been suggested previously but has not been generally accepted. Blume (1855) transferred Angelesia splendens, the type species, to Licania but made an illegitimate name change to Licania angelesia. Hallier (1903) suggested that Licania, Moquilea and Angelesia should be united, but did not make the necessary new combinations. Angelesia splendens is transferred below.

Licania splendens (Korth.) Prance, comb. nov.

Type: Korthals, South Borneo (not seen)

Angelesia splendens Korth. in Nederl. Kruidk. Arch. 3:384 (1854); Boerlage Koorders, Ic. Bogor 4:59-60, t.96 (1901).

Licania angelesia Blume, Mélanges Bot. (1855); Hasskl. in Flora 41:256 (1858) nom illegit.

Trichocarya splendens (Korth.) Miq., Fl. Ind. Bat. 1:358 (1855).

Chrysobalanus splendens (Korth.) Miq. loc. cit. in syn.

Parinarium nitidum Hook. f., Fl. Brit. Ind. 2:310 (1878).

Coccomelia nitida (Hook. f.) Ridl. in Journ. As. Soc. Str. Branch 72:183 (1920).

Parinari philippinensis Elmer, Leafl. Philipp. Bot. 10:3809 (1939) nom. nud.

Distribution: Malay Peninsula, Borneo, Sarawak, Indonesia, Philippines.

In an important paper Merrill (Philipp. Journ. Sci. 10:307 (1915)) gives good reasons for regarding Trichocarya and Parinarium nitidum as synonyms of Angelesia. The other species of Angelesia are accounted for as follows.

1. Angelesia racemosa (Korth.) Kuntze, Rev. Gen.: 215 (1891) (Diemenia racemosa Korth. in Nederl. Kruidk. Arch, 3:388 (1855).) = Parastemon urophyllus (A.DC.) A.DC.

2. Angelesia papuana Bak. f. in Journ. of Bot. 61, Suppl.:13 (1923). = Hunga papuana (Bak. f.) Prance.

(7) Reasons for transferring Geobalanus to Licania are given under the genus Chrysobalanus. The nomenclature of the species is complicated and it has not yet been possible to decide which would be the legitimate specific epithet under Licania. Until further type-specimens have been seen the new combination will not be made.

Although the author is not yet in a position to revise Licania at the species level, he thinks that the following list of excluded species is complete, or almost so.

Species exclusae

Moquilea aubletiana Blume, Mus. Bot. Lugd. Bat. 2:92 (1852) = Acioa guianensis Aubl.

Licania aubletiana (Blume) Lemée, Fl. Guyane Franç. 2:23 (1952) = *Acioa guianensis* Aubl.

Licania balansae Guillaumin in Bull, Soc. Bot. France 67:346 (1921) = *Hunga gerontogea* (Schlecht.) Prance.

Moquilea bracteosa (Benth.) Walp., Rep. 2 (1843) = *Couepia bracteosa* Benth.

Moquilea canomensis Mart., Nov. Gen. et Sp. 2:80.t.166 (1827) = *Couepia canomensis* (Mart.) Benth.

Moquilea chrysocalyx Poepp. & Endl., Nov. Gen. et Sp. 3:75.t.286 (1845) = *Couepia chrysocalyx* (Poepp. & Endl.) Benth. ex Hook. f.

Moquilea comosa (Benth.) Walp., Rep. 2:6 (1843) = *Couepia bracteosa* Benth.

Moquilea couepia Steud., Nom. ed. 2, 2:159 (1849) = *Couepia guianensis* Aubl.

Licania celativenia Standl. in Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser., 17:254 (1937) = *Vantanea cupularis* Huber.

Licania diamenia Blume, Mélanges Bot. (1855); Hasskl. in Flora 41:256 (1858) nom illegit. = *Parastemon urophyllus* (A.DC.) A.DC.

Moquilea eliti Walp., Rep. 2:6 (1843) (= *M. uiti*) = *Couepia uiti* (Mart. & Zucc.) Benth.

Licania gerontogaea Schlecht. in Engl. Jahrb. 40. Beibl. 92:25 (1908) = *Hunga gerontogaea* (Schlecht.) Prance.

Moquilea glandulosa (Miq.) Walp., Ann. 2:463 (1852) = *Couepia glandulosa* Miq.

Moquilea grandiflora Mart. & Zucc. in Abhandl. Akad. Münch. 1:388 (1832) = *Couepia grandiflora* (Mart. & Zucc.) Benth.

Moquilea inaequalis Poepp. ex Fritsch in Annal. Naturh. Hofmus. Wien 5:12 (1890) (given solely as a synonym from the Poeppig herbarium) = *Couepia amazonica* Fritsch.

Moquilea kuntheana Mart. & Zucc. in Abhandl. Akad. Münch. 1:390 (1832) = *Couepia kuntheana* (Mart. & Zucc.) Benth.

Licania lifouana Däniker in Vierteljahrschr. Nat. Ges. Zürich 76:166 (1931) = *Hunga lifouana* (Däniker) Prance.

Moquilea multiflora (Benth.) Walp., Rep. 2:7 (1843) = *Couepia multiflora* Benth.

Moquilea paraënsis Mart. & Zucc. in Abh. Akad. Münch. 1:320 (1832) = *Couepia paraënsis* (Mart. & Zucc.) Benth.

Moquilea parilla (DC.) Steud., Nom. ed. 2, 2:159. (1841) = *Couepia parillo* DC.

Licania rhamnoides Guillaum. in Bull. Soc. Bot. France 67:346 (1921) = *Hunga rhamnoides* (Guillaum.) Prance.

Moquilea rufa Barb. Rodr., Hort. Flumin 1893:165 (1895), parte = Couepia rufa (Barb.) Ducke parte = Parinari montana (Aubl.)

Moquilea steudeliana (Miq.) Walp., Ann. 2:463 (1852) = Couepia steudeliana Miq. = C. cognata (Steud.) Fritsch.

Moquilea uiti Mart. & Zucc. in Abh. Akad. Münch. 1:390 (1832) = Couepia uiti (Mart. & Zucc.) Benth.

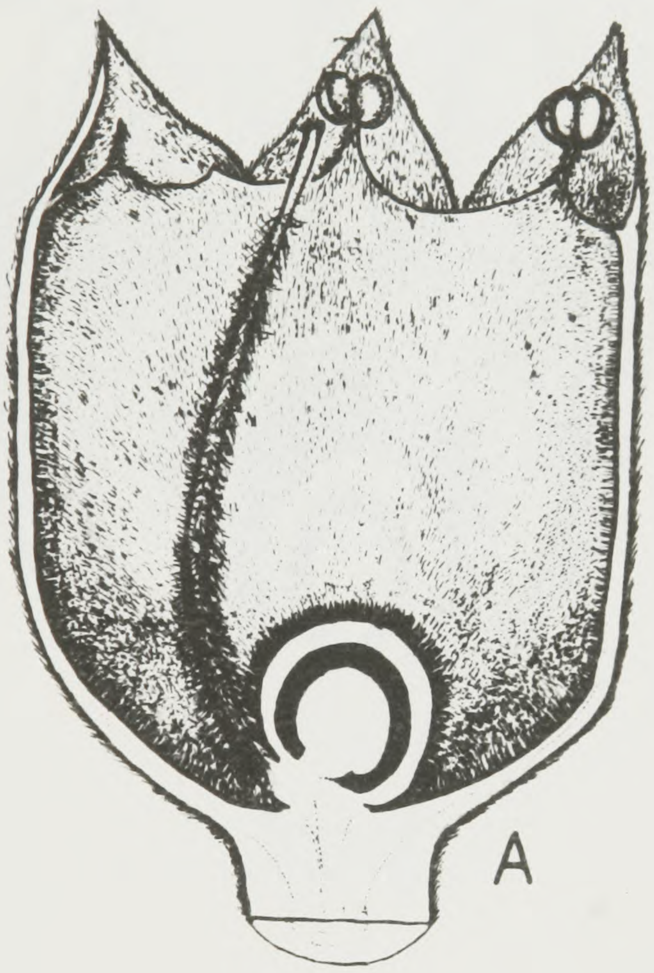


Plate XXXI.- LICANIA KUTHIANA Hook.f.
flower (x40).

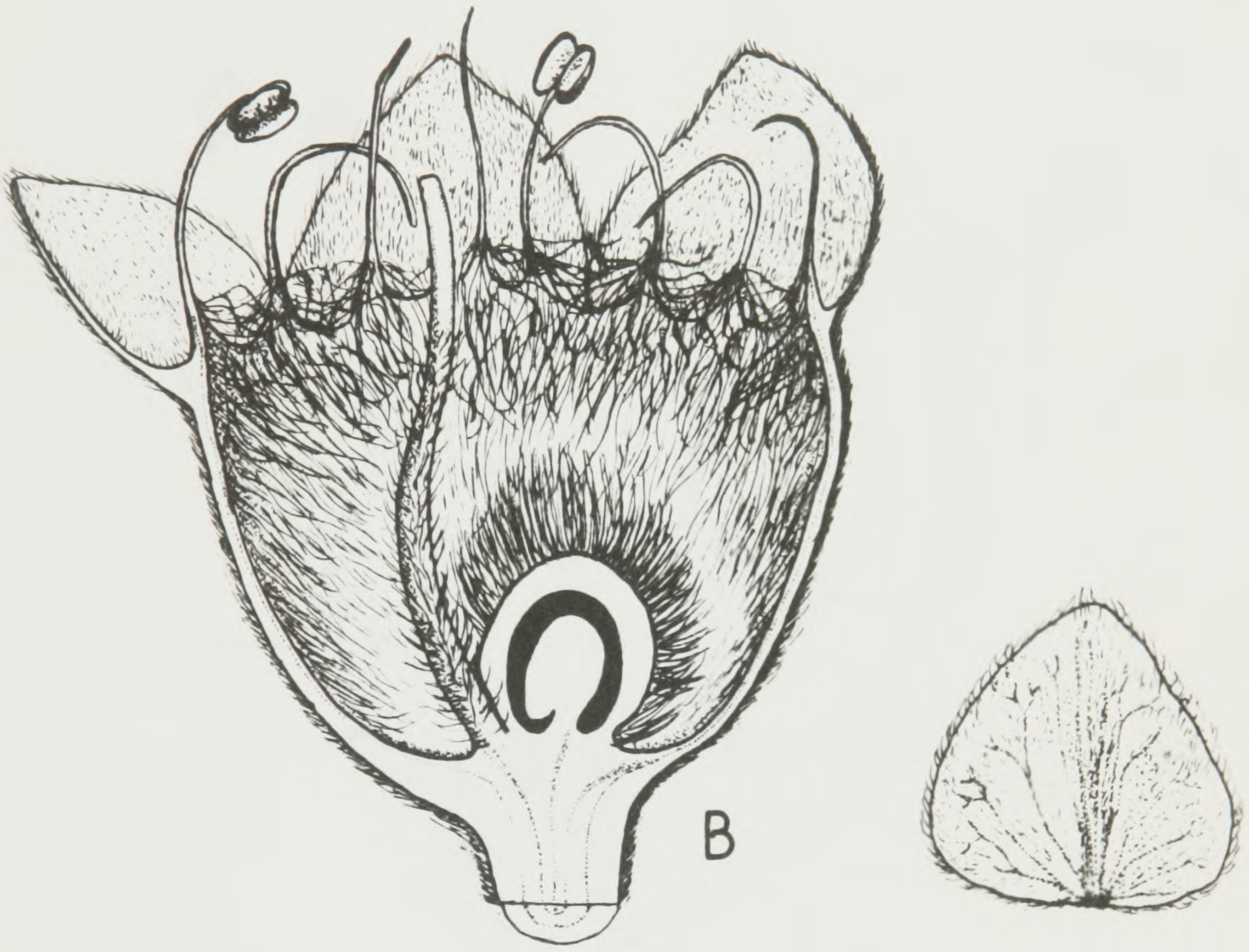


Plate XXXII.- LICANIA PLATYPUS (Hemsl.)Fritsch flower and petal (x20).

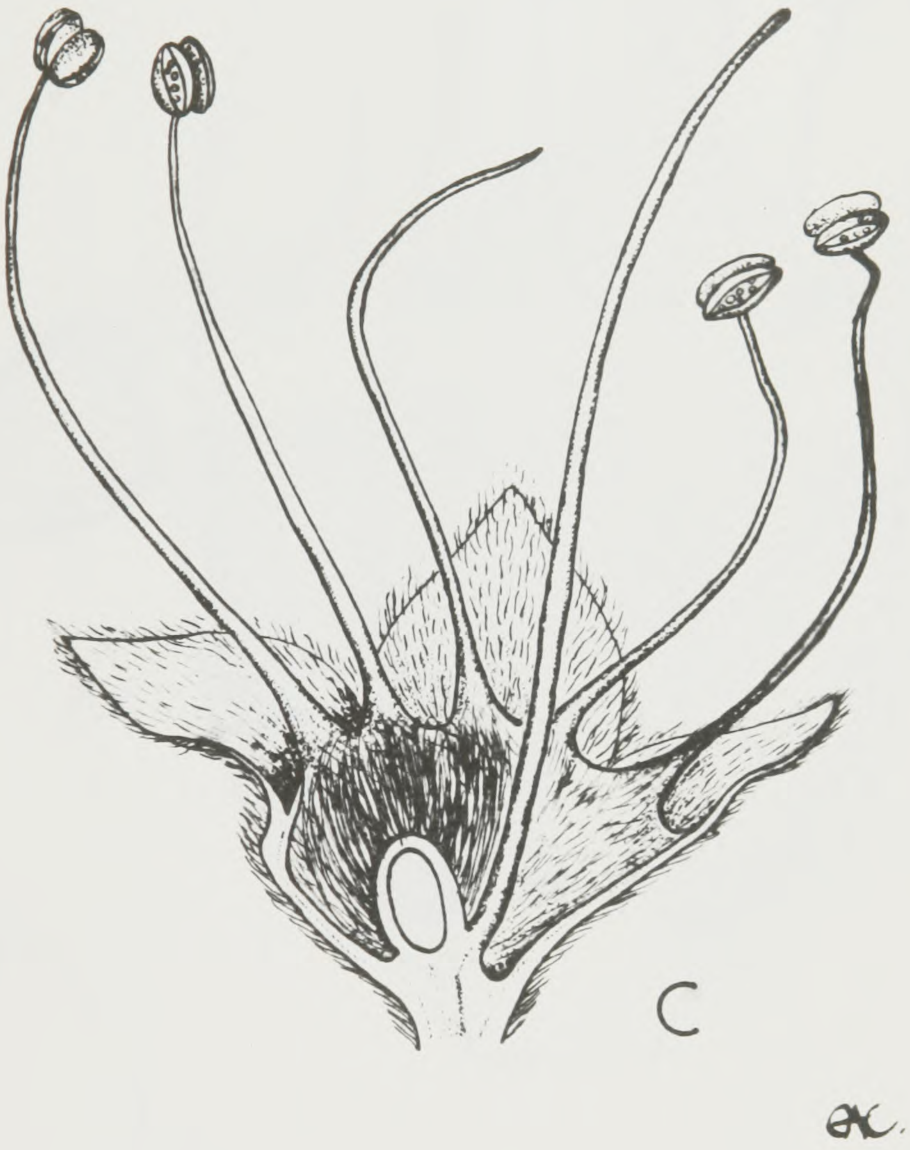


Plate XXXIII.- LICANIA SCLEROPHYLLA (Mart.ex Hook.f.)Fritsch flower (x20).

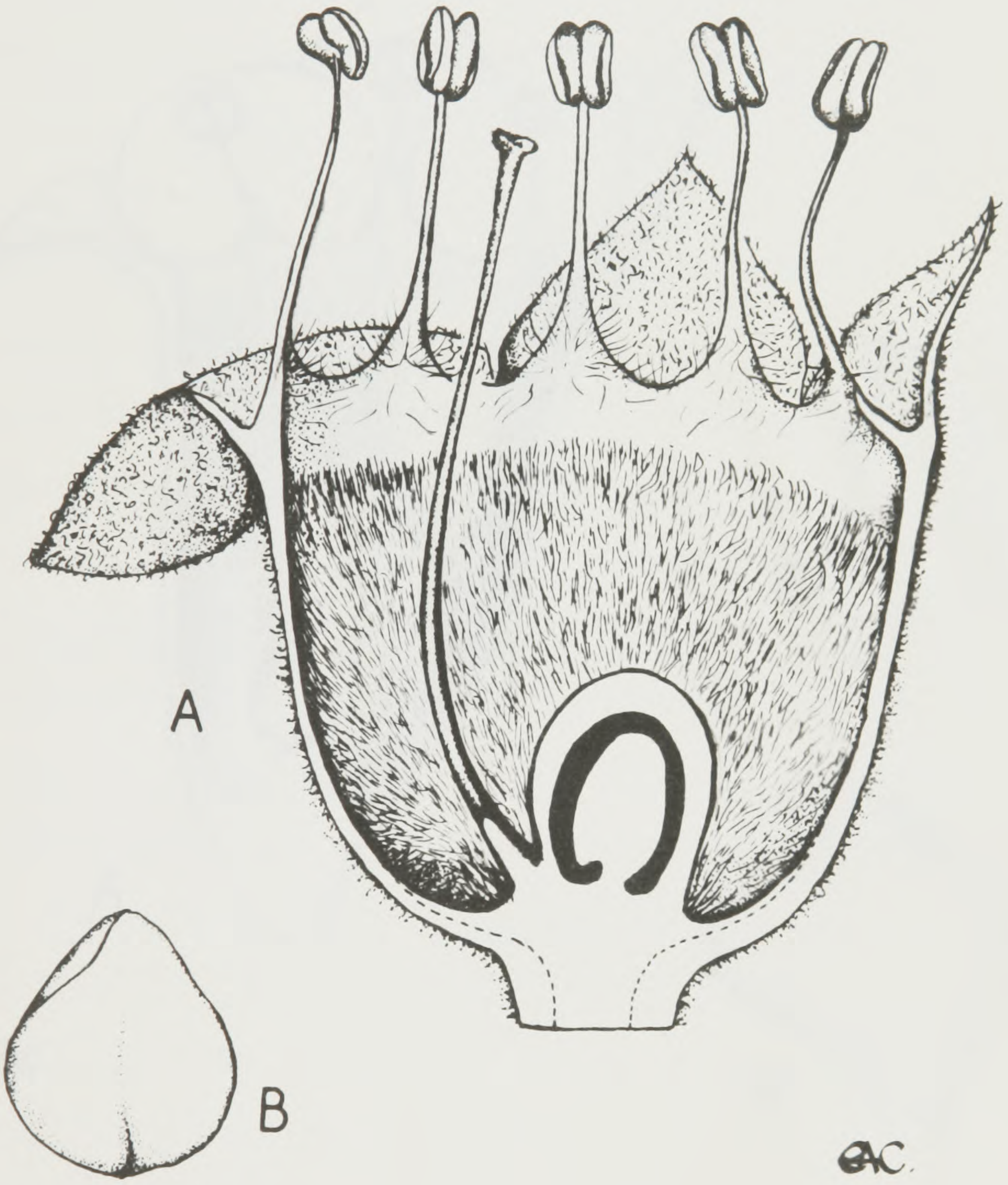


Plate XXXIV.- LICANIA (GEOBALANUS) Sp.
A,flower (x30); B,petal (x30).

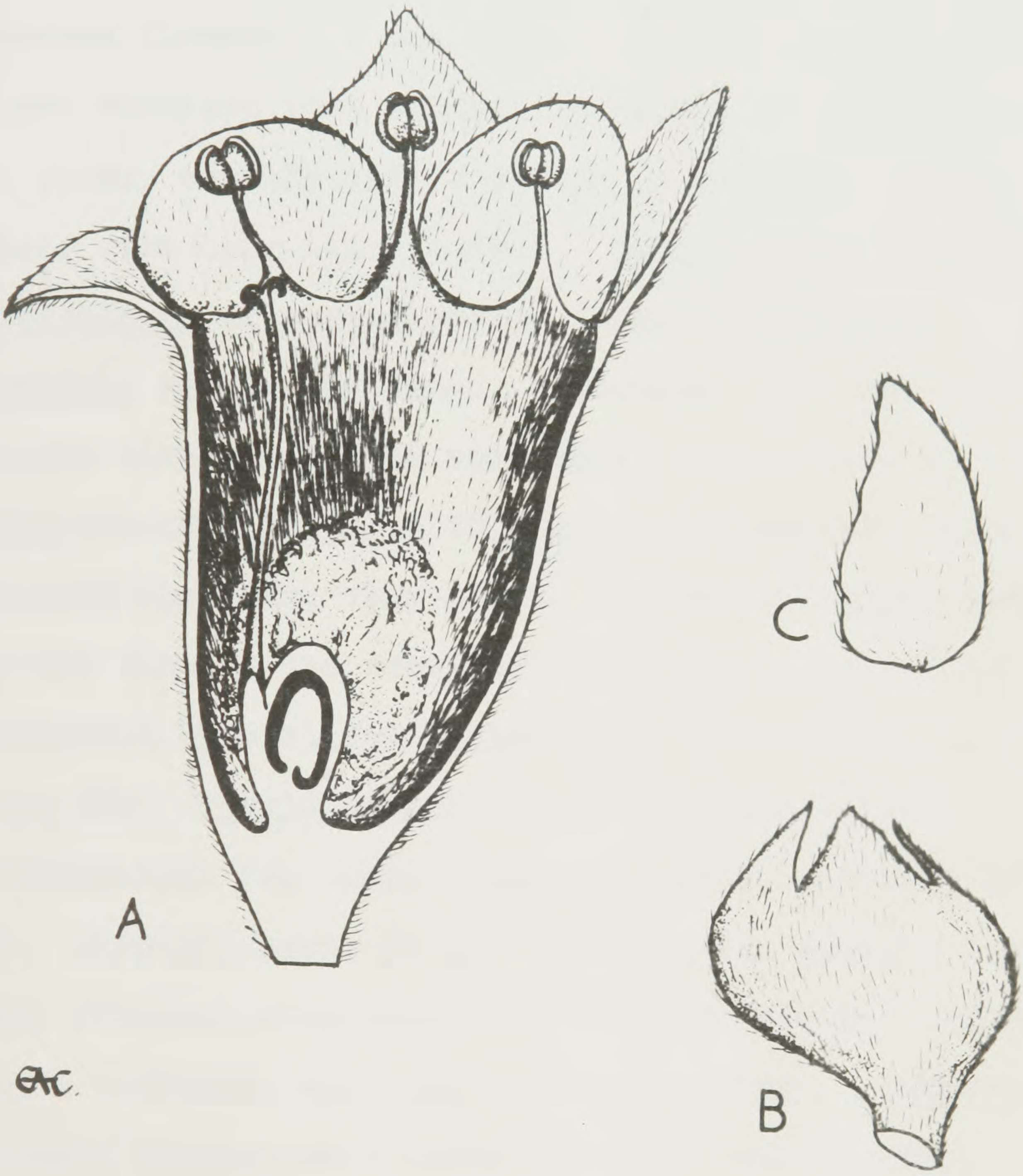


Plate XXXV.- LICANIA SPLENDENS (Korth.)Prance
A,flower (x50); B,flower-bud (x20); C,petal (x20).

3. AFROLICANIA

Mildbraed in Notizbl. Bot. Gart. Berlin, 7:484 (1921); Dalziel, Useful Pl. W. Trop. Afr.: 167 (1937).

Small to medium-sized trees with polygamous andro-dioecious flowers ± 2 mm. long. Leaves usually glabrous on both surfaces when mature, tomentose on undersurface when young, usually with 2 glands on petiole; young petiole with long silky hairs. Bracts small, membranaceous. Inflorescence of many-flowered terminal panicles. Receptacle small, flattened, turbinate, interior pubescent, exterior with short grey tomentum; calyx-lobes 5, acute. Petals absent. Stamens 20, forming a complete circle; filaments glabrous, very short, included. Ovary inserted near the base of the receptacle, absent in male flowers but represented by a slight swelling, carpel unilocular; ovules two. Style basal; stigma shortly 3-lobed. Fruit a medium-sized dry drupe, epicarp warted, mesocarp thin soft; endocarp hard, thin, with granular exterior, not easily detached from mesocarp, interior hairy; without special mechanism allowing seedling escape. Germination hypogeal, first leaves alternate with lower surface sparsely tomentose. (Plate XXXVI).

Distribution: widespread in West Africa from Sierra Leone to Gabon.

Type species: *A. elaeosperma* Mildbr.

Note - This unispecific genus is widespread in the coastal regions of West Africa, where its seeds are transported by water (Deighton, m.s. in Herb. Kew). It is clearly distinct from all other genera of the Chrysobalanaceae, but is nearest to Licania from which it differs in the andro-dioecious flowers, the flattened receptacle and the petiole furnished with long silky hairs when young. These hairs encompass the petiole like a little tuft of spider's threads. The genus is also well differentiated by its wood structure for the arrangement of the vessels and parenchyma distinguish it from Licania and indeed all other genera of the Chrysobalanaceae (see Plates I-C, II-A).

Afrolicania elaeosperma Mildbr. in Notizbl. Bot. Gart. Berl. 7:483 (1921); Burnner in Notizbl. Bot. Gart. Berl. 8:188 (1924).

Type specimens: Dinklage 2761, 1969, Liberia (not seen; Huckstädt 170, Cameroons (not seen); Zenker 1629, Cameroons, fl. (K;M;P); Mildbraed 7730, Cameroons, fl. (K).

Parinarium glabrum auct. non Oliv.; Hutch. & Dalz., Fl. W. Trop. Afr. 1(2):317 (1928) pro parte quoad Chipp 299 tantum.

Distribution: As for the genus.

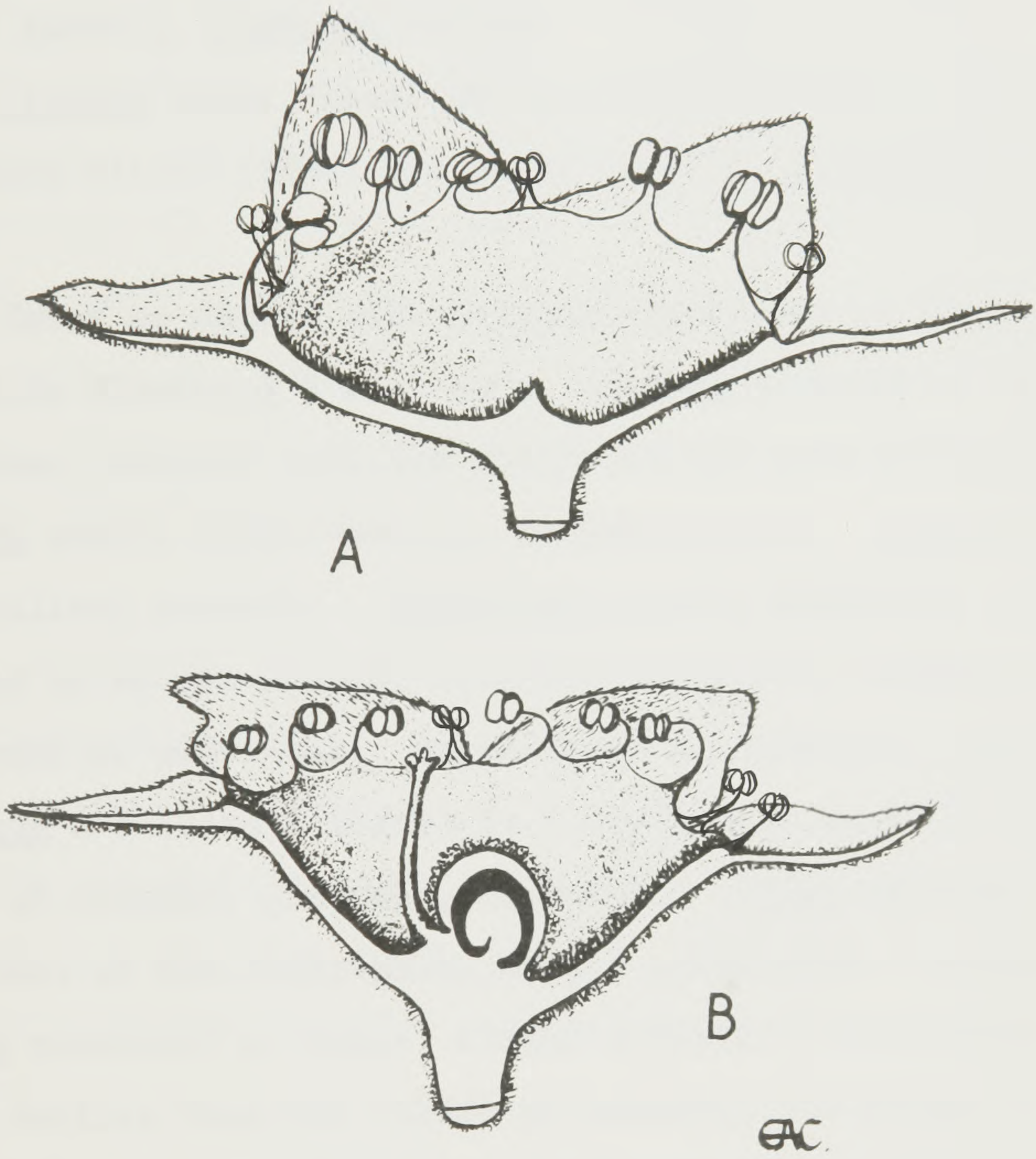


Plate XXXVI.- AFROLICANIA ELAEOSPERMA Mildbr.
A,male flower (x30); B,hermaphrodite flower (x30).

4. PARASTEMON

A. De Candolle in Ann. Sc. Nat. Sér. 2, 18:208 (1842); Boerlage & Koorders, Ic. Bogor 4:61-2 (1901); Merrill & Perry in Journ. Arn. Arb. 21:197 (1940).

Diemenia Korth. in Nederl. Kruidk. Arch. 3:388 (1854).

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

Licania sensu Blume, Mélanges Bot. (1855); Hasskl. in Flora 41:256 (1858) pro parte quoad L. diemenia tantum.

Trees or shrubs with polygamo-dioecious or hermaphrodite flowers ± 2 mm. long. Leaves glabrous on both surfaces, usually with two glands at the base of the lamina. Bracts small, linear-oblong, membranaceous. Inflorescence of axillary racemes. Receptacle small, shallowly cup-shaped or saucer-shaped, interior pubescent, exterior glabrous or pubescent; calyx-lobes 5, pointed. Petals 5. Stamens 2-5 (when 2 there are 3 staminodes opposite the pair of stamens) glabrous, included. Ovary inserted near the base of the receptacle, carpel unilocular; ovules 2. Style pubescent at base; stigma 3-lobed, 1 lobe often much smaller than the others or obscure, the other two large, distinct. Fruit a small hard drupe; epicarp smooth, interior glabrous; endocarp thin, hard, bony, smooth, with two lateral plates which break away during germination and allow the seedlings to escape. (Plates XXXVII, XXXVIII).

Distribution: from the Malay Peninsula to New Guinea.

Type species: P. urophyllus (A.DC.) A.DC.

Notes - (1) In much of the literature, this genus is distinguished from others by the two stamens and the polygamo-dioecious flowers. Merrill & Perry loc. cit. in describing P. versteeghii, which has neither of these characters, placed it in Parastemon with hesitation. They made the correct decision. Their doubts about possible confusion between Parastemon and Angelesia are removed in the light of the greater amount of herbarium material, which now exists. Parastemon is distinct from Licania (Angelesia) splendens in many features:- the racemose inflorescence, the basal style, the lobed stigma, the fewer stamens and the fruit which has two plates on the endocarp and a glabrous interior. Parastemon is in fact a distinct genus, which is not easily confused with any other genus of the Chrysobalanaceae.

(2) Miquel united the species Diemenia racemosa and Angelesia splendens to form the illegitimate genus Trichocarya, both Boerlage and Koorders loc. cit., and Merrill (in Philipp. Journ. Sci. 10:307 (1915)) give reasons for uniting Diemenia racemosa with Parastemon (the former authors had seen the type specimens concerned) and Korthals incorrectly described Diemenia as having 10 stamens and a two seeded fruit, otherwise his description is accurate.

1. Parastemon urophyllus (A.DC.) A.DC. in Ann. Sci. Nat. Sér. 2, 18:208 (1842).

Type: Wallich 2309, Malay Peninsula, fl. (BM).

Embelia urophylla [Wall., Cat. n.2309 (1830) nom. nud.] A.DC. in Trans. Linn. Soc. Lond. 17:131 (1837).

Diemenia racemosa Korth. in Nederl. Kruidk. Arch. 3:388 (1854).

Trichocarya racemosa (Korth.) Miq. Fl. Ind. Bat. 1(1):358 (1855).

Licania diamenia Blume, Mélanges Bot. (1855); Hasskl. in Flora 41:256 (1858) nom. illegit.

Parastemon spicatus Ridley in Journ. Roy. As. Soc. Str. Branch 75:29 (1917) synon. nov.

Distribution: Nicobars, Malay, Indonesia, Sarawak, Borneo, Philippines.

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 may be small trees. There appears to be insufficient reason for maintaining P. spicatus as a species. Anderson, however, (personal communication) says that in Sarawak the sessile flowered plant has a distinctive bark and has a distinct ecology. Further work may show that it is worth recognizing as a subspecies.

This species is here referred to as P. urophyllus, not P. urophyllum which has more generally been used. This is in accordance with the International Code of Botanical Nomenclature, Article 75 recommendation 75A.

2. Parastemon versteeghii Merrill & Perry in Journ. Arn. Arb. 21:197 (1940).

Type: Brass & Versteegh 13544, Indonesian New Guinea.

Distribution: New Guinea and Eastern Indonesia (Sangihe and Talaud Islands).

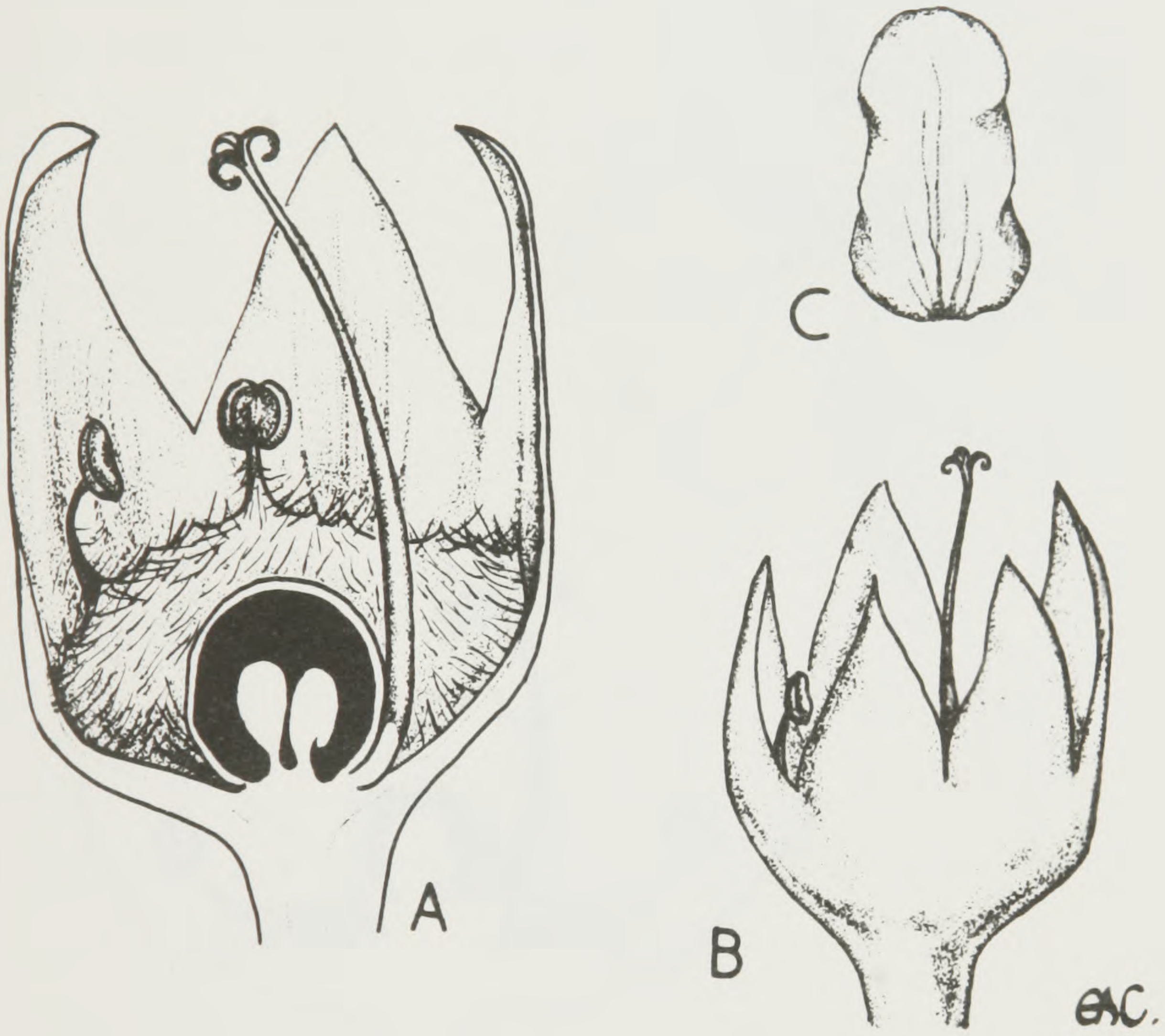


Plate XXXVII.- PARASTEMON UROPHYLLUS (A.DC.)A.DC.
A,flower (x40); B,flower (x25); C,petal (x25).

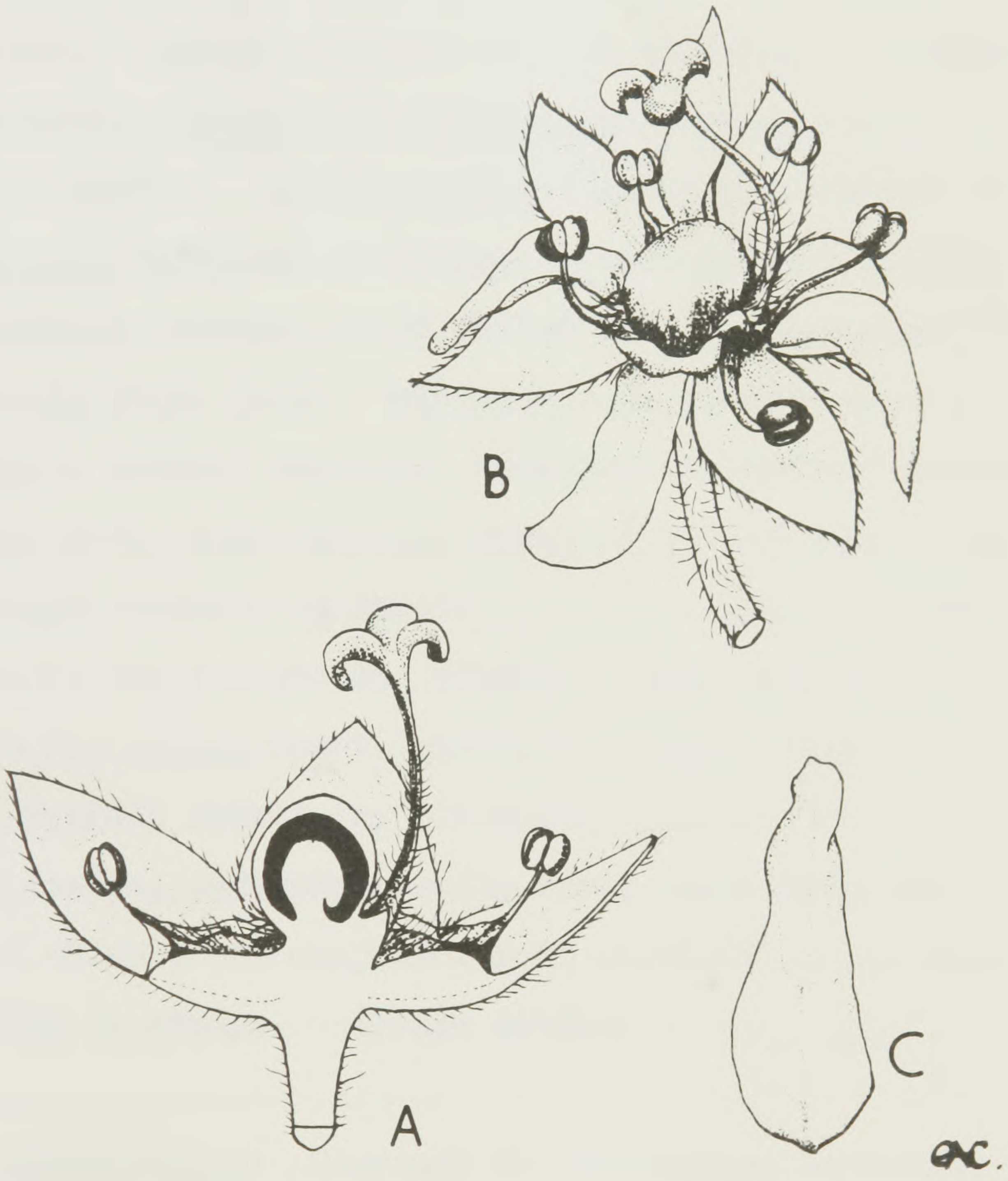


Plate XXXVIII.- PARASTEMON VERSTEEGHII Merrill & Perry
A, flower (x25); B, flower (x25); C, petal (x25).

5. GRANGERIA

Commers ex Juss., Gen.:340 (1789); Baillon in Adansonia 8:200 (1868).

Hirtella sensu Drake, Hist. Pl. Madag. 1:30 (1886).

Small trees or shrubs with hermaphrodite flowers 2-3 mm. long. Leaves glabrous on both surfaces. Petioles eglandular. Bracts and bracteoles sometimes with a few sessile glands. Inflorescence a short distinctive raceme. Receptacle turbinate, glabrous at base inside, puberulous or glabrous outside, mouth filled with a conspicuous mass of woolly white hair; calyx-lobes 5, rounded or acute. Petals 5, minute, caducous, inserted at mouth of receptacle. Stamens 8-15, only slightly exserted beyond calyx-lobes, forming a complete or partial circle. Ovary inserted ± midway up the receptacle, woolly; carpel unilocular; ovules 2. Style short, glabrous, stigma slightly 3-lobed. Fruit a small nearly dry trigonous drupe, epicarp smooth, hairy inside, endocarp smooth, hard, bony, with two lateral plates which break away easily on germination and allow the seedling to escape. (Plate XXXIX).

Distribution: Confined to Madagascar, Mauritius and Réunion.

Type species: G. borbonica Lam.

Notes - (1) A number of early workers state that Grangeria is closely related to Hirtella. In fact the only genus it is at all closely related to is Parastemon. The most striking difference between Grangeria and Hirtella concerns the dehiscence of the endocarp. An almost diagnostic character is found in the position of the ovary. In Grangeria it is inserted about half-way up the receptacle-tube and has disc-tissue distal to it. This condition is only found in two species of Hirtella. In all others the ovary is inserted at the mouth of the receptacle. A multitude of smaller characters contribute to the totally different aspects of the two genera.

(2) In Grangeria and Parastemon the endocarp dehisces on germination by means of two large lateral plates. The only other genus in the family which shows this feature is Maranthes which differs in other fruit characters, and indeed, in nearly all other respects. It has not been possible to study the germination of Grangeria and Parastemon but the structure of the endocarp suggests that as in Maranthes it is epigeal. In general facies Grangeria and Parastemon are similar. The fruits of Parastemon are not not trigonous and are glabrous inside. In Parastemon there are only 2-5 stamens and the ovary is inserted at the base of the receptacle; its stigma is distinctly 3-lobed.

(3) There are only two species in Grangeria. Baillon (1868), questioned whether they belong to the same genus. They are similar in all important respects.

1. Grangeria borbonica Lam., Encyc. 3:21 (19 Oct. 1789).

Type: Commerson s.n., Réunion (P-LAM, not seen).

Grangeria buxifolia Sm. in Rees, Cyclop 16:n.2 (1811).

Distribution: Mauritius and Réunion.

Note. Early collectors frequently stated that this species was plentiful.

2. Grangeria porosa Boiv. ex Baill. in Adansonia 8:200 (1868).

Type specimens: Richard 220, Madagascar (P); 582 (P); Pervillé 354, Madagascar (P); 507 fr. (P); Boivin 2210, Madagascar (P).

Grangeria madagascariensis O. Hoffmann, Sert. Plant. Madag.:15 (1881).

Hirtella porosa (Boiv. ex Baill) Drake. Hist. Pl. Madag. 1:30 (1886).

Species exclusa

G. brasiliensis Hofmgg. ex Mart. & Zucc. in Abh. Akad. Münch 1:378 (1830) in syn. = Hirtella ciliata Mart. & Zucc.

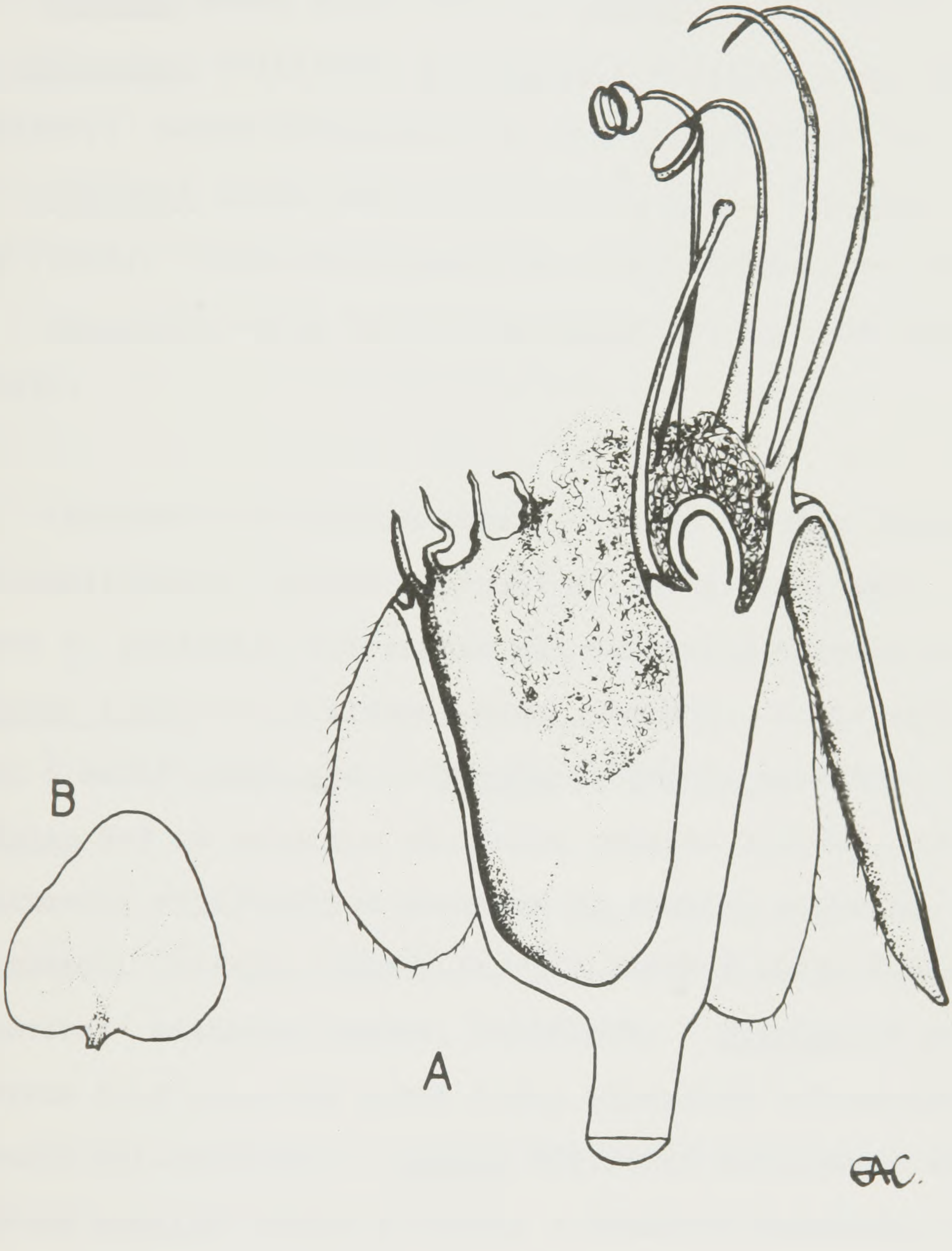


Plate XXXIX.- GRANGERIA POROSA Boiv.ex Baill.
A,flower (x50); B,petal (x30).

6. HUNGA

Hunga Pancher ex Prance, genus novum.

Hunga Pancher ex Guillaum. in Ann. Mus. Col. Marseille 2:91 (1911) in syn. sub Chrysobalano.

Licania sensu auct. viz. L. gerontogea Schlecht., L. rhamnoides Guillaum., L. balansae Guillaum., L. lifouana Däniker.; sensu Guillaum., Fl. Nouv. Calédonie: 143 (1948).

Parinari sensu Bak. f. in Journ. Linn. Soc. Bot. 45: 298 (1921); sensu Guillaum., Fl. Nouv. Calédonie: 143 (1948).

Angelesia sensu Bak. f. in Journ. of Bot. 61 suppl.:13 (1923).

Frutices vel arbores parvi. Folia integra oblonga vel oblongolinearia glabra vel subtus lanato-tomentosa. Flores parvi in paniculas terminales vel axillares dispositi. Calycis tubus campanulatus, extus puberulus, intus pilosus; lobi 5 acuti imbricati. Petala 5, parva, sessilia, decidua. Stamina 5-9 ad marginem adaxialem calycis tubi disposita, filamentis filiformibus brevibus in annulum connatis; staminodia (stamina ananthera) 3-7 parva stamina diametricale opposita; antherae parvae, basifixae. Ovarium ad medium calycis tubi insertum extus dense puberulum 2-loculare, loculis uni-ovulatis. Stylus basilaris filiformis ut videtur simplex revera e stylis 3 connatis formatus, stigmate truncato, breviter 3-lobo. Fructus drupaceus 1 vel 2 loculearis extus laevis intus dense pilosus, endocarpio duro tenue extus laeve longitudinaliter in partibus 4-6 dehiscente.

Typus generis: Hunga rhamnoides (Guillaum.) Prance.

Shrubs or small trees with hermaphrodite flowers ± 2 mm. long. Leaf-undersurface glabrous or with a woolly tomentum, stomata visible at X 25 magnification. Bracts and bracteoles small, membranaceous. Inflorescence of small terminal or axillary panicles. Receptacle campanulate, shortly puberulous outside, hairy inside throughout; calyx-lobes 5, acute. Petals 5, small not exceeding the calyx-lobes. Stamens 5-9, included, filaments short, grouped towards one side of the receptacle and with 3-7 small, free staminodes opposite to them. Ovary inserted mid-way up the receptacle, densely hairy outside; carpel bilocular with 1 ovule in each loculus. Style-apex truncate but distinctly 3 lobed, base hairy. Fruit a small fleshy drupe, bilocular or often with one loculus underdeveloped, epicarp smooth, dark coloured; endocarp hard, thin, bony with a smooth surface, interior very hairy, with 4-6 longitudinal lines of weakness which allow the seedling to escape. (Plate XL).

Type species: H. rhamnoides (Guillaum.) Prance

Distribution: New Caledonia, Loyalty Islands, Papua.

Notes - (1) In 1907 Schlechter described Parinarium myrsinoides from New Caledonia. The holotype of this is now destroyed and no other type-material has yet been traced so that its identity is doubtful. The type-description mentions a receptacle-tube densely lined with hairs so that in all probability the plant belongs to Chrysobalanaceae and as all the known Chrysobalanaceae from New Caledonia are species of Hunga one might expect it to belong to that genus, were it not for one discordant fact in the description. Schlechter says that the ovary contains a single ovule. In all species of Hunga the carpel is bilocular with two ovules.

In the absence of material it would be unwise to transfer this species to _Hunga_.

(2) The species now gathered together in _Hunga_ were originally described in three different genera, but two of these (_Licania_ and _Angelesia_) are in my opinion synonymous. In 1908 Schlechter described _Licania gerontogea_ from New Caledonia and 13 years later Guillaumin described two more Licanias also from New Caledonia. One of these, _L. rhamnoides_ is distinct, the other _L. balansae_ is the same as Schlechter's species. On the very next day E.G. Baker independently published two new species of _Parinari_ from New Caledonia. In my opinion these are also synonyms of _L. gerontogea_. Baker compared both his species with _Parinari myrsinoides_ but there is no evidence that he actually saw the type. In 1923 Baker described _Angelesia papuana_. Although somewhat different from the other species of _Hunga_ in facies it has almost identical flowers and similar distinctive stomata and clearly belongs with them. Finally in 1931, Däniker described _Licania lifouana_, a good species, from the Loyalty Islands. A second species from Papua has remained up till now undescribed.

(3) Despite the conflicting views of previous authors there is no doubt that all these species belong together in the same genus. Apart from the bilocular ovary _Hunga_ shares no important characters with _Parinari_. It is, however, quite closely related to, though in my opinion distinct from, _Licania_. _Hunga_ differs from _Licania_ in having a bilocular ovary which is inserted half-way to two-thirds of the way up the receptacle-tube and in having the stamens grouped to one side of the flower. It differs from all species of _Licania_

known to me in its very large stomata. Although these differences are not appreciable the statistical analysis shows that Hunga is clearly distinct from Licania. If its species were to remain in Licania a consequence would be that most genera in the family would also need to be amalgamated.

1. Hunga rhamnoides (Guillaum.) Prance, comb. nov.

Type specimens: New Caledonia, Pancher 26 fl. (P); 13, fl. (P) s.n., fr. (P; Z); Balansa 1334, (P); 2335, fr. (P); 3549, fl. (P; Z); Deplanche 519, fr. (P; Z); 40, (P); Vieillard 239, (P); 238, (P).

Licania rhamnoides Guillaum. in Bull. Soc. Bot. France 67:346 (1921).

Hunga rhamnoides Panch. ex Guillaum. in Ann. Mus. Col. Marseille 2 (9):132 (1911) in syn. sub Chrysobalano sp.

Distribution: New Caledonia.

2. Hunga gerontogea (Schlecht.) Prance, comb. nov.

Type specimens: Cribs 1248, New Caledonia, fl. (P); Le Rat 460, New Caledonia, fl. (P).

Licania gerontogea Schlecht. in Engl. Bot. Jahrb. 40, Beibl. 9:25 (1908).

Parinarium minutiflorum Bak. f. in Journ. Linn. Soc. Bot. 45:298 (6.9.1921), synon. nov.

P. neocaledonium Bak. f. loc. cit., synon. nov.

Licania balansae Guillaum. in Bull. Soc. Bot. France 67:346 (7.9.1921), synon. nov.

Distribution: New Caledonia.

3. *Hunga lifouana* (Däniker) Prance, comb. nov.

Type: Däniker 2470, Loyalty Isles, fl. (Z; P).

Licania lifouana Däniker in Vierteljahrschr. Nat. Ges. Zürich 76:166 (1931).

Distribution: Loyalty Islands.

4. *Hunga papuana* (Bak. f.) Prance, comb. nov.

Type: Forbes 257, Papua, fl. (BM).

Angelesia papuana Bak. f. in Journ. of Bot. 61 suppl.: 13 (1923).

Distribution: Papua.

5. *Hunga longifolia* Prance sp. nov.

Arbor 15 m. alta, ramis ramulisque teretibus glabris. Folia coriacea oblongo-lanceolata (7-10 cm. longa 2-3 cm. lata), apice breviter acuminata, basi cuneata, supra glabra infra adpresse, puberula, petiolo ad 5 mm. longo. Stipulae parvae, caducae. Flores in paniculas axillares vel terminales breviter fulvo-tomentosas dispositi. Bracteae parvae acuminatae membranaceae. Calycis tubus campanulatus breviter fulvo-tomentosus, intus pilis deflexis instructus, lobis 5 triangularibus pubescentibus. Petala 5 parva glabra (praeter margines ciliolatae) quam sepala breviora. Stamina 8, unilateralis, haud exserta; staminodiia 3-5 staminibus opposita. Ovarium ad medium calycis tubi insertum, dense pubescens, biloculare loculis 1-ovulatis, ovulis basalibus. Stylus basalis, filamenta aequans, basi pilosus, stigmate truncato. Fructi mihi ignoti.

Papua - Mount Sisa, Misima isle. Typus L.J. Brass 27462 (L. holo., K, iso.)

This species is distinct from all other species of <u>Hunga</u> in the shape and length of the leaves and in the sparse appressed indumentum of the lower surface of the leaves. <u>H. longifolia</u> and <u>H. papuana</u> are the only two species of <u>Hunga</u> so far recorded outside the New Caledonia group of islands, and they unquestionably belong to the same genus as the New Caledonian species. <u>H. papuana</u> has more distinctly acuminate leaves, secondary nerves which curve and anastomose and are impressed on the upper surface. <u>H. longifolia</u> is probably most closely related to <u>H. lifouana</u> from which it differs, in addition to the leaf shape and indumentum, in the longer more branched inflorescence with a rust-coloured pubescence, the more prominent secondary nerves on both surfaces of the leaf, and the shorter more swollen petioles.

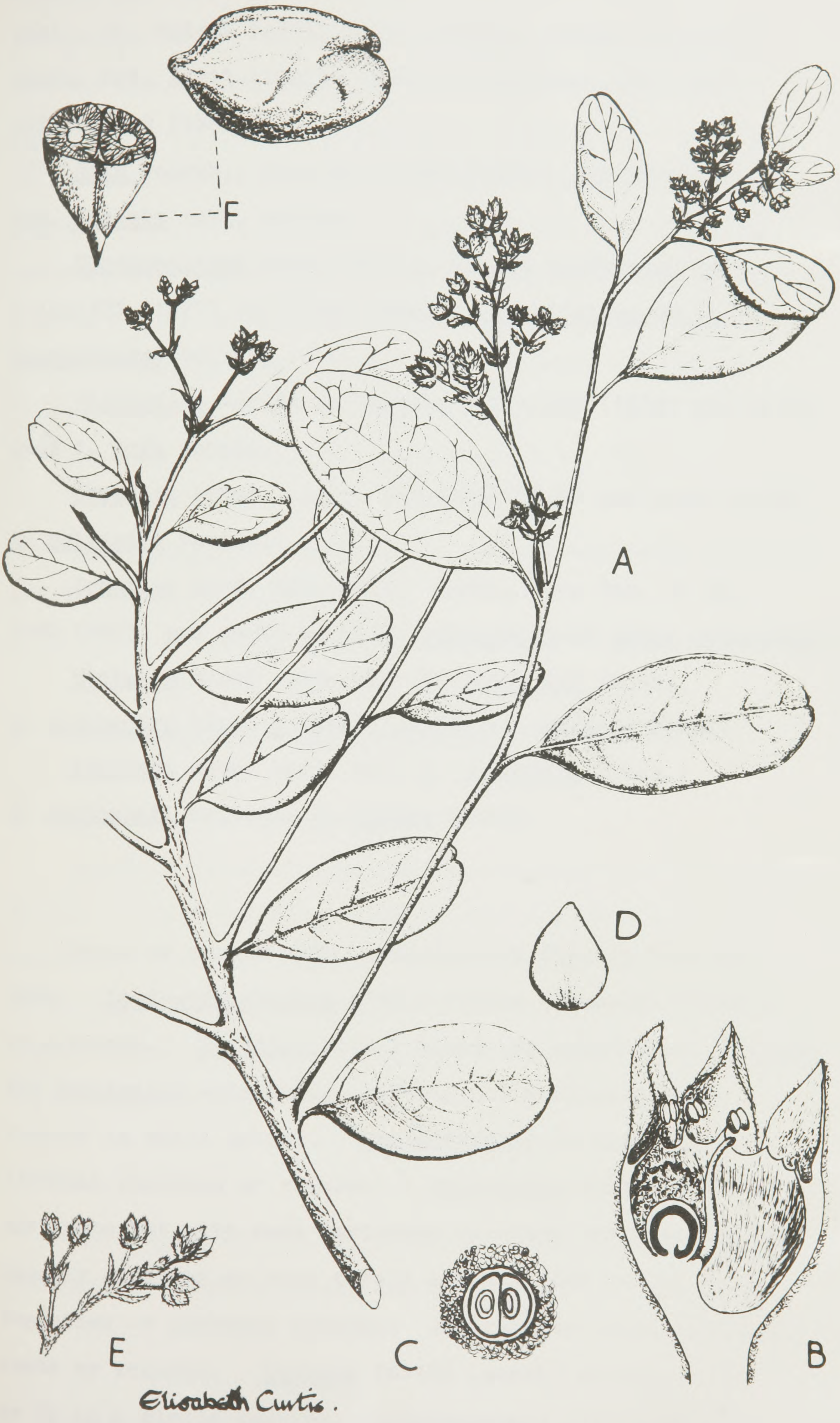


Plate XL.- HUNGA GERONTOGEA (Schlecht.)Prance

A,flowering branch (x1); B,flower (x20); C,ovary (x25); D,petal (x20); E,inflorescence (x2); F,fruit (x1).

7. COUEPIA

Aubl., Pl. Guian. 1:519, t.221 (1775); Benth. in Hook. Journ. Bot. 2:215 (1840); Hook. f. in Mart., Fl. Bras. 14(2):40-49 (1867).

Acia Schreb., Gen. Pl. 2:458 (1791), pro parte, quoad syn. Couepia Aubl. tantum.

Chrysobalanus auct. non L., Schott in Spreng. Syst. 4 App:407 (1827) pro parte quoad C. ovalifolius et C. macrophyllus tantum.

Pleraginea Arruda ex Koster, Trav.:499 (1816) pro parte quoad P. rufa tantum.

Grymania Presl., Epim. Bot.:193 (1849) pro parte quoad G. polyandra tantum.

Moquilea auct. non Aubl.; Mart., Nov. Gen. et Sp. 2:80 (1827) pro parte excl. M. guianensis et Acioa guianensis.

Hirtella sensu auct. viz. H. polyandra Kunth., H. dodecandra (Moc. & Sessé) ex DC., H. cognata Steud.

Parinari sensu auct. viz. P. canescens Gleas., P. hostmannii Fritsch, P. pilosa Standl.

Trees or shrubs with hermaphrodite flowers 7-40 mm. long. Leaf-undersurface with a woolly arachnoid tomentum or glabrous. Petioles with 2 glands or eglandular. Bracts and bracteoles eglandular, usually not enclosing young flowers in small groups. Inflorescence of axillary or terminal panicles or racemes. Receptacle cylindrical-turbinate but with much variation in shape and size, hollow, usually glabrous or very rarely hairy inside at the base; tomentose or glabrous outside; calyx-lobes often reflexed, acute or rounded. Stamens 14-100 (rarely to 300 and as few as 10 in a single species, C. dodecandra), far exserted, often in a complete circle, less frequently grouped towards one side of the receptacle in which case there are usually a few staminodes as well; filaments usually twisted around each other and forming a tangled mass. Ovary of 1 (2-3) carpels, inserted laterally at the mouth of the receptacle, carpels unilocular. Fruit a hard or fleshy drupe, with a verrucose, smooth or hairy epicarp; endocarp hard and roughish, with a characteristically granular exterior, on germination breaking up in an irregular manner. Germination hypogeal, first leaves alternate. (Plates XLI, XLII).

Distribution: widespread in Central and South America, and the West Indies.

Type species: Couepia guianensis Aubl.

Notes - (1) This study has not resulted in any changes to the circumscription of Couepia as currently understood. Because of this, and because of the large number of species in the genus, detailed work has not been done at the species-level. Work already done indicates that some of the species listed below may be synonyms.

(2) Couepia is closely related to Hirtella. Their relationships are discussed under the latter genus.

1. Couepia guianensis Aubl., Pl. Guian. 1:519, t.221 (1775).

Type: Aublet s.n., French Guiana, fr. (BM).

Acia amara Willd., Sp. Pl. 3(1):717 (1800).

C. versicolor Benoist in Bull. Mus. Hist. Nat. Paris 29:596 (1923) synon. nov.

C. surinamensis Kleinh. in Rec. Trav. Bot. Néerl. 22:390 (1925) synon. nov.

Distribution: French Guiana, Suriname.

2. Couepia bracteosa Benth. in Hook., Journ. of Bot. 2:215 (1840).

Type: Schomburgk 485, British Guiana, fl. (K; BM).

Distribution: British Guiana, Brazil.

3. Couepia canescens (Gleason) Prance, comb. nov.

Type: Tate 870, Venezuela, fl. (K).

Parinari canescens Gleason in Bull. Torr. Bot. Cl. 63:370 (1931).

Distribution: Venezuela.

An examination of the type shows that this species has several characters that exclude it from Parinari. The 13 stamens are exserted, the inside of the receptacle is glabrous, the ovary is unilocular, the bracts do not enclose the flowers in small groups and the leaves do not have stomatal cavities, but rather, the tomentum characteristic of Couepia. Gleason himself, in the type description, pointed out the anomalous position of this species within Parinari on account of the staminal number. It fits perfectly into Couepia, where it is now placed.

4. Couepia canomensis (Mart.) Benth. ex Hook. f. in Mart., Fl. Bras. 14(2):42 (1867).

Type: Martius s.n., Brazil-Paré, st. (M; K; BR).

Moquilea canomensis Mart., Nov. Gen. et Sp. 2:80 (1827).

Hirtella canomensis (Mart.) Spreng., Syst. 4; Cur. Post:341 (1827).

Parinari pilosa Standl. in Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser. 17:259 (1937) Synon. nov.

Distribution: Brazil, British Guiana, Peru.

This species has usually be cited as "C. canomensis" Benth. but Bentham did not publish the combination.

5. Couepia caryophylloides Benoist in Bull. Mus. Hist. Nat. Paris 28:253 (1922).

Type specimens: Wachenheim Second Series 274, French Guiana, st. (K; BM); Third Series 11, French Guiana, fl. (P).

Distribution: French Guiana, Suriname.

6. Couepia cataractae Ducke in Arquiv. Serv. Florest., Rio de Janeiro 1(1):31 (1939).

Type specimens: Ducke H.A.M.P. 16388, Brazil-Pará, fl. K; H.J.B.R. 15136 (not seen).

Distribution: Brazil.

7. Couepia chrysocalyx (Poepp. & Endl.) Benth. ex Hook. f. in Mart., Fl. Bras. 14(2):42 (1867).

Type: Poeppig 2177, Brazil, Maynas, fl. (P).

Moquilea chrysocalyx Poepp. & Endl., Nov. Gen. et Sp. 1:75 (1827).

Distribution: Brazil, Peru, Ecuador.

8. Couepia cognata (Steud.) Fritsch in Ann. Naturh. Hofmus. Wien 4:60 (1889).

Type: Hostman 795, Suriname, fl. (K).

Hirtella cognata Steud. in Flora 26:761 (1843).

Couepia steudeliana Miq., Stirp. Surin. Sel.:28 (1850).

Moquilea steudeliana Walp., Ann. 2:463 (1851-52).

Parinari hostmannii Fritsch in Ann. Nat. Hofmus. Wien 5:13 (1890).

Distribution: British Guiana, Suriname.

9. Couepia comosa Benth. in Hook., Journ. of Bot. 2:215 (1840).

Type: Schomburgk 28, British Guiana, fl. (K; BM).

Distribution: British Guiana.

10. Couepia dahlgrenii Standl. in Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser. 17:249 (1937).

Type: Dahlgren 986, Brazil Piauhy, (F, holo, not seen).

Distribution: Brazil.

11. Couepia divaricata Huber in Bol. Mus. Pará 6:75 (1910).

Type: Huber H.A.M.G. 2030, Brazil-Amazonas (not seen).

Distribution: Brazil.

12. Couepia dodecandra (Moc. & Sessé ex DC.) Hemsl. in Hook., Ic. Pl. 27, 6.2620 (1901).

Type: Mocino & Sessé tabula 302 (original drawing, not lost). Tracing, tabula 302 in A.L.P.P. de Candolle, Calq. des Dess. Fl. Mex. (Neotype).

Hirtella dodecandra Moc. & Sessé ex DC. Prodr. 2:529 (1825).

Distribution: Mexico, British Honduras.

13. Couepia duckei Huber in Bol. Mus. Pará 5:271 (1909).

Type: Ducke 8536, Brazil-Amazonas, fl. (P).

Distribution: Brazil.

14. Couepia elata Ducke in Arquiv. Inst. Biol. Veg. Rio de Janeiro 2:35 (1935).

Type: Ducke H.J.B.R. 25001, Brazil-Amazonas, fl. (K; P).

Distribution: Brazil.

15. Couepia eriantha Spruce ex Hook. f. in Mart., Fl. Bras. 14(2):45 (1867).

Type specimens: Spruce 313 and 1138, Brazil-Pará, fl. (K; OXF).

Distribution: Brazil.

16. Couepia excelsa Ducke in Arch. Jard. Bot. Rio de Janeiro 5:116 (1930).

Type: Ducke H.J.B.R. 19758, Brazil-Amazonas fl. (P; K).

Distribution: Brazil.

17. Couepia exflexa Fanshawe & Maguire in Bull. Torr. Bot. Cl. 75:376 (1948).

Type specimens: Fanshawe 722 (F.D. 3458), British fl. (NY, holo not seen; K, iso); 722a (F.D. 3458), British Guiana, fr. (NY not seen; K).

Distribution: British Guiana.

18. Couepia formosana Taub. in Engl. Jahrb. 21:429 (1896).

Type: Ule 2881, Brazil (not seen).

Distribution: Brazil.

19. Couepia glandulosa Miq., Stirp. Surin. Sel.: 28 (1850).

Type: Hostman 859, Suriname, fl. (K; BM).

Distribution: Suriname, British Guiana.

20. Couepia glaucescens Spruce ex Hook. f. in Mart., Fl. Bras. 14(2):49 (1867).

Type: Spruce 1752, Brazil-Amazonas, fl. (K; OXF; M; P).

Distribution: Brazil.

21. Couepia glazioviana Pilger in Notizbl. Bot. Gart. Berlin 8:537 (1923).

Type: Glaziou 18217, Brazil-Rio de Janeiro, fl. (K; P).

Distribution: Brazil.

22. Couepia grandiflora (Mart. & Zucc.) Benth. ex Hook.f. in Mart., Fl. Bras. 14(2):46 (1867).

Type: Martius s.n., Brazil-Goyaz, fl. (M).

Moquilea grandiflora Mart. & Zucc. in Abh. Akad. Münch. 1:388 (1932).

Distribution: Brazil.

23. Couepia habrantha Standl. in Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser., 17:249 (1937).

Type: Krukoff 7252, Brazil-Amazonas, fl. (F, holo not seen; NY not seen; BR; K).

Distribution: Brazil, British Guiana.

24. Couepia insignis Fritsch in Ann. Naturh. Hofmus. Wien 5:11 (1890).

Type: Blanchet 3209, Brazil-Bahia, fl. (P).

Distribution: Brazil.

25. Couepia krukovii Standl. in Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser. 17:250 (1937).

Type specimens: Krukoff 6208, Brazil-Amazonas, fl. (F, holo not seen; NY not seen; BR; K); 6007, Brazil-Amazonas, st. (F not seen; NY not seen; BR; K).

Distribution: Brazil.

26. Couepia latifolia Standl. in Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser. 17:251 (1937).

Type: Krukoff 6005, Brazil-Amazonas, fr. (F, holo not seen; NY not seen; BR; K).

Distribution: Brazil.

27. Couepia leptostachya Benth. ex Hook. f. in Mart., Fl. Bras. 14(2):44 (1867).

Type: Spruce 1536, Brazil-Amazonas, fl. (OXF: K: P: M).

Distribution: Brazil.

28. Couepia longipendula Pilger in Notizbl. Bot. Gart. Berlin 6:141 (1914).

Type: Ule 8854, Brazil-Amazonas, fl. (K).

Distribution: Brazil.

29. Couepia macrophylla Spruce ex Hook. f. in Mart., Fl. Bras. 14(2):41 (1867).

Type: Spruce 4049, Peru, fl. (OXF).

Couepia speciosa Pilger in Bot. Jahrb. 37:539 (1906).

Distribution: Peru, Brazil.

30. Couepia magnolifolia Benth. ex Hook. f. in Mart., Fl. Bras. 14(2):43 (1867).

Type: Spruce 1414, Brazil-Amazonas, fl. (OXF; K; P).

Distribution: Brazil.

31. Couepia martiana Hook. f. in Mart., Fl. Bras. 14(2):47 (1867).

Type specimens: Martius s.n., Brazil-Piauhy, fr. (M); Gardner 1283, Brazil-Piauhy, fr. (K).

Distribution: Brazil.

32. Couepia multiflora Benth. in Hook. Journ. of Bot. 2:215 (1840).

Type: Schomburgk 112, Br. Guiana, fl. (OXF; K; BM).

Distribution: British Guiana, Brazil.

33. Couepia myrtifolia Benth. ex Hook. f. in Mart., Fl. Bras. 14(2):44 (1867).

Type specimens: Spruce 174, Brazil-Pará, Alto Amazonas fl. (K); 2262 fl. (M; K); 3072, fl. (BR); Sagot 262, Fr. Guiana (not seen).

Distribution: Brazil, British Guiana, French Guiana.

34. Couepia obovata Ducke in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:35 (1935).

Type: Ducke H.J.B.R. 24 495, Brazil-Amazonas, fl. (P; K).

Distribution: Brazil.

35. Couepia ovalifolia (Schott) Benth. in Hook., Journ. of Bot. 2:216 (1840).

Type: Schott s.n., Brazil, fl. (K).

Chrysobalanus ovalifolius Schott in Spreng., Syst. 4, App.: 406 (1827).

Couepia hypoleuca Miq. in Linnaea 19:438 (1847).

Distribution: Brazil.

36. Couepia panamensis Standl. in Tropical Woods 44:22 (1935).

Type: G.P. Cooper 279 (Yale 24041), Panama (F not seen).

Distribution: Panama.

37. Couepia paraënsis (Mart. & Zucc.) Benth. in Hook. Journ. of Bot. 2:216 (1840).

Type: Sieber (Eq. de Martius) s.n., Brazil-Pará, fl. (M).

Moquilea paraensis Mart. & Zucc. in Abh. Akad. Münch. 1:390 (1832).

Distribution: Brazil, Venezuela, Peru.

38. Couepia paraguariensis Hassler in Fedde Repert. Nov. Sp. 7:375 (1909).

Type: Fiebrig 1379, Paraguay, fl. (K).

Distribution: Paraguay.

39. Couepia parillo DC., Prod. 2:526 (1825).

Type: Ventenat s.n., French Guiana (G not seen).

Distribution: French Guiana.

40. Couepia pauciflora Huber in Bol. Mus. Pará 5:372 (1909).

Type: Ducke 8630, Brazil-Amazonas (not seen).

Distribution: British Guiana, Brazil.

41. Couepia platycalyx Cuatrec. in Fieldiana, Bot. 27:66 (1950).

Type: Cuatrecasas & Arbelaez 5336, Colombia, (F not seen).

Distribution: Colombia.

42. Couepia polyandra (Kunth) Rose in U.S. Dept. Agric. Contrib. Nat. Herb. 5:196 (1899).

Type: Humbolt & Bonpland s.n., Mexico (not seen)

Hirtella polyandra Kunth, Nov. Gen. et Sp. 6:246 (1823).

Moquilea kunthiana Mart. & Zucc. in Abh. Akad. Münch. 1:390 (1830).

Couepia kunthiana (Mart. & Zucc.) Benth. in Hook., Journ. of Bot. 2:216 (1840).

Grymania polyandra (Kunth) Presl, Epim. Bot.:193 (1849).

Couepia floccosa Fritsch in Ann. Naturh. Hofmus.

Wien 5:12 (1890).

Distribution: Costa Rica, Mexico, Guatemala.

43. Couepia racemosa Benth. ex Hook. f. in Mart., Fl. Bras. 14(2):43 (1867).

Type specimens: Spruce 1776. Brazil-Amazonas, fl. (OXF; P; K); 2322 Brazil-Amazonas, fl., fr. (K; M; OXF).

Couepia calophlebia Standl. in Publ. Field. Mus. Nat. Hist., Chicago, Bot. Ser., 17:249 (1937), see Ducke in Arquiv. Serv. Florest. 1(1):29 (1939).

Distribution: Brazil.

44. Couepia reflexa Ducke in Arch. Jard. Bot. Rio de Janeiro 5:118 (1930).

Type: Ducke H.J.B.R. 19 757, Brazil-Amazonas, fl. (K; P).

Distribution: Brazil.

45. Couepia robusta Huber in Bol. Mus. Pará 6:76 (1910).

Type: R.S. Rodrigues H.A.M.G. 9651, Brazil-Amazonas, fl. (P; K).

Distribution: Brazil.

46. Couepia rufa Ducke in Arch. Mus. Nac. Rio de Janeiro 22:66 (1919).

Type: Lutz H.A.M.G. 3575, Brazil-Pernambuco, fl. (P; BM).

Pleragina rufa Arruda Camara in Koster, Trav.: 499 (1816).

Moquilea rufa Barbosa Rodrigues, Hort. Flum.: 165 (1895) pro parte.

Distribution: Brazil.

47. Couepia schottii Fritsch in Ann. Naturh. Hofmus. Wien 5:13 (1890).

Type: Schott s.n., Brazil (not seen).

Chrysobalanus macrophyllus Schott in Sprengel, Syst. 4, App.: 407 (1827).

Distribution: Brazil.

48. Couepia spicata Ducke in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:36 (1933).

Type: Ducke H.J.B.R. 25 002, Brazil-Amazonas, fl. (K; P).

Distribution: Brazil.

49. Couepia steyermarkii Maguire in Fieldiana, Bot. 28(2): 252 (1952).

Type: Steyermark 60025, Venezuela (F, holo not seen; NY, iso not seen).

Distribution: Venezuela.

50. Couepia stipularis Ducke in Archiv. Inst. Biol. Veg. Rio de Janeiro 4:3 (1938).

Type: Ducke H.J.B.R. 35583, Brazil-Amazonas fl. (K; P).

Distribution: Brazil.

51. Couepia subcordata Benth. ex Hook. f. in Mart., Fl. Bras. 14(2):46 (1867).

Type: Spruce 1423, Brazil-Amazonas, fl. (OXF; K; P).

C. amazonica Fritsch in Ann. Naturh. Hofmus. Wien 5:2 (1890).

Distribution: Brazil, Peru.

52. Couepia suberosa Pilger in Notizbl. Bot. Gart. Berlin 8:538 (1923).

Type: Riedel 504, Brazil-Minas Geraes (OXF).

Distribution: Brazil.

53. Couepia thrysiflora Hook. f. in Mart., Fl. Bras. 14(2): 45 (1867).

Type: Spruce 3681, Brazil-Amazonas, fl. (K; P).

Distribution: Brazil.

54. Couepia trapezioana Cuatr. in Brittonia 8:197 (1956).

Type: Schultes 8266, Colombia (F, holo not seen).

Distribution: Colombia.

55. Couepia uiti (Mart. & Zucc.) Benth. ex Hook. f. in Mart. Fl. Bras. 14(2):47 (1867).

Type: Martius s.n., Brazil-Bahia, fl. (M).

Moquilea uiti Mart. & Zucc. in Abh. Akad. München. 1:390 (1832).

Distribution: Brazil.

56. Couepia ulei Pilg. in Verh. Bot. Ver. Brand. 47:149 (1950).

Type: Ule 5547, Brazil-Amazonas, fl. (K).

Distribution: Brazil, Peru.

57. Couepia villosa Fanshawe & Maguire in Bull. Torr. Bot. Cl. 75:378 (1948).

Type: Maguire 24782, British Guiana, fl. (NY, holo not seen; K; M; BR).

Distribution: British Guiana.

58. *Couepia williamsii* Macbride in Candollea 5:366 (1934).

Type: *Williams* 2975, Peru (F, holo not seen).

Distribution: Peru.

Species exclusa

Couepia laurifolia Cuatr. = *Persea laurifolia* (Cuatr.) Cuatr.

Plate XLI.- COUEPIA HABRANTHA Standl.
A,flower (x10); B,ovary and style (x10); C,ovary (x15); D,petal (x10).

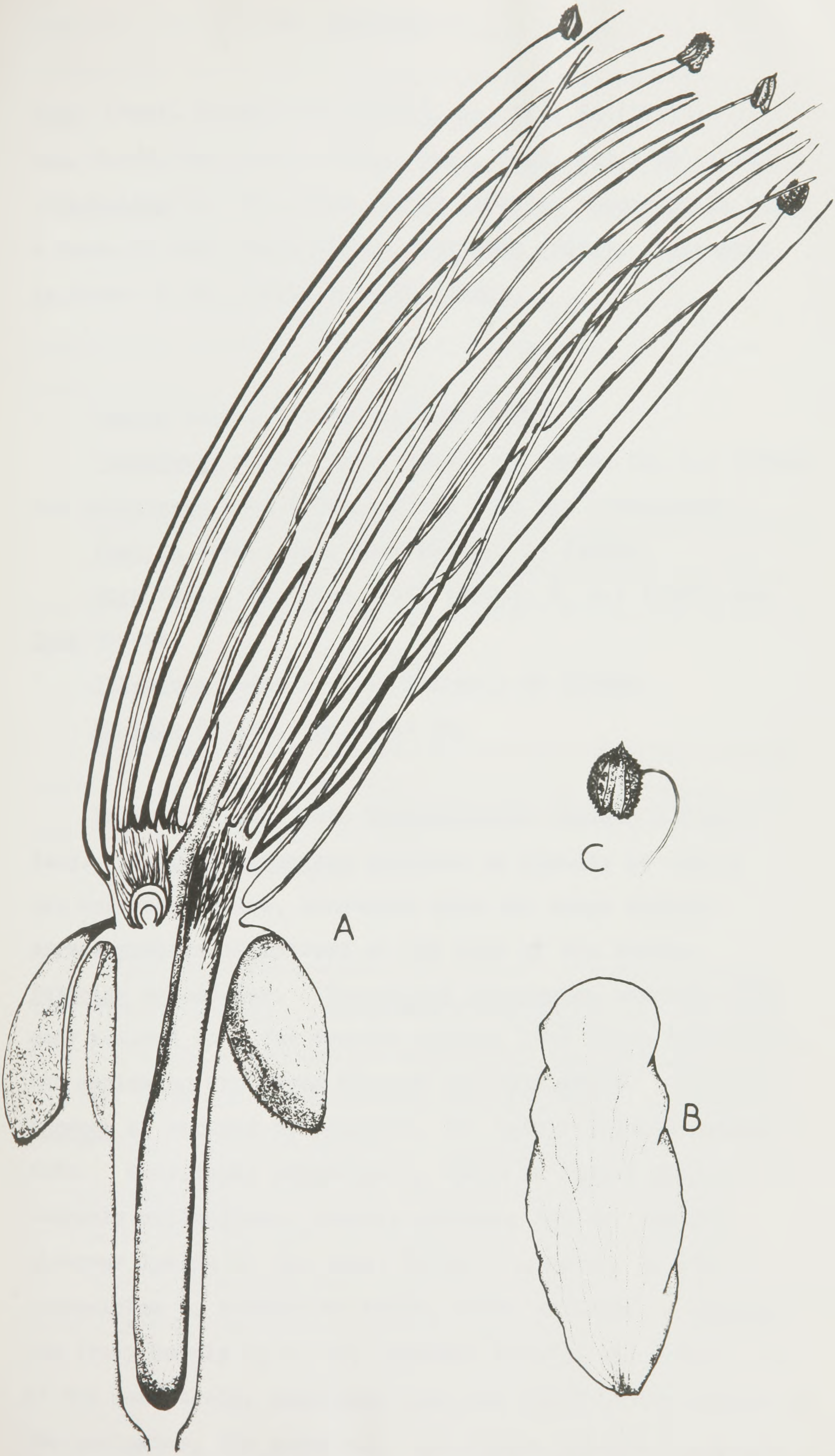


Plate XLII.- COUEPIA CHRYSOCALYX (Poepp.& Endl.)Benth. ex Hook.f
A,flower (x6); B,petal (x5); C,anther (x10).

8. HIRTELLA

Linn. [Hort. Cliff.: 17 (1737)], Sp. Pl.: 34 (1753); Gen. Plant. ed. 5:20 (1754); Dum., Anal. Fam.: 40 (1829) ["Hirtellia"]; DC., Prod. 2:528 (1825); Zuccarini in Mart. & Zucc. in Abh, Akad. Münch. 1:373-380 (1832); Zuccarini in Flora 15 (2), Beibl.: 78-79 (1832).

Causea Scop., Introd. n. 928 (1777).

Cosmibuena Ruiz & Pav., Prodr. Fl. Peru: 10, t.2 (1794); non Cosmibuena Ruiz & Pav. of Fl. Peru 3:3 (1789-1802).

Thelyra Thou., Gen. Nov. Madag.: 21 (1806).

Brya Vell., Fl. Flum.: 147 (1825), 4, t.1 (1827) non Brya Browne.

Sphenista Rafin., Sylva Tellur.: 91 (1838).

Zamzela Rafin., tom cit.: 90.

Trees or shrubs with hermaphrodite flowers 4-8 mm. long. Leaf-undersurface glabrous or hirsute or with a few appressed hairs, sometimes with two large bulbous myrmecophilous inflations at the base of the lamina. Petioles eglandular. Bracts and bracteoles commonly with many stalked to a few sessile glands, less often eglandular, not enclosing the young flowers in small groups. Inflorescence of racemes or panicles, the latter usually racemiform. Receptacle campanulate, short or rather elongate to narrowly cylindrical, usually gibbous, hollow, usually glabrous inside at the base, hairy or glabrous outside; calyx-lobes 5, rounded or acute, often reflexed. Stamens 3-8 (very rarely up to 10) inserted towards the abaxial rim of the receptacle, occupying from one third to two thirds of the perimeter, far exserted; staminodes inserted opposite the stamens, short free. Ovary inserted laterally at the mouth of, or rarely midway up, the receptacle, carpel unilocular, ovules 2. Style filiform, far exserted. Fruit a fleshy drupe, often ellipsoid in shape, epicarp smooth or rarely with a dense rust-coloured tomentum; endocarp thin, hard not granular with a smooth, but channelled surface, hairy inside, with 4-7 longitudinal lines of weakness which allow the seedling to escape. Germination hypogeal, first leaves alternate. (Plates XLIII, XLIV).

Type species: Hirtella americana L., Sp. Pl.: 34 (1753). Type: a specimen in cover representing page 17 of the Hortus cliffortianus in the Clifford Herbarium, fl. (BM).

Distribution: widespread in Central and South America and the West Indies, and with 3 species in East Africa and Madagascar.

Notes - (1) The majority of earlier workers starting with Aublet, wrongly interpreted H. americana L., and much material which should be referred to H. racemosa Lam., was confused with it. For an explanation of this see Sandwith in Kew Bull. 1931:376 (1931). H. mollicoma Kunth., H. gautemalensis Standl. and Central American material previously wrongly named H. glandulosa Spreng. are conspecific with true H. americana L. Brazilian material of H. glandulosa, including the type, is a distinct species.

(2) The statistical work confirms that Magnistipula as defined by Graham (1957) is distinct from Hirtella. This

is discussed in Chapter 10 and under Magnistipula. This leaves only three species outside the New World, two in Africa and one in Madagascar.

There are nearly 100 American species. Many of these, covering the whole morphological range of the genus have been examined, but it has not been possible to study them all. In view of this, and the fact that the circumscription of Hirtella has not been altered in this study, details of the American species are not given below.

(3) The statistical work shows that Hirtella and Couepia are as closely related to each other as are any two genera within the family, although still separable. They are separated by one diagnostic character and a number of differential characters one of which is almost diagnostic. (The terms diagnostic and differential are used in the sense of White, 1962, p. 75.) The single diagnostic character is that of the fruit first pointed out by Zuccarini (1832). In Couepia the endocarp is thick and hard with a granular exterior. It breaks easily in no particular pattern. In Hirtella the endocarp is thin and bony. It does not readily fracture as in Couepia but instead opens by splitting longitudinally along the lines of weakness occupied by vascular strands. Nearly all previous works separate these two genera entirely by the number of fertile stamens. This feature is almost diagnostic but there is a slight overlap. Most species of Hirtella have from 3-8 fertile stamens but in H. angustifolia, H. enneandra and H. floribunda there are 7-9 fertile stamens and very rarely in occasional flowers there may be 10. Most species of Couepia have more than 15 fertile stamens, the majority have a considerably higher number, but in C. dodecandra, C. cognata and C. polyandra

the number may be less than 15. In C. dodecandra especially, it is common to find flowers with only 10 fertile stamens. These three related species, however, resemble Couepia in all other respects including the fruit and although they were all originally described in the genus Hirtella they are best placed in Couepia. An additional feature of the staminal filaments must also be mentioned as a differential character. In most species of Couepia the filaments are twisted and form a tangled mass around each other. This is never so in Hirtella.

Other differential features are now given. In both genera a small proportion of the species have glabrous leaves but, when hairs are present they are of a different type in the two genera. In Couepia (see Plate XXVII-D) the leaf-undersurface has a dense woolly arachnoid tomentum which is very distinctive. In Hirtella (see Plate XXVII-C) the hairs are never dense and are stiff and appressed forming a strigose tomentum or often there are just a few appressed hairs along the secondary nerves and reticulations. About 60 per cent of the species of Hirtella have glandular bracts and bracteoles. These do not occur at all in Couepia. In Hirtella the flowers are 4-8 mm. long and the receptacle is not usually elongated in the way that it is in Couepia, its base is most often gibbous a feature which does not occur in Couepia. In Couepia the receptacle is 7-40 mm. long.

The extremes of the two genera are very different. Those species that are anomalous for one character are invariably typical for the others so that if all characters are considered their placing presents no difficulty.

The Extra-American Species of Hirtella

1. Hirtella thouarsiana Baill. ex Laness., Pl. Util. Colon. Franç.: 874 (1886).

Type: Dupetit-Thouars s.n., Madagascar, fl. (P).

This species known only from Madagascar is closely related to the African H. zanzibarica. Baillon (1868) gives good reasons for merging Thelyra Thouars, which was published without a specific name, with Hirtella. Its type was made the type of H. thouarsiana by Lanessan.

2. Hirtella zanzibarica Oliv. in Hook., Ic. Pl. 12:81, t. 1193 (1876); Brenan in Trop. Woods 86:5 (1946).

Type: Kirk s.n., Mafia Isl., fl., fr. (K).

Acioa goetzeana Engl. in Bot. Jahrb. 30:315, t. 12 (1901).

Distribution: Kenya, Tanganyika, Zanzibar, Nyasaland, Mozambique.

3. Hirtella megacarpa R. Graham in Kew Bull. 1957:231 (1957).

Type: Drummond & Hemsley 2614, Tanganyika, fr. (K).

Distribution: confined to Tanganyika.

Species exclusae

Hirtella apetala E. Mey. in Nov. Act. Phys.-Med. Acad. Caes. Leop. Car. Nat. Cur. 21:803 (1825) = Licania apetala (E. Mey.) Fritsch.

H. bangweolensis (R.E. Fr.) Greenway in Kew Bull. 1928: 199 (1928) = Magnistipula bangweolensis (R.E. Fr.) R.A. Graham.

H. butayei (De Wild.) Brenan in Trop. Woods 86:4 (1946) = Magnistipula butayei De Wild.

H. canomensis (Mart.) Spreng., Syst. 4. Cur. Post: 341 (1827) = Couepia canomensis (Mart.) Benth. ex Hook. f.

H. cognata Steud. in Flora 26:761 (1843) = _Couepia cognata_ (Steud.) Fritsch.

H. conrauana (Engl.) A. Chev. in Bull. Mus. Hist. Nat. Paris, Sér. 2, 3:194 (1931) = _Magnistipula conrauana_ Engl.

H. cupheiflora (Mildbr.) Mildbr. ex A. Chev. in Bull. Mus. Hist. Paris Sér. 2, 3:193 (1931) = _Magnistipula cupheiflora_ Mildbr.

H. dodecandra Moc. & Sessé ex DC., Prodr. 2:529 (1825) = _Couepia dodecandra_ (Moc. & Sessé ex DC.) Hemsl.

H. eglandulosa Greenway in Kew Bull. 1928:199 (1928) = _Magnistipula eglandulosa_ (Greenway) R.A. Graham.

H. fleuryana A. Chev., tom. cit.: 192 = _Magnistipula fleuryana_ (A. Chev.) Hauman.

H. fruticulosa Hauman in Bull. Jard. Bot. Brux. 21:182 = _Magnistipula eglandulosa_ (Greenway) R.A. Graham.

H. glaberrima Steud. in Flora 26:761 (1843) = _Crudia obliqua_ Griseb.

H. glaberrima (Engl.) A. Chev. tom. cit.: 195 = _Magnistipula glaberrima_ Engl.

H. katangensis Hauman, tom. cit.: 179 = _Magnistipula katangensis_ (Hauman) E.J. Mendes.

H. montana Hauman, tom. cit.: 180 = _Magnistipula montana_ (Hauman) Prance.

H. octandra Hoffmgg. ex Roem & Schult., Syst. 5:274 (1819) = _Licania octandra_ (Hoffmgg. ex Roem & Schult.) Kuntze.

H. oliviformis Poir., Encyc., Suppl. 3:53 (1823) = _Icacina senegalensis_ A. Juss.

H. polyandra Kunth., Nov. Gen. et Sp. 6:246 (1823) = _Couepia polyandra_ (Kunth) Rose.

H. porosa (Boiv. ex Baill.) Drake, Hist. Pl. Madag. 1:30 (1895) = _Grangeria porosa_ Boiv. ex Baill.

H. sapinii (De Wild.) A. Chev., tom. cit.: 195 = _Magnistipula sapinii_ De Wild.

H. zenkeri (Engl.) A. Chev., tom. cit.: 195 = _Magnistipula zenkeri_ Engl.

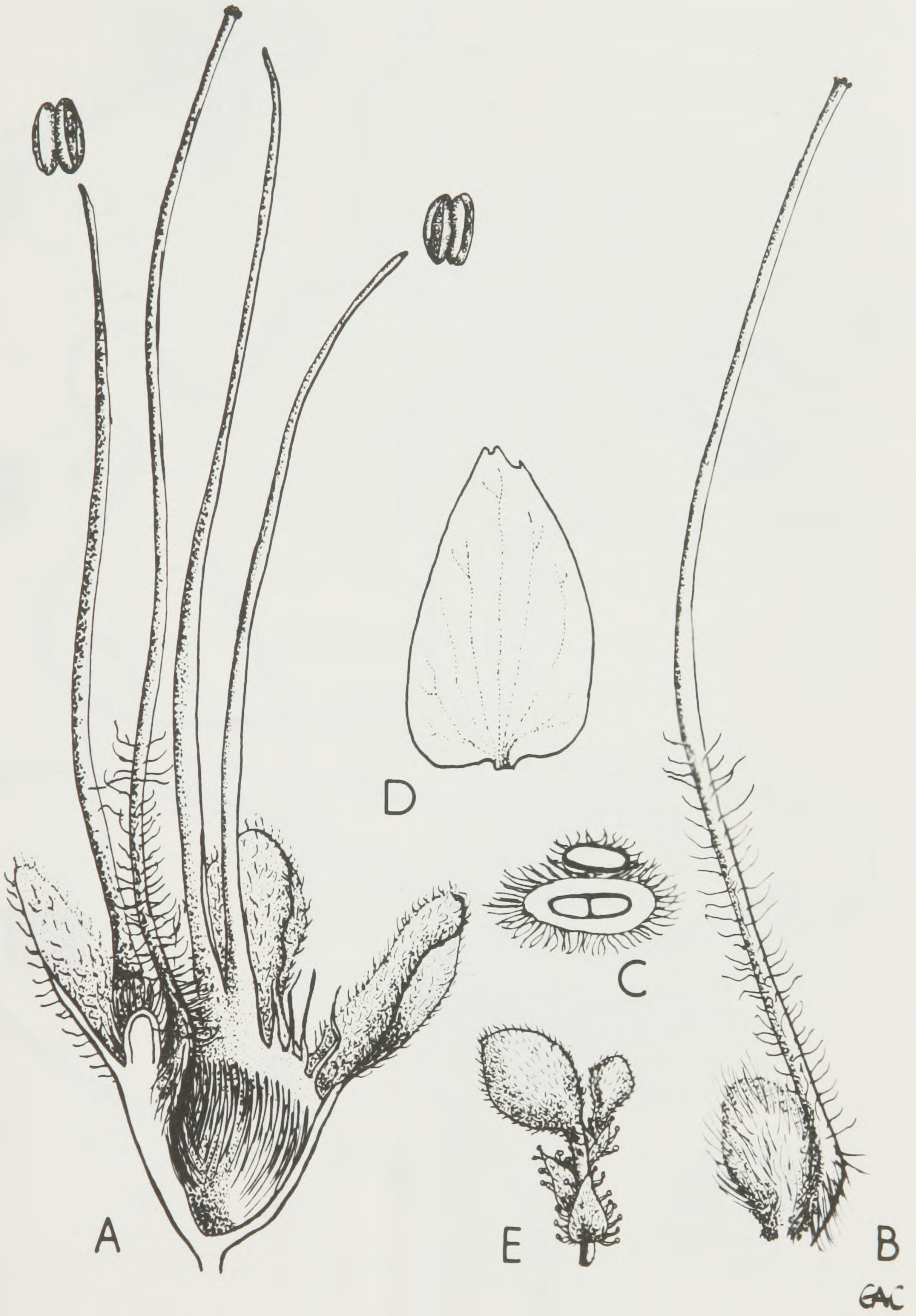


Plate XLIII.- HIRTELLA GLANDULOSA Spreng.

A, flower (x10); B, ovary and style (x15); C, ovary (x20); D, petal (x10); E, bud and bracteoles (x15).

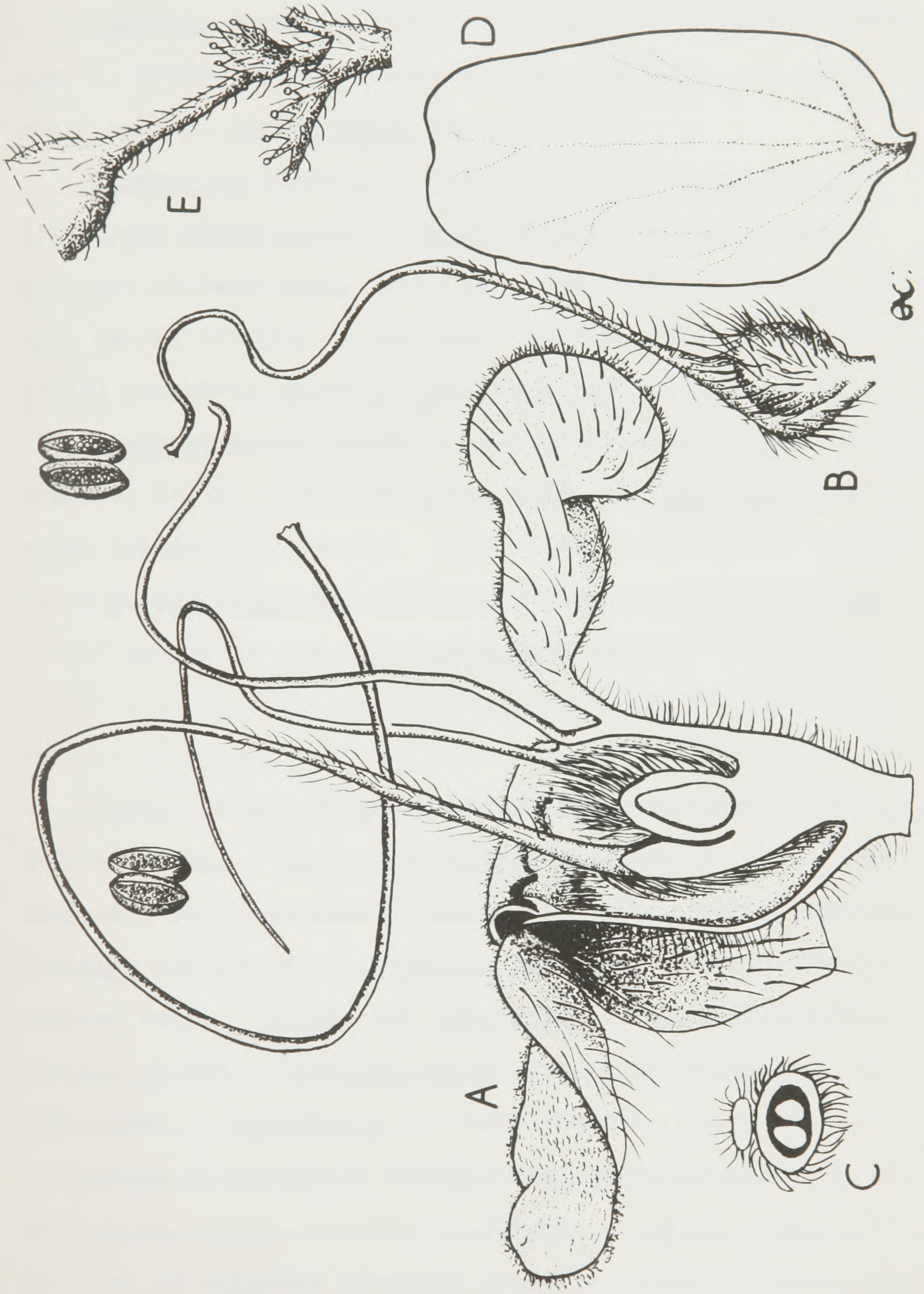


Plate XLIV.- HIRTELLA PANICULATA Sw.

A,flower (x20); B,ovary and style (x13);C,ovary (x20); D,petal (x20); E,bracteoles and glands (x20).

9. MAGNISTIPULA

Engl. in Bot. Jahrb. 36:226 (1905); Hauman in Bull. Jard. Bot. Brux. 21:173 (1951); R.A. Graham in Kew Bull. 1957:30 (1957), in Fl. Trop. E. Afr., Rosaceae: 55 (1960).

Hirtella sensu A. Chev. in Bull. Mus. Hist. Nat. Paris, Sér. 2, 3:192 (1931); sensu Hauman, loc. cit. pro parte quoad subgen. Afrohirtella tantum.

Parinarium sensu R.E. Fries in Fedde Repert. 12:540 (1913) pro parte quoad P. bangweolense tantum; sensu Pellegr. in Bull. Mus. Hist. Nat. Paris 26:349 (1920), tom. cit. 29:267 (1923); sensu Engl. in Bot. Jahrb. 46:139-142 (1912) pro parte quoad P. tessmannii and P. versicolor tantum.

Parinari sensu Aubrév. & Pellegr. in Not. Syst. ed. Humbert, 14:58 (1950) pro parte quoad P. tisserantii tantum; sensu Aubrév. Fl. Forest. Côte d'Iv. 1:153 (1936) pro parte quoad P. fleuryana tantum; sensu Hauman tom. cit.: 189 (1951) pro parte quoad P. tessmannii tantum.

Trees, shrubs or suffrutices with hermaphrodite flowers, 5-22 mm. long. Leaf-undersurface glabrous or with a few strigose, rust-coloured hairs, never with a dense tomentum. Petioles eglandular. Stipules large and persistent in some species only. Bracts and bracteoles occasionally with a few sessile glands. Inflorescence usually of panicles, rarely of racemes. Receptacle of characteristic shape, gibbous, ventricose or obliquely campanulate, hairy or glabrous inside; calyx-lobes acute, usually tomentose. Fertile stamens 5-9, included or slightly exserted, arcuate, grouped towards one side of receptacle; staminodes inserted opposite the stamens, free or united to form a short comb or an elevated tongue. Ovary inserted at the mouth of the receptacle; carpels unilocular (bilocular in M. tessmannii). Style slightly exserted, ± arcuate. Fruit a fleshy drupe, epicarp with a dense rusty tomentum (smooth and glabrous in M. fleuryana), endocarp hairy inside, usually soft and consisting of a few fibres only, and breaking up in no special way on germination; hard and smooth in M. tessmannii. Germination hypogeal, first leaves opposite. (Plates XLV, XLVI).

Distribution: Africa with most species in Cameroun, Gabon and the Congo.

Type Species: M. conrauana Engl.

Notes - (1) Magnistipula was first described in 1905 by Engler who did not compare it with any other genus of Chrysobalanaceae but said that it was unique in having large, foliaceous "intrapetiolar"* stipules, an obliquely campanulate ventricose receptacle and the staminodes united to form a comb-shaped structure. Between 1905 and 1921 four more species were described by Engler, De Wildeman and Mildbraed, but only one of these M. glaberrima Engl. has persistent stipules and they are small. The others (M. butayei De Wild., M. sapinii De Wild. and M. cupheiflora Mildbr.) have small caducous stipules.

In 1913 R.E. Fries described Parinarium bangweolense which is now included in Magnistipula. He drew attention to its unilocular ovary and pointed out that his new species was unique in Parinari in this respect. In 1928 Greenway transferred P. bangweolense to Hirtella without comment and described a new species, H. eglandulosa. Another African

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* The stipules are in fact laterally inserted.

Hirtella (H. fleuryana) was described by Chevalier in 1931. In the same paper Chevalier transferred Engler's original two species of Magnistipula and M. cupheiflora Mildbr. and M. sapinii De Wild. to Hirtella but apparently overlooked De Wildeman's other species of Magnistipula (M. butayei). This latter species was transferred by Brenan in 1946. In 1951 Hauman revived Magnistipula and placed in it four species with larger flowers and more completely united staminodes. His line of separation between Magnistipula and Hirtella is artificial and some of the species he left in Hirtella must be placed next to some he transferred, whether one splits or unites these genera. In connection with his revision for the Flora of Tropical Africa, Graham (1957) transferred H. bangweolensis and H. eglandulosa, two species left in Hirtella by Hauman, to Magnistipula.

(2) At first sight M. conrauana and M. zenkeri with their large persistent foliaceous stipules, less markedly zygomorphic receptacles and their longer, almost completely united staminodes which form a tongue-like structure appear to stand apart from M. bangweolensis and its allies which have small caducous stipules, markedly asymmetric receptacles and very short staminodes not forming a tongue-like structure. Other species, however, provide connecting links. M. glaberrima has persistent stipules combined with the M. bangweolensis type of flower and M. fleuryana and M. cuneatifolia lack stipules but have the M. conrauana type of flower.

(3) Although _Magnistipula_ is distinct from _Hirtella_, the two genera are closely related. The principal differences separating _Magnistipula_ from _Hirtella_ are its markedly asymmetric receptacle (not ± symmetric), its included (not far exserted stamens and style) and its endocarp which lacks a special mechanism of dehiscence. The species of _Magnistipula_ whose receptacle is least asymmetric and therefore most likely to be confused with _Hirtella_ on that account are those in which the staminodes are fused for the greater part of their length - a character unknown in _Hirtella_ as at present circumscribed.

(4) It is necessary to discuss the placing of _Parinari tessmannii_ Engl. This species has placed in _Parinari_ because of its bilocular ovary, although it shares few other characters with that genus. In the statistical work it was consistently associated with _Magnistipula_. Besides its bilocular ovary it differs from _Magnistipula_ in having a thick, hard, smooth endocarp. It seems to be best treated as a subgenus of _Magnistipula_.

Subgenus _Pellegriniella_ (Hauman) Prance, comb. nov.

Parinari subgenus _Pellegriniella_ Hauman in Bull. Jard. Bot. Brux. 21:188 (1951) pro parte quoad _P_. _tessmannii_ tantum.

1. _M_. _tessmannii_ (Engl.) Prance, comb. nov.

Type: _Tessman_ 81, Gabon, fl. (P; K).

Parinarium _tessmannii_ Engl., Bot. Jahrb. 46:139 (1912).

Parinari _ingangensis_ (sic) Pellegr. in Bull. Mus. Nat. Hist. Paris 29:267 (1923).

Parinari nyangensis Pellegr. in Exell, Journ. of Bot. 1928 Suppl. 1:161 (1928).

Distribution: Nigeria, Rio Muni, Gabon, Cabinda.

Hauman based his diagnosis of Parinari subgenus Pellegriniella on P. tessmannii which he clearly regarded as an anomalous member of Parinari. He associated two other anomalous species with it, P. coriacea Benth. and P. gardneri Hook. f. They have no important features in common with P. tessmannii and are here placed in the genus Duckea.

Subgenus Magnistipula

2. M. butayei De Wild. in Ann. Mus. Congo Sér. 2, 2:255 (1908).

Type specimens: Butaye 1440, Congo, fl. (BR); Gillet s.n. (not seen).

Hirtella butayei (De Wild.) Brenan in Trop. Woods 86:4 (1946).

Parinarium sargosii Pellegr. in Bull. Mus. Hist. Paris 26:347 (1920).

Parinarium tisserantii Aubrév. & Pellegr. in Humbert, Not. Syst. 14:58 (1950).

Distribution: Ivory Coast, Ubangui-Chari, Gabon, Congo.

3. M. bangweolensis (R.E. Fries) R.A. Graham in Kew Bull. 1957: 230 (1957).

Type specimens: N. Rhodesia, Fries 732, fl. (K, UPS, BR); 780, (UPS not seen); 780a, (UPS not seen).

Parinarium bangweolense R.E. Fries in Fedde Repert. 12:540 (1913).

Hirtella bangweolensis (R.E. Fries) Greenway in

Kew Bull. 1928: 199 (1928).

<u>Distribution</u>: Congo, Tanganyika, Nyasaland, Northern Rhodesia.

4. <u>M</u>. <u>conrauana</u> Engl., Bot. Jahrb. 36:226 (1905).

<u>Type</u>: <u>Conrau</u> 65, Cameroons, fl. (E).

<u>Hirtella</u> <u>conrauana</u> Engl. A. Chev. in Bull. Mus. Hist. Nat. Paris Sér. 2, 3:194 (1931).

<u>Distribution</u>: Cameroons.

5. <u>M</u>. <u>cuneatifolia</u> Hauman in Bull. Jard. Bot. Brux. 21:175 (1951).

<u>Type</u>: <u>Le Testu</u> 9376, Gabon, fl. (P; BR).

<u>Distribution</u>: Gabon.

6. <u>M</u>. <u>cupheiflora</u> Mildbr. in Notizbl. Bot. Gart. Berlin 8:57 (1921).

<u>Type</u>: <u>Mildbraed</u> 8307, Cameroun, st. (K).

<u>Hirtella</u> <u>cupheiflora</u> (Mildbr.) Mildbr. ex A. Chev. in Bull. Mus. Hist. Nat. Paris Sér. 2, 3:195 (1931).

<u>Distribution</u>: Sierra Leone, Cameroun.

7. <u>M</u>. <u>eglandulosa</u> (Greenway) R.A. Graham.

<u>Type</u>: <u>Borle</u> 254, N. Rhodesia, fl. (K; FHO).

<u>Hirtella</u> <u>eglandulosa</u> Greenway in Kew Bull. 1928: 199 (1928).

<u>H</u>. <u>fruticulosa</u> Hauman in Bull. Jard. Bot. Brux. 21:175 (1951).

<u>Distribution</u>: Congo, Rhodesia.

8. M. fleuryana (A. Chev.) Hauman in Bull. Jard. Bot. Brux. 21:175 (1951).

Type: Chevalier s.n., Ivory Coast, fl. (P).

Hirtella fleuryana A. Chev. in Bull. Mus. Hist. Nat. Par. Sér. 2, 3:192 (1931).

Parinari fleuryana (A. Chev.) Aubrév., Fl. For. Côte d'Ivoire 1:153 (1936).

Distribution: Liberia, Ivory Coast, Gabon.

9. M. glaberrima Engl. in Notizbl. Bot. Gart. Berlin 6:35 (1913).

Type: Zenker 4509, Cameroun, fl. (P; M; E).

Hirtella glaberrima (Engl.) A. Chev. in Bull. Mus. Hist. Nat. Paris Sér. 2, 3:194 (1931).

Distribution: Cameroun.

10. M. katangensis (Hauman) E.J. Mendes in Trab. Centr. Bot. Junt. Invest. Ultram. No. 1:3 (1962).

Type: Duvigneaud 139, Congo (Katanga), fl. (BR; FHO).

Hirtella katangensis Hauman in Bull. Jard. Bot. Brux. 21: 179 (1951).

Distribution: Congo.

11. M. montana (Hauman) Prance, comb. nov.

Type: Michelson 741, Congo (Kivu), fl. (BR).

Hirtella montana Hauman in Bull. Jard. Bot. Brux. 21:175 (1951).

Distribution: Congo.

12. *M. pallidiflora* Engl., Pflanzenw. Afr. 3(1):308 (1915) nom. nud.

Distribution: Cameroun.

This species has not yet been described but the herbarium material of it indicates that it is probably a good species.

13. *M. sapinii* ["sapini"] De Wild. in Bull. Jard. Bot. Brux. 3:262 (1911).

Type: Sapin s.n., Congo, fl. (BR).

Hirtella sapini (De Wild.) A. Chev. in Bull. Mus. Hist. Nat. Paris Sér. 2, 3:195 (1931).

14. *M. youngii* E.J. Mendes, loc. cit.

Type: Young 410, Angola, fl. (LISC; K).

Distribution: Angola.

15. *M. zenkeri* Engl. loc. cit.

Type: Zenker 2469, Cameroun, fl. (BR; P; E).

Hirtella zenkeri (Engl.) A. Chev. in Bull. Mus. Hist. Nat. Paris Sér. 2, 3:195 (1931).

Distribution: Cameroun.

16. *Magnistipula albida* Prance, sp. nov.

Arbor vel frutex?, ramulis juvenibus glabris aetate lanticellatis. Stipulae parvae, lineares, caducae, 4-5 mm. longae. Folia alterna, breviter petiolata, petiolo c. 3 mm. longo, oblongo-elliptica 6-9 cm. longa 3-4 cm. lata, marginine integra apice acuninata acumine ad 15 mm. longo, basi rotundata, utrinque glabra, nervis secondariis 6-9 paris subtus prominentibus. Flores in racemose axillares 3-10 floros, breviter pedunculatos dispositi, breviter et sparsiuscule argenteo-griseo-tomentosi: pedicelli 3-4 mm. longi. Bracteae parvae, lineares, 1.5 - 2 mm. longae, eglandulosae. Calycis tubus obliquus, 6 mm. longus, extus argenteo-griseo-tomentosus, intus prope faucem dense tomentosus, pilis longis deflexis infra stamina et staminodia dispositis, parte basali glabra, lobis 5, anguste lanceolatis 2.5 mm. longis, pubescentibus. Petala 5, decidua, glabra praeter margines hirsutae, apice acuta, calycis lobos aequantia. Stamina 5, unilateralia, filamentis 2.5 - 3 mm. longis glabris, complanatis ad medium connatis dispositis, antheris parvis basifixis, staminodiis 6, liberibus staminibus oppositis, pectinatim dispositis. Ovarium ad faucem calycis tubi insertum dense pubescens, uniloculare, loculo glabro, ovulis 2 basalibus. Stylus basalis, filamenta aequans, ± arcuatus, basi pilosus. Fructi mihi ignoti.

Gabon - Haut Ngounyé, Le Testu 5472 (P holotypus; FHO isotypus).

Nearest to M. cupheiflora Mildbr. but differs in having rather sparse silver-grey tomentum, more rounded leaf base, the axillary and more crowded inflòrescence, the flowers borne on short pedicels and the young branches being almost glabrous. There are also floral similarities to M. glaberrima Engl. but it differs in the tomentose inflorescence, the absence of glands on the bracts and bracteoles, the dull upper leaf-surface, and the very small stipules. The distinctive inflorescence differentiates it from any other species of Magnistipula.

Species dubia

Parinarium versicolor Engl., Bot. Jahrb. 46:142 (1911).

Hauman (loc. cit.) gives reasons for regarding this species as a Magnistipula. I have been unable to find any additional information or specimens of this species.

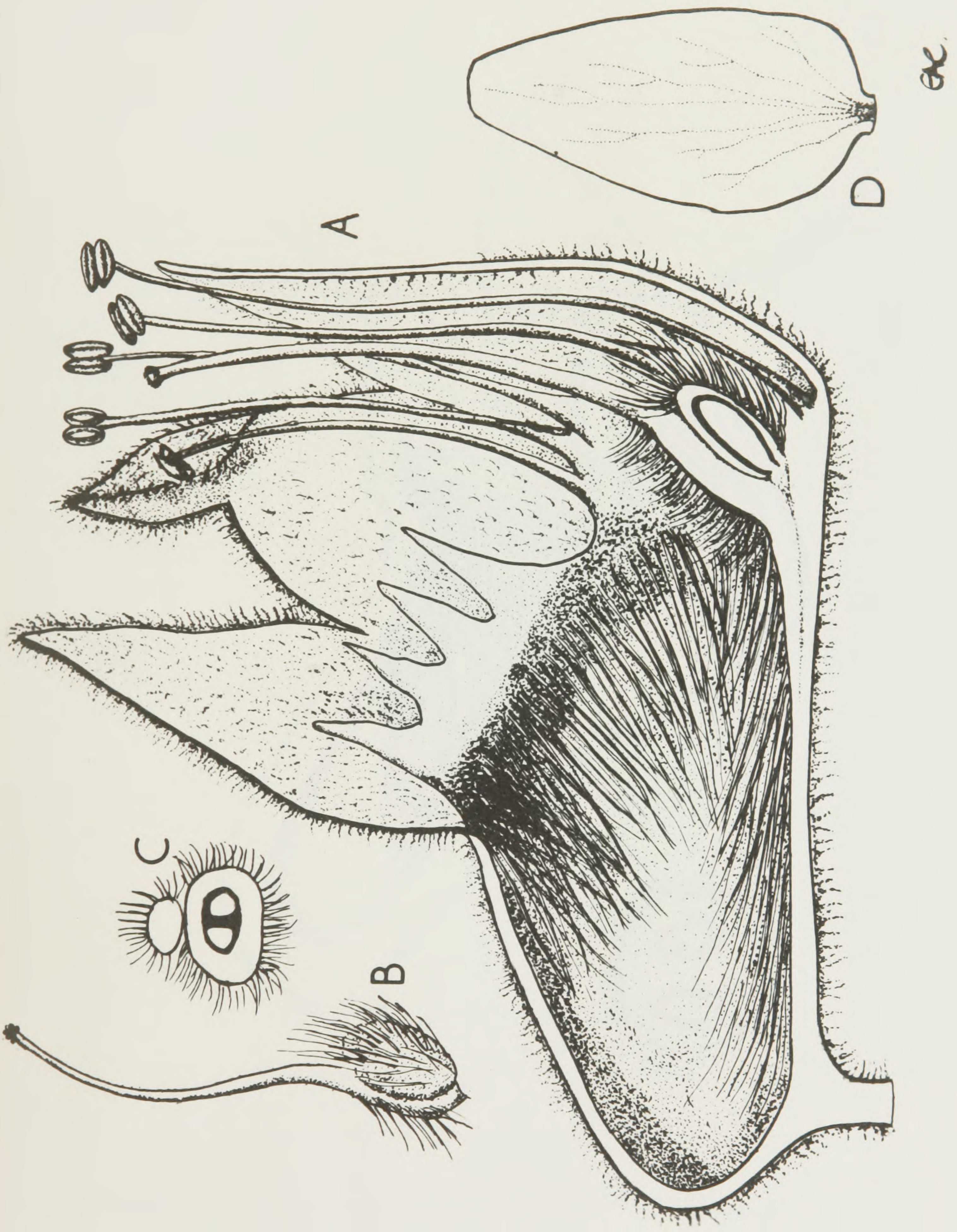

Plate XLV.- MAGNISTIPULA BUTAYEI De Wild.
A,flower (x23); B,ovary and style (x20); C,ovary (x20); D,petal (x20).

Plate XLVI.- MAGNISTIPULA TESSMANNII (Engl.)Prance
flower,ovary,and petal (all x25).

10. ACIOA

Aubl., Pl. Guian. 2:698, t. 280 (1775); Baillon in Adansonia 7:223 (1867); De Wildeman in Bull. Jard. Bot. Brux. 7:21 (1920); Maguire in Brittonia 7:271 (1951).

Dulacia Neck., Elem. Bot.: 414 (1790), non Dulacia Vell. (1823).

Acia Schreb., Gen. Pl. 2:458 (1791) pro parte excl. syn. Couepia.

Moquilea sensu Martius, Nov. Gen. et Sp. 79 (1826) pro parte quoad syn. Acioa tantum; sensu Blume, Mus. Bot. 2:92 (1852) pro parte quoad subgen. Acioa tantum.

Dactyladenia Welw., Apont. in Ann. Cons. Ultram. 55:572 (1859).

Griffonia Benth. in Benth. & Hook., Gen. Pl. 1:608 (1865) non Griffonia Baill. (1863).

Couepia sensu Benth. loc. cit. pro parte quoad syn. Acioa tantum.

Shrubs or small trees with hermaphrodite flowers 12-40 mm. long. Leaves usually with two glands towards the base of the lamina, leaf-undersurface glabrous or with stiff rust-coloured hairs, rarely with a white lanate tomentum; petiole eglandular. Bracts and bracteoles eglandular or with many stalked glands, not enclosing the flowers in groups. Inflorescence of branched or dichotomous racemes or less frequently of panicles. Receptacle usually elongate, obconic-tubular, rarely campanulate; hollow, glabrous within, tomentose or glabrous outside; calyx-lobes rounded or acute, puberulous inside. Stamens 10-65; filaments ligulately connate for most of their length, inserted laterally on rim of the receptacle; staminodes sometimes present, opposite the stamens. Ovary inserted laterally at the mouth of the receptacle; carpels unilocular. Fruit a hard or fleshy drupe, markedly tapered towards the base or apex, epicarp often with rusty tomentum, less often glabrous; mesocarp thin; endocarp usually hard, thin, with a roughish surface, hairy inside with no special mechanism allowing seedling escape. Germination hypogeal, first leaves opposite (observed in African species). (Plate XLVII).

Distribution: confined to West Africa and the Congo Basin except for 3 species in South America.

Type species: *Acioa guianensis* Aubl.

Notes - (1) *Acioa guianensis*, the type of the genus, was described by Aublet in 1775 and remained the only known American species until a few years ago. All subsequent workers up to the time of Baillon (1867) mistakenly united *Acioa* with *Couepia* or *Moquilea*, but none of them saw the type specimen which is now in the British Museum. In their 'Genera Plantarum' (1865) Bentham and Hooker cite *Acioa* as a synonym of *Couepia*. Their next genus, *Griffonia*, which was based on some specimens from West Africa in the Kew Herbarium, did not differ in essential characters from Aublet's original description of *Acioa*. In 1867 Baillon pointed out that *Griffonia* of Bentham was antedated by his own genus of that name in the *Caesalpinioideae* by a few days. Oliver (Fl. W. Trop. Afr. 2:371 (1871)) disputes this statement but Keay (F.W.T.A., ed. 2, 1:444) clearly shows that it is correct.

Baillon was the first to point out that Griffonia Benth. was the same as *Acioa* Aublet, and described three African species. In the Flora of Tropical Africa, Oliver, who had no material of Acioa from America for comparison continued to use Griffonia Benth. and mistakenly believed that it had priority over Griffonia Baill. He transferred Baillon's three species of Acioa to Griffonia and added two new ones. All botanists since Oliver have followed Baillon.

(2) Maguire (loc. cit.) has recently described two new American species (A. somnolens and A. schultesii) and discussed their relationships to A. guianensis, the type of the genus and previously the only known American representative. Both new species were based on single gatherings. A. somnolens is very closely related to A. guianensis, but A. schultesii, as indicated by Maguire is anomalous in certain respects. It differs from all other species of Acioa in having a shallowly cup-shaped (not narrowly tubular) receptacle and in having a short and broad staminal ligule. In other respects it resembles typical Acioa. As its fruit is still unknown it is impossible to decide whether it is best treated as an anomalous Acioa or as a distinct genus.

(3) Acioa appears to be most closely related to Magnistipula, and to Kostermansia, the only other genera in which the stamens are appreciably fused. It differs from Magnistipula chiefly in the receptacle and androecium. The receptacle of Acioa is elongate and tubular not obliquely ventricose. Acioa has 15-65 (or as few as 10 in A. somnolens and 14 in A. schultesii) far-exserted stamens whose filaments are united to form a strap-shaped structure. In Magnistipula the stamens are never more than 9, and are never exserted beyond the petals. They are fused for about half their length in two species but never form a strap-shaped structure.

Relationships with Kostermansia are discussed under that genus.

(4) The differences separating many of the species listed below are slight and a revision would almost certainly reduce their number.

American species

1. Acioa guianensis Aubl. Pl. Guian. 2:698 (1775).

Type: Aublet s.n., French Guiana, fl.-buds (BM).

Acia dulcis Willd., Sp. Pl. 3:717 (1800).

Acioa dulcis (Willd.) Steud., Nom. ed 1:9 (1821).

Distribution: French Guiana.

2. Acioa somnolens Maguire in Brittonia 7:272 (1951).

Type: Melinon 230, French Guiana, fl. (P).

Distribution: French Guiana.

3. Acioa schultesii Maguire in Brittonia 7:272 (1951).

Type: Schultes & Lopez 9958, Brazil-Amazonas, fl. (NY; K).

Distribution: Brazil.

African species

4. Acioa barteri (Oliv.) Engl. in Bot. Jahrb. 26:383 (1899).

Type specimens: Barter 2183, S. Nigeria, fl. (K); Thomson 66, S. Nigeria, fl. (K).

Griffonia barteri Oliv., Fl. Trop. Afr. 2:373 (1871).

A. tenuiflora Dinkl. & Engl. in Bot. Jahrb. 26:382 (1899).

A. eketensis De Wild. in Bull. Jard. Bot. Brux. 7:214 (1920).

Distribution: Guinea, Liberia to Nigeria, Cameroons, Congo.

5. Acioa bellayana Baill. in Adansonia 7:224 (1867).

Type: Griffon du Bellay s.n. (1864), Gabon, fl. (P).

Griffonia bellayana (Baill.) Oliv., Fl. Trop. Afr. 2:371 (1871).

Distribution: Gabon, Congo, Angola.

6. Acioa brazzai De Wild. in Bull. Jard. Bot. Brux. 7:202 (1920).

Type specimens: Thollon 565, Moyen Congo, fl. (P); 4209 fl. (P).

Distribution: Moyen Congo.

7. Acioa buchneri Engl. in Bot. Jahrb. 17:88 (1893).

Type: Buchner 10, Angola (not seen).

Distribution: Angola.

8. Acioa campestris Engl. in Bot. Jahrb. 17:88 (1893).

Type: Soyaux 362, Gabon, fl. (P; K).

Distribution: Gabon.

9. Acioa chevalieri De Wild. in Bull. Jard. Bot. Brux. 7:213 (1920).

Type specimens: Chevalier 26665, Moyen Congo, fl. (P); Dybowski 118, Moyen Congo, fl. (P; BR).

Distribution: Moyen Congo.

10. _Acioa_ _cinerea_ Engl. ex De Wild. in Bull. Jard. Bot. Brux. 7:211 (1920).

Type: _Zenker_ 2903, Cameroun, fl. (K; BR).

Distribution: Cameroun.

11. _Acioa_ _dawei_ E.J. Mendes in Trabh. Centr. Bot. Jun. Invest. Ultram. 1:3 (1962).

Type: _Dawe_ 225, Cabinda, (K; PHO).

Distribution: Cabinda.

12. _Acioa_ _dewevrei_ De Wild. & Dur. in Ann. Mus. Congo, Sér. 2, 1 (2):19 (1900).

Type: Dewèvre 743, Congo, (not seen).

_A._ _van-houttei_ De Wild. in Ann. Mus. Congo, Sér. 5, 2:235 (1908).

_A._ _reygaertii_ De Wild. in Bull. Jard. Bot. Brux. 7:201 (1920).

_A._ _seretii_ De Wild. in Ann. Mus. Congo, Sér. 5, 2:254 (1908).

_A._ _gilletii_ De Wild. in Ann. Mus. Congo, Sér. 5, 1:47 (1903).

Distribution: Congo, Angola.

13. _Acioa_ _dichotoma_ De Wild. in Bull. Jard. Bot. Brux. 7:216 (1920).

Type: _Talbot_ 3048, Nigeria, fl. (BM).

Distribution: Nigeria.

14. Acioa dinklagei Engl. in Bot. Jahrb. 26:381 (1899).

Type specimens: Dinklage 1648, Liberia, fl. (BM); 2023, fl. (BM).

Distribution: Liberia, Ghana.

15. Acioa floribunda (Welw.) Exell in Journ. of Bot. 66. Suppl. 1:161 (1928).

Type: Welwitsch 1289, 1289b, Angola, fl. (K).

Dactyladenia floribunda Welw., Apont., in Ann. Cons. Ultram. 55:572 (1859).

Acioa icondere Baill. in Adansonia 7:223 (1867).

Griffonia icondere (Baill.) Oliv., Fl. Trop. Afr. 2:371 (1871).

Distribution: Gabon, Congo, Angola.

16. Acioa hirsuta A. Chev. ex De Wild. in Bull. Jard. Bot. Brux. 7:200 (1920).

Type: Chevalier 19738, Ivory Coast (P).

Distribution: Ivory Coast.

17. Acioa johnstonei Hoyle in Kew Bull. 1932:258 (1932); op. cit. 1947:71 (1947).

Type: Johnstone 74/31, Cameroons, fl. (FHO; K).

Distribution: Cameroons.

18. Acioa klaineana Pierre ex De Wild. in Bull. Jard. Bot. Brux. 7:196 (1920).

Type: Klaine 12, Gabon (P).

Distribution: Nigeria, Cameroons, Cameroun, Gabon.

19. Acioa laevis Pierre ex De Wild. in Bull. Jard. Bot. Brux. 7:205 (1920).

Type: Klaine 1890, Gabon (P).

Distribution: Gabon.

20. Acioa lanceolata Engl. in Bot. Jahrb. 26:383 (1899).

Type: Dinklage 925, Cameroun (not seen).

Distribution: Cameroun.

21. Acioa lujai De Wild. in Bull. Jard. Bot. Brux. 7:209 (1920).

Type: Luja 38, Congo, fl. (BR).

A. gossweileri Cavaco in Bull., Mus. Hist. Nat. Paris Sér. 2, 26:638 (1954).

Distribution: Congo, Angola.

22. Acioa mannii (Oliv.) Engl. in Bot. Jahrb. 26:384 (1899).

Type: Mann 1427, Fernando Po, fl. (K).

Griffonia mannii Oliv., Fl. Trop. Afr. 2:372 (1871).

Distribution: Cameroons, Fernando Po.

23. Acioa pallescens Baill. in Adansonia 7:224 (1867).

Type: Griffon du Bellay 261, Gabon (P).

Griffonia pallescens (Baill.) Oliv., Fl. Trop. Afr. 2:372 (1871).

Distribution: Nigeria, Cameroons, Cameroun, Rio Muni, Gabon.

24. Acioa parvifolia Engl. in Bot. Jahrb. 26:380 (1899).

Type: Afzelius s.n., Sierra Leone (not seen).

Distribution: Sierra Leone.

25. Acioa pierrei De Wild. in Bull. Jard. Bot. Brux. 7:212 (1912).

Type specimens: Klaine 196, Gabon, fl. (P; K; E); 420 fl. (P).

Distribution: Gabon.

26. Acioa rudatisii De Wild. in Bull. Jard. Bot. Brux. 7:215 (1920).

Type specimens: Rudatis 30, Cameroons, fl. (K; BM); Diestel 654, Cameroons, fl. (K).

Distribution: Cameroons, Nigeria.

27. Acioa sapinii De Wild. in Bull. Jard. Bot. Brux. 4:80 (1914).

Type: Sapin s.n., Congo, fl. (BR).

Distribution: Congo.

Known only from Type collection.

28. Acioa scabrifolia Hua in Bull. Mus. Hist. Nat. Paris 3:328 (1897).

Type: Miquel 24, French Guinea, fl. (P).

A. lehmbachii Engl. in Bot. Jahrb. 26:379 (1899).

Distribution: French Guinea, Sierra Leone, Liberia, Ivory Coast, Rio Muni, Cameroons, Gabon.

29. Acioa smeathmannii Baill. in Adansonia 10:244 (1872).

Type: Smeathman s.n., Sierra Leone (not seen).

Distribution: Sierra Leone.

30. Acioa staudtii Engl. in Bot. Jahrb. 26:379 (1899).

Type: Staudt 263, Cameroons, fl. (K).

Distribution: Cameroons.

31. Acioa talbotii Bak. f. in Cat. Talbot's Nigerian Pl.: 29 (1913).

Type: Talbot 1533, Nigeria, fl. (K; BM).

Distribution: Nigeria.

32. Acioa thollonii De Wild. in Bull. Jard. Bot. Brux. 7:208 (1920).

Type: Thollon 794, Moyen Congo, fl. (P).

Distribution: Moyen Congo.

33. Acioa unwinii De Wild. in Bull. Jard. Bot. Brux. 7:198 (1920).

Type: Unwin & Smyth 36, Sierra Leone, fl. (K).

Distribution: Sierra Leone, Nigeria.

34. Acioa whytei Stapf in Journ. Linn. Soc. 27:97 (1905).

Type: Whyte s.n., Liberia, fl. (K).

Acioa stapfiana De Wild. in Bull. Jard. Bot. Brux. 7:204 (1920).

Distribution: Sierra Leone, Liberia.

Species exclusae

Acioa amara Steud., Nom. ed. 1:9 (1821) = *Couepia guianensis* Aubl.

A. goetzeana Engl. in Bot. Jahrb. 30:315 (1902) = *Hirtella zanzibarica* Oliv.

Plate XLVII.- ACIOA BELLAYANA Baill.
A,flower (x3); B,petal (x4); C,anthers (x10).

11. PARINARI

Aubl., Pl. Guian. 1:514 (1775); Hauman in Bull. Jard. Bot. Brux. 21:185 (1951) pro parte quoad subgen. Euparinari tantum.

Parinarium Juss., Gen.:342 (1789); DC., Prodr. 2:526 (1825) pro parte quoad Sectio Petrocarya et Sectio Neocarya excl. P. senegalense; Benth. in Hook., Niger Fl.: 335 (1849) pro parte quoad Sectio Petrocarya tantum; Blume, Mélange Bot. 2:10 (1855), Hasskl. in Flora 16:254 (1858) pro parte quoad subgen. Euparinarium tantum; C. Muell. in Walp., Ann. Bot. Syst. 4:644 (1857) pro parte quoad sectio Euparinarium tantum; Miquel., Fl. Ind. Bat. 1(1):353 (1853) pro parte quoad subgen. Petrocarya tantum.

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

Petrocarya Schreb., Gen. Pl.: 245 (1789).

Balantium Desv. in Ham., Prod. Fl. Ind. Occ.: 34 (1825).

Lepidocarpa Korth. in Nederl. Kruidk. Arch. 3:385 (1855); Miq., Fl. Ind. Bat. 1(1):353 (1855) as Lepidocarya (Sphalm.).

Small or large trees or rarely suffruticose with hermaphrodite flowers 4-7 (11) mm. long. Leaf-undersurface nearly always with stomatal cavities filled with hairs, rarely glabrous. Petiole usually with 2 glands. Bracts and bracteoles eglandular, usually enclosing the young flowers in small groups. Inflorescence of much branches panicles. Receptacle turbinate-campanulate, slightly swollen to one side, hollow, usually hairy inside throughout, tomentose outside; calyx-lobes 5, acute. Stamens 6-8, included, grouped on one side of the receptacle, staminodes inserted opposite to them. Ovary inserted laterally at the mouth of the receptacle, carpel bilocular. Fruit a fleshy drupe with verrucose epicarp; endocarp hard, thick and with a rough fibrous surface with two basal plugs or stoppers the detachment of which allows the seedlings to escape. Germination hypogeal, first leaves alternate (Plate XLVIII).

Distribution: pan-Tropical.

Type species: P. campestris Aubl.

Notes - (1) The great majority of species of Parinari sens. strict. share a number of distinctive characters which only occur sporadically elswehere in the family. Nearly all species have stomatal cavities filled with hairs on the leaf-undersurface (elsewhere only known in a few species of Licania and in Neocarya and Bafodeya). All species but one have the flower-buds enclosed in small groups by the bracts and bracteoles (elsewhere found only in 2 species of Couepia and 4 spp. of Licania which comprise subgenus Parinariopsis). All species have a verrucose epicarp and a rough fibrous endocarp of varying thickness with two basal plugs or stoppers which enable the seedlings to escape on germination. The epicarp character is shared by a few species of Couepia and Licania and by Neocarya and Bafodeya. Only Neocarya has a similar endocarp. These distinctive characters are reinforced by others, particularly of the flower, which, in combination, elsewhere in the family, are of the kind on which generic distinctions are based.

The statistical work shows that Parinari sens. strict. is the most compact genus in the family and the most distinct from all the others. Nevertheless its exact circumscription is a matter of judgement. Those species which share all the distinctive features mentioned above form an indivisible unit. There are about 40 of them and they occur throughout the Tropics (except for Central America). Despite the very wide range of ecological conditions they occupy, the differences between species, other than differences of life-form, are slight (White, 1962, p. 97). Geographically widely separated species are often very similar.

In addition to this remarkably uniform group there are two anomalous species, the placing of which raises important taxonomic issues. P. sericeo-argentea only differs from typical Parinari in having glabrous leaves. A closely related species, P. canarioides, also has glabrous leaves and its flower-buds are not enclosed by the bracts. This species was used in the statistical analysis (see Chapter 10). It is tempting to exclude these species from Parinari in order to preserve the latter's purity and some taxonomists would unquestionably do this. But if this were done innumerable anomalous species in the other genera would likewise have to be removed and a plethora of small new genera would result. These two species are so close to Parinari in all other respects that their inclusion scarcely enlarges the variation of that genus.

However, having included these slightly anomalous species it is important to decide if other species somewhat more anomalous should also be included. Neocarya differs from Parinari in a number of small floral characters (shape of receptacle which is glabrous at the base inside, more numerous stamens, bracts not enclosing flowers, racemose inflorescence); there are also some slight differences in wood anatomy (Chapter 3). It does, however, share the distinctive leaf-undersurface and fruit of Parinari. Bafodeya has fewer floral differences (receptacle-shape and flowers not enclosed by bracts) and has the Parinari-type of leaf-undersurface but a different fruit structure. Somewhat more distinct is Duckea which is very similar to Parinari in its floral structure and inflorescence, but differs in its leaf-undersurface and fruit structure. Other genera show increasing degrees of divergence.

The situation is that the differences between Parinari and Neocarya or between Parinari and Bafodeya are as great as those separating long-established genera in the group. If Bafodeya and Neocarya are united with Parinari the process of lumping could not be stopped there and all members of the family would have to be amalgamated to form a single genus. A wise taxonomist starting de novo could justifiably do this but for practical considerations it would be unthinkable now. Although many of the characters used to distinguish genera are individually slight it so happens that all species of all genera of the Hirtelleae recognized in this work differ from all other species in at least four such characters (three only in Bafodeya), and as the statistical work confirms, all the genera are discrete though closely related entities.

(2) Aublet based Parinari on two species, P. campestris and P. montana. Hauman (1951) chose the former as the type of the genus because the figure and description of the latter are not quite accurate. Furthermore the type material of P. montana is mixed and is contaminated with P. rodolphii Hub. (Ducke, 1935).

(3) Ferolia Aubl. (Pl. Guian. Suppl.: 8 (1775) is usually cited as a synonym of Parinari. The name Ferolia was first used by Barrère (Essai ... France équin.:51 (1741)) who described the use of its wood by the South American Indians. Aublet's type sheet of Ferolia is at the British Museum and although it is sterile it is certainly not Parinari nor indeed any other genus of Chrysobalanaceae. The type of leaf-

venation and the absence of stomatal cavities on the leaf-undersurface would exclude it from the South American Parinari. Kuntze (Rev. Gen. 1891) mistakenly transferred all species of Parinari known to him to Ferolia.

(4) Most authors who have described species of Parinari have used Juisseau's latinized form Parinarium. I consider the latter to be a mere orthographic variant of the former and so it is not in my opinion necessary to make new combinations for all species described under the name Parinarium, as is done, for instance, by Dandy in Andrews, Fl. Pl. Anglo-Egypt. Sudan: 105 (1952).

1. Parinari campestris Aubl., Pl. Guian. 1:514, t. 206 (1775).

Type: Aublet s.n., French Guiana, fr. (BM).

Distribution: West Indies, Guiana, Brazil.

This species is recorded from Africa by Kleinhoonte (in Pulle, Fl. Suriname 2(1):426 (1939)) but I have seen no evidence that this is true.

2. Parinari montana Aubl., Pl. Guian. 1:514, t. 204, 205 (1775) pro parte; quoad fruct. excl. fol. et ramul.; Huber in Bol. Mus. Pará. 6:77 (1910); Ducke in Rev. Bot. Appl. 163:180 (1935).

Type: Aublet s.n., French Guiana, fr. (only, excluding leaves), (BM).

Parinari pajura R. Ben. in Bull. Mus. Hist. Nat. Paris 28:232 (1922).

Moquilea rufa B. Rodr. Hort. Flumin.: 165 (1895) pro parte quoad fruct. tantum.

Petrocarya montana (Aubl.) Willd., Sp. Pl. 2:287 (1800).

Parinari lucidissima Standl. in Lloydia 2:183 (1939).

Distribution: Guianas, Brazil, Venezuela.

This species and related species are remarkable for the long-haired rusty indumentum of the young branches and inflorescence and for the long linear stipules.

3. Parinari ["Parinarium"] anamensis Hance in Journ. of Bot. 15:333 (1877).

Type: Pierre 339, S. Vietnam, fl. fr. (BM; K).

Parinari ["Parinarium"] albida Craib in Kew Bull. 1912:152 (1912).

Distribution: Indo China.

4. Parinari bicolor Merr. in Philipp. Journ. Sci. Bot. 10:309 (1915).

Type: Ruzon, For. Bur. 28022, Philippines, fl. (K).

Distribution: Philippines.

This species has large persistent stipules resembling those of P. montana Aubl.

5. Parinari ["Parinarium"] boivinii Fritsch in Annal. Naturh. Hofmus. Wien 5:14 (1890).

Type: Boivin s.n., Madagascar.

Distribution: Madagascar.

6. Parinari ["Parinarium"] borneensis Merr. in Univ. Calif. Publ. Bot. 15:93 (1929).

Type: Elmer 27396, Borneo fl. (BR; M).

Distribution: Borneo, Brunei.

7. Parinari ["Parinarium"] brachystachya Benth. in Hook. Journ. of Bot. 2:213 (1840).

Type: Schomburgk 785, British Guiana, fl. (K; OXF).

Parinari ["Parinarium"] amazonica Mart. ex Hook. f. in Mart., Fl. Bras. 14(2):52 (1867) nom. nud. in syn.

Parinari excelsa auct. non Sabine; Oliv., Fl. Trop. Afr. 2:367 (1871); Kleinhoonte in Pulle, Fl. Suriname 2(1):426 (1939); pro parte quoad syn. Parinarium brachystachyum tantum.

Kleinhoonte united P. brachystachya with the African P. excelsa. They are certainly closely related, but I consider them to be specifically distinct.

8. Parinari ["Parinarium"] brasiliensis (Schott) Hook. f. in Mart. Fl. Bras. 14(2):51 (1867).

Type specimens: Pohl s.n., Brazil-Minas fl., (BR); Schott s.n., Brazil-Rio de Janeiro fl. (K).

Petrocarya brasiliensis Schott in Spreng. Syst. 4. App. 405 (1827).

Distribution: Brazil.

9. Parinari canarioides Kosterm., New & Crit. Mal. Fl. 3:25 (1955).

Type: Kostermans 7152, Sumatra, fl. (BO not seen; K).

Distribution: Sumatra, Borneo.

10. Parinari ["Parinarium"] capensis Harv. in Harv. & Sond., Fl. Cap. 2:597 (1894).

Type specimens: Zeyher 537, South Africa st. (K syn.); Burke 518, South Africa, fl. (K. syn.).

Parinarium latifolium (Oliv.) Exell in Journ. of

Bot. 66, Suppl. 1:160 (1928) (P. capense Harv. var. latifolium Oliv., Fl. Trop. Afr. 2:369 (1871)).

Parinari ["Parinarium"] pumilum Mildbr. in Wiss. Ergebn. Deutsch. Zentr. Afr. Expd. 1910-11, 2:10 (1922) nom. nud.

Distribution: Congo to South Africa.

11. Parinari ["Parinarium"] cardiophylla Ducke in Archiv. Inst. Biol. Veg., Rio de Janeiro 2:33 (1935).

Type specimens: Ducke H.J.B.R. 24182, Brazil-Amazonas, fl. (RB not seen; P, iso); H.J.B.R. 24183, fl. (K, para).

Distribution: Brazil.

12. Parinari ["Parinarium"] chapelieri Baill. in Adansonia 9:148 (1869).

Type: Chapelier s.n., Madagascar, fl. (P).

Distribution: Madagascar.

13. Parinari ["Parinarium"] congensis Didr. in Kjoeb. Vidensk. Meddel. 1854:197 (1854).

Type specimens: C. Smith 67/366 (not seen), Congo, 52/295 (not seen).

Parinari ["Parinarium"] subcordata Oliv., Fl. Trop. Afr. 2:367 (1871).

Distribution: French Guinea, Sierra Leone, Ivory Coast, Ghana, Togo, Dahomey, Nigeria, Ubangui-Shari, Cameroons, Congo.

14. Parinari ["Parinarium"] congolana Th. & H. Dur., Syll. Fl. Congo: 189 (1909).

Type specimens: Laurent s.n., Congo, fl. (BR); Camp 691, Congo, fl. (BR).

Parinari ["Parinarium"] congoensis Engl. in Bot. Jahrb. 26:377 (1899).

P. minus H. Bn. ex Aubrév., Contr. paleohist. forêts de l'Afr. Trop.: 92 (1949) nom. nud.

Distribution: Congo.

This species is remarkable in this genus for the size of its flowers (up to 11 mm. long) and the glandular calyx-lobes. The receptacle is elongate and the exterior is covered in a long rust coloured tomentum. The leaves and fruit are typical of Parinari and it has bracts which enclose groups of flowers.

15. Parinari ["Parinarium"] costata (Korth.) Blume, Mélang. Bot. 2:10 (1855); C. Muell. in Walp., Ann. Bot. Syst. 4:644 (1857); Hasskl. in Flora 41:255 (1858).

Type: Korthals, Sumatra (not seen).

Lepidocarpa costata Korth. in Nederl. Kruidk. Arch. 3:397 (1855).

L. ovalis Korth. tom cit.: 386 (1855).

Parinari ["Parinarium"] ovalis (Korth.) Blume ex Miq. Fl. Ind. Bat. 1(1):353 (1855).

P. elmeri Merr. in Univ. Calif. Publ. Bot. 15:92 (1929).

Distribution: Malay Penin., Indonesia, Borneo.

The specimens distributed under the type number of P. elmeri represent two species. The sheets of Elmer 20806 at Kew and Munich belong to P. costata and they correspond to the original description. Elmer 20806 at the British Museum and Brussels belongs to Kostermansia myriandra (Merr.) Prance.

16. Parinari ["Parinarium"] curatellifolia Planch. ex Benth. in Hook. Niger Fl.: 333 (1849).

Type specimens: Heudelot 362, Senegal, fl. (OXF; K);

Vogel 177, Sierra Leone, fl. (K).

Parinari mobola Oliv., Fl. Trop. Afr. 2:368 (1871).

P. ["Parinarium"] gardineri Hemsl. in Journ. of Bot. 54 Suppl. 2:13 (1916).

Distribution: Senegal to Angola, Southern Rhodesia, Mozambique.

The type of P. gardineri comes from the Seychelles, where it was probably introduced.

17. Parinari ["Parinarium"] excelsa Sabine in Trans. Hort. Soc. 5:451 (1824).

Type: Don s.n., Sierra Leone, fl., fr. (K; lecto).

Petrocarya excelsa (Sabine) Steud. Nom. ed. 2. 2:309 (1841) non Jack.

Parinari ["Parinarium"] holstii Engl. Pflanzenw. Ost.-Afr. C. Add. : 423 (1896).

P. ["Parinarium"] elliotii Engl. in Bot. Jahrb. 26:377 (1899).

P. ["Parinarium"] whytei Engl. tom. cit.: 378 (1899).

P. ["Parinarium"] tenuifolia A. Chev., Vég. Ut. Afr. trop. Franç. 5:225 (1909).

P. ["Parinarium"] nalaensis De Wild., Pl. Bequaert 50:289 (1931).

P. ["Parinarium"] riparia R.E. Fr. in Fedde Rep. 12:539 (1913).

P. ["Parinarium"] salicifolia Engl. in Abh. Preuss. Akad. Wiss.: 54 (1894) nom illegit. non (Presl) Miq.

P. mildbraedii Engl. in Wiss. Ergebn. Deutsch. Zentr. Afr. Exped. 1907-8, 2:227 (1911).

Distribution: Guinea to Tanganyika and Northern Rhodesia, Mozambique.

18. Parinari ["Parinarium"] glazioviana Warm. in Kjoeb. Vidensk. Meddel. 1874:72 (1874).

Type specimens: Brazil-Rio de Janeiro Glaziou 752 fl. (P); 2128, 2560, fl. (BR; K; P).

Distribution: Brazil.

19. Parinari ["Parinarium"] gracilis Kuhlm. in An. Prim. Reun. Sul-Amer. Bot. 3:78 (1940).

Type: Kuhlmann 279 (H.J.B.R. 34160), Brazil-Expírito Santo (not seen).

Distribution: Brazil.

I have not seen material of this species.

20. Parinari ["Parinarium"] helferi Hook. f., Fl. Brit. Ind. 2:311 (1879).

Type: Helfer s.n., Burma, st. (K).

Parinari ["Parinarium"] sumatrana sensu Kurz, For. Fl. Brit. Burma 1:433 (1877) non Benth.

Distribution: Burma.

21. Parinari ["Parinarium"] insulara A. Gray, Bot. U.S. Expl. Exped. 1:488 (1854).

Type: Herb. U.S. Expl. Exped. s.n., Samoa, fr. (K).

Distribution: Fiji, Samoa.

22. Parinari ["Parinarium"] laxiflora Ducke in Arch. Jard. Bot. Rio de Janeiro 3:44 (1922).

Type specimens: Ducke H.J.B.R. 11051, Brazil-Amazonas, fl. (K); 15244 fr. (P).

Distribution: Brazil, Bolivia.

23. Parinari ["Parinarium"] nonda F. Muell. ex Benth., Fl. Austral. 2:426 (1804).

Type specimens: Liechart s.n., N. Territory Australia (not seen); Mueller s.n., N. Territory Australia, fl. (K); M'Gillivray s.n., N. Territory Australia fl. (BM).

Distribution: New Guinea, Australia.

24. Parinari ["Parinarium"] oblongifolia Hook.f., Fl. Brit. Ind. 2:309 (1879).

Type specimens: Griffith s.n., Malay Peninsula (not seen); Maingay 623, Malay Peninsula, fl. (K).

Parinari ["Parinarium"] wallichiana R.Br. in Wall. Cat. n. 7520 (1832).

Distribution: Malay Peninsula, Borneo, Sumatra.

25. Parinari ["Parinarium"] obtusifolia Hook.f. in Mart., Fl. Bras. 14(2):52 (1864).

Type: Gardner 3137, Brazil-Goyaz fl. (K; OXF).

Distribution: Brazil.

26. Parinari ["Parinarium"] pachyphylla Rusby, Descr. New Sp. S. Am. Pl.: 26 (1920).

Type: H.H. Smith 1775, Colombia, fl., fr. (K; P).

Distribution: Colombia.

27. Parinari ["Parinarium"] papuana C.T. White in Journ. Arn. Arb. 31:86 (1950).

Type specimens: L.S. Smith N.G.F. 1019, New Guinea, fr. (not seen); 1004, New Guinea, st. (L para).

Distribution: New Guinea.

28. Parinari ["Parinarium"] parilis Macbride in Candollea 5:367 (1934).

Type: Williams 1140, Peru, fl. (not seen).

Distribution: Peru.

29. Parinari parvifolia Sandw. in Kew Bull. 1931:374 (1931).

Type: Sandwith 139, British Guiana, fl. (K).

Distribution: British Guiana.

30. Parinari ["Parinarium"] pohlii Hook. f. in Mart., Fl. Bras. 14(2):51 (1867).

Type: Pohl s.n., Brazil-Minas, fl. (M; BR).

Distribution: Brazil.

31. Parinari ["Parinarium"] polyneura Miq., Fl. Ind. Bat. Suppl.: 306 (1860).

Type: Teysmann s.n., Sumatra, st. (K).

Distribution: Malay Peninsula, Sumatra.

32. Parinari ["Parinarium"] rodolphii Huber in Bol. Mus. Pará 6:77 (1910); Ducke in Rev. Bot. Appl. 163:181 (1935).

Type: Rodrigues H.A.M.G. 9648, Brazil, fl. (K).

Parinari montanum Aubl., Pl. Guiane 1:514 (1775), pro parte quoad fol. et ramul. tantum.

Distribution: Brazil.

33. Parinari ["Parinarium"] rubiginosa Ridl. in Journ. As. Soc. Straits Br. 75:29 (1917).

Type: Ridley 16016, Malay Penins., fl. (K).

Distribution: Malay Peninsula.

34. Parinari salomonensis C.T. White in Journ. Arn. Arb. 31:87 (1950).

Type specimens: Walker & White B.S.I.P. 149a, British Solomon Isles (not seen); 149 fr. (K).

Distribution: Solomon Isles, New Guinea.

35. Parinari ["Parinarium"] sprucei Hook. f. in Mart., Fl. Bras. 14(2):53 (1867).

Type: Spruce 2539, Brazil-Amazonas, fl. (K; OXF).

Distribution: Brazil.

36. Parinari ["Parinarium"] sumatrana (Jack.) Benth. in Hook., Niger Fl.: 335 (1849).

Type: Koorders 8562B, Sumatra, fr. (K).

Petrocarya sumatrana Jack. in Malay Misc. 2, n.7: 67 (1822).

Distribution: Sumatra.

37. Parinari verdickii De Wild. in Ann. Mus. Congo Sér. 4:182 (1903).

Type: Verdick 568, Congo, fl. (BR).

Parinari whytei sensu Hauman in Bull. Jard. Bot. Brux. 21:192 (1951) non Engl.

Distribution: Congo, Angola.

I think this might be a hybrid between P. excelsa and P. curatellifolia.

38. Parinari parya Kosterm. ined.

Type: Boden-Kloss 14676, Sumatra, fl. (K).

Distribution: Sumatra.

39. Parinari sericeo-argentea Kosterm. ined.

Type: Mail B.N.B.F.D. 2875; North Borneo, fl. (K; FHO).

Distribution: Borneo.

Species exclusae

P. asperulum Miq.	= Cyclandrophora asperula (Miq.) Prance
P. aubrevillei Pellegr.	= Maranthes aubrevillei (Pellegr.) Prance
P. bangweolense R.E. Fr.	= Magnistipula bangweolensis (R.E. Fr.) R.A. Graham.
P. baoulense A. Chev.	= Maranthes polyandra (Benth.) Prance
P. barbatum Ducke	= Duckea barbata (Ducke) Prance
P. benna Sc. Elliot	= Bafodeya benna (Sc. Elliot) Prance
P. bequaerti De Wild.	= Maranthes polyandra (Benth.) Prance
P. canescens Gleas.	= Couepia canescens (Gleas.) Prance
P. chrysophyllum Oliv.	= Maranthes chrysophylla (Oliv.) Prance
P. coccineum Elm.	= Pygeum coccineum (Elm.) Elm.
P. cordatum Hook. f.	= Duckea cordata (Hook. f.) Prance
P. coriaceum Benth.	= Duckea coriacea (Benth.) Prance
P. corymbosum (Bl.) Miq.	= Maranthes corymbosa Bl.
P. curranii Merr.	= Cyclandrophora glaberrima Hasskl.
P. dillenifolium R. Br.	= Dipterocarpus cornutus Dyer
P. elatum King	= Cyclandrophora elata (King) Prance
P. emirnense Bak. f.	= haud Chrysobalanaceae
P. fleuryana (A. Chev.) Aubrév.	= Magnistipula fleuryana (A. Chev.) Hauman
P. floribundum Bak. f.	= Maranthes polyandra (Benth.) Prance
P. gabunense Engl.	= Maranthes gabunensis (Engl.) Prance
P. gardneri Hook. f.	= Duckea gardneri (Hook. f.) Prance
P. gilletii De Wild.	= Maranthes glabra (Oliv.) Prance
P. glaberrimum Hasskl.	= Cyclandrophora glaberrima Hasskl.
P. glabrum Oliv.	= Maranthes glabra (Oliv.) Prance
P. goetzenianum Engl.	= Maranthes goetzeniana (Engl.) Prance
P. griffithianum Benth.	= Maranthes corymbosa Bl.
P. guyanense Fritsch	= Hirtella guyanensis (Fritsch) Sandw.

P. heteropetalum Scortech. ex King	= Kostermansia heteropetala (Scortech. ex King) Prance
P. hostmanni Fritsch	= Couepia cognata (Steud.) Fritsch
P. indicum Bedd.	= Cyclandrophora indica (Bedd.) Prance
P. ingangense Pellegr.	= Magnistipula tessmannii (Engl.) Prance
P. iodocalyx Mildbr.	= Maranthes iodocalyx (Mildbr.) Prance
P. kerstingii Engl.	= Maranthes kerstingii (Engl.) Prance
P. klaineanum Pierre ex A. Chev.	= Maranthes robusta (Oliv.) Prance
P. krukovii Gleas.	= Couepia sp.
P. kunstleri King	= Cyclandrophora asperula (Miq.) Prance
P. lanceolatum Teijsm. & Binn.	= Cyclandrophora glaberrima Hasskl.
P. latifolia Henders.	= Cyclandrophora latifolia (Henders.) Prance
P. laurinum A. Gray	= Cyclandrophora glaberrima Hasskl.
P. macrophyllum Sabine	= Neocarya macrophylla (Sabine) Prance
P. macrophyllum Teijsm. & Binn.	= Cyclandrophora glaberrima Hasskl.
P. maingayi King	= Cyclandrophora asperula (Miq.) Prance
P. maranthes Bl.	= Maranthes corymbosa Bl.
P. mindanaense Perk.	= Cyclandrophora glaberrima Hasskl.
P. minutiflorum Bak. f.	= Hunga gerontogea (Schlecht.) Prance
P. montanum Engl.	= Maranthes glabra (Oliv.) Prance
P. multiflorum Miq.	= Maranthes corymbosa Bl.
P. myriandrum Merr.	= Kostermansia myriandra (Merr.) Prance
P. myrsinoides Schlecht.	= ? Hunga sp.
P. neocaledonicum Bak. f.	= Hunga gerontogea (Schlecht.) Prance
P. nitidum Hook. f.	= Licania splendens (Korth.) Prance
P. palauensis Kanehira	= Maranthes corymbosa Bl.
P. petiolata V. Malm.	= Maranthes corymbosa Bl.

P. philippinensis Elm.	= Licania splendens (Korth.) Prance
P. pilosa Standl.	= Couepia canomensis (Mart.) Benth.
P. poggei Engl.	= Maranthes poggei (Engl.) Prance
P. polyandrum Benth.	= Maranthes polyandra (Benth.) Prance
P. polystachyum Poepp. ex Fritsch	= Couepia amazonica Fritsch
P. racemosum Merr.	= Cyclandrophora glaberrima Hasskl.
P. racemosum Vid.	= Maranthes corymbosa Bl.
P. robustum Oliv.	= Maranthes robusta (Oliv.) Prance
P. salicifolium Miq.	= Maranthes corymbosa Bl.
P. sargosii Pellegr.	= Magnistipula butayei De Wild.
P. scabrum Hasskl.	= Cyclandrophora glaberrima Hasskl.
P. senegalense Perr. ex DC.	= Neocarya macrophylla (Sabine) Prance
P. tessmannii Engl.	= Magnistipula tessmannii (Engl.) Prance
P. tibatense Engl.	= Maranthes glabra (Oliv.) Prance
P. tisserantii Aubrév. & Pellegr.	= Magnistipula butayei De Wild.
P. tranvancoricum Bedd.	= Cyclandrophora travancorica (Bedd.) Prance
P. vassonii A. Chev.	= Maranthes glabra (Oliv.) Prance
P. versicolor Engl.	= Magnistipula ? zenkeri Engl.
P. villamilii Merr.	= Cyclandrophora villamilii (Merr.) Prance

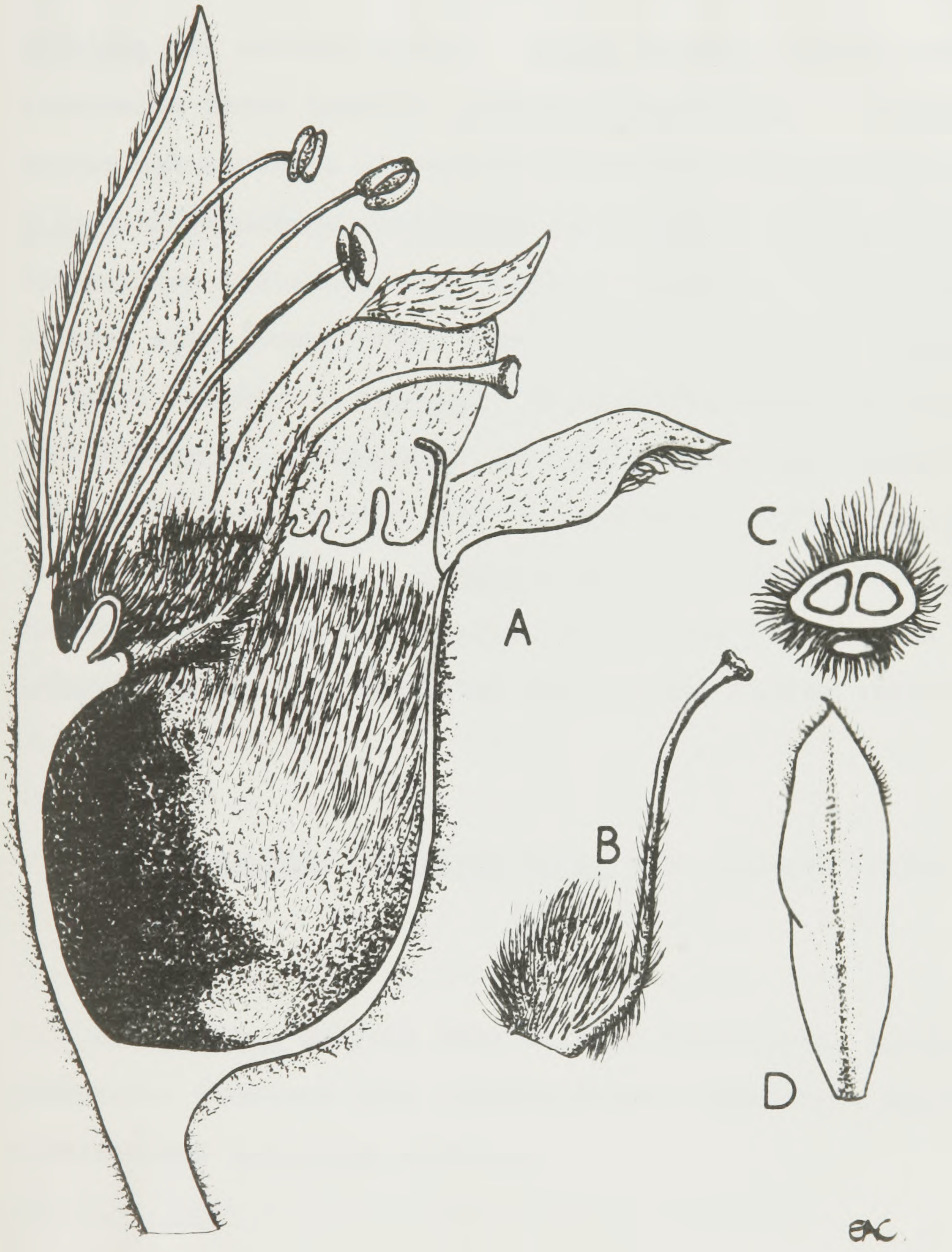

Plate XLVIII.- PARINARI MONTANA Aubl.
A,flower (x15); B,ovary and style (x15); C,ovary (x20); D,petal (x20).

12. BAFODEYA Prance, genus novum

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

Frutices vel arbores parvi. Folia integra, subtus cum cavis stomatalis dense lanatis, petiolo eglanduloso. Bracteolae parvae eglandulosae alabastris floralibus haud includentae. Flores in paniculas terminales dispositi. Calycis tubus lateraliter inflatus, ventricosus, excavatus, intus ubique pilosus extus tomentosus, lobi 5 acuti imbricati. Petala 5 sessilia decidua. Stamina 7 ad marginem adaxialem calycis tubi disposita, staminodiis stamina diametricale opposita orta. Ovarium ad orem calycis tubi lateraliter insertum biloculare, loculis uni-ovulatis. Stylus basilaris filiformis. Fructus drupaceus carnosus extus sparse verrucosus, endocarpio laeve indurato demum unilateraliter dehiscente, semine erecto.

Typus generis: Bafodeya benna (Sc. Elliot) Prance

Ab Parinari calycis tubo oblique ventricoso, bracteolis glomerulos florales haud includentibus, endocarpio laeve sine obturamentis basilibus differt.

Shrubs with hermaphrodite flowers ± 6 mm. long. Leaf-undersurface with stomatal cavities filled with dense woolly hairs. Petioles eglandular. Bracts and bracteoles small, eglandular, not enclosing the young flowers in groups. Inflorescence of terminal panicles. Receptacle swollen laterally, ventricose, hollow, hairy inside throughout, tomentose outside; calyx-lobes acute. Stamens 7, shorter than the calyx lobes, grouped to one side of the receptacle with the staminodes inserted opposite to them. Ovary inserted laterally at the mouth of the receptacle, pilose, carpel bilocular. Fruit a fleshy drupe, sparsely warted; endocarp hard, smooth, dehiscing on germination. (Plate XLVIX).

Distribution: confined to West Africa.

Notes - (1) The generic name is taken from the type locality of *Parinari benna*, Bafodeya, a range of hills in Sierra Leone.

(2) *Bafodeya* differs from *Parinari* in having flowers not enclosed by bracts in the bud and with a different receptacle-shape; the endocarp dehisces by a single line of weakness and not by broad stoppers. The stomatal cavities of the lower leaf surface are similar to those of *Parinari*. The distinctive receptacle-shape only occurs elsewhere in *Magnistipula*.

Bafodeya benna (Scott Elliot) Prance, comb. nov.

Type specimens: Scott Elliot 5052, 5480, Sierra Leone, fl. (K; P).

Parinarium benna Scott Elliot in Journ. Linn. Soc. Bot. 30:78 (1894).

Distribution: Senegal, French Guinea, Sierra Leone.

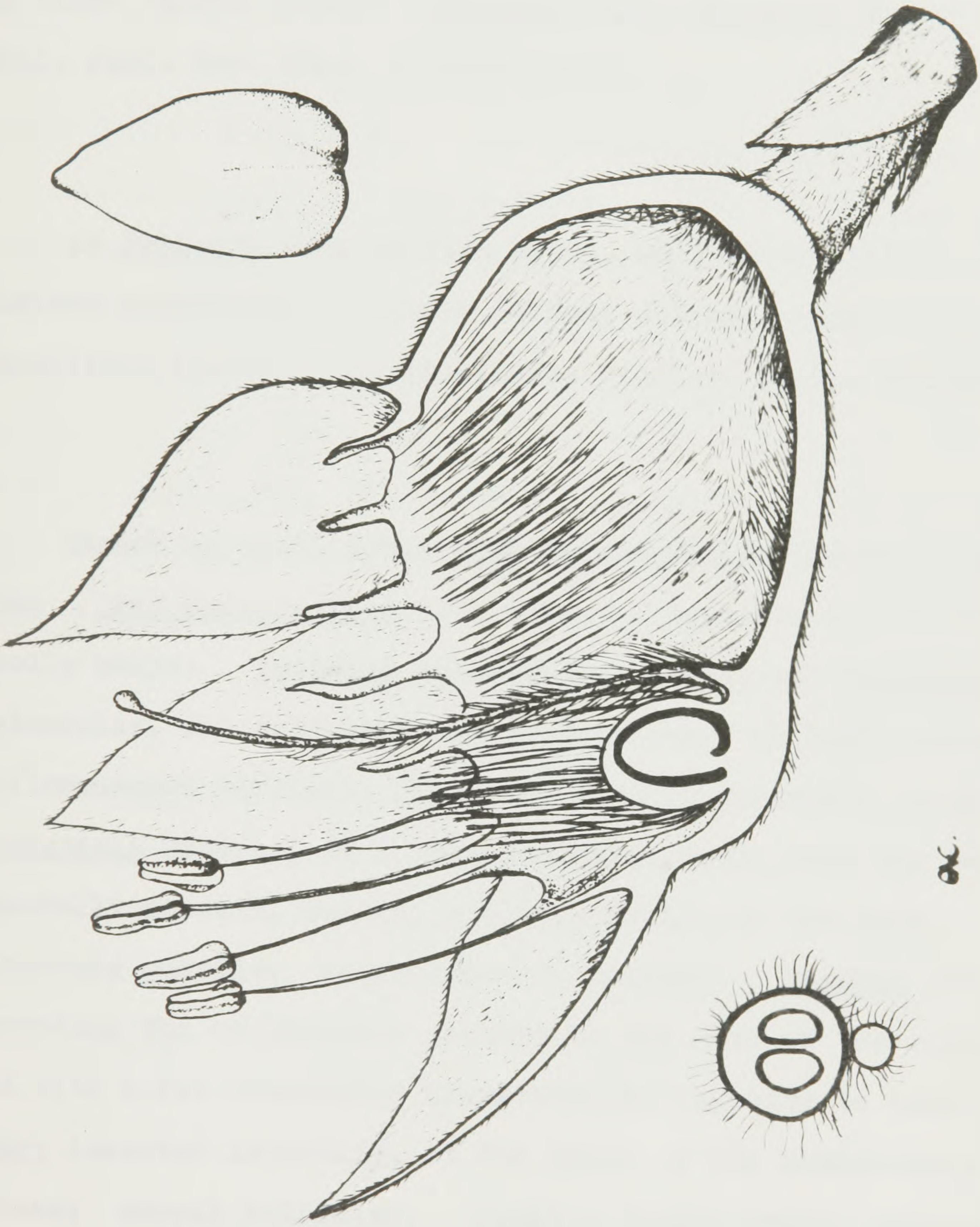

Plate XLIX.- BAFODEYA BENNA (Sc.Elliot)Prance flower,ovary,and style (all x20).

13. NEOCARYA [DC.] Prance, genus novum

Parinarium sect. Neocarya DC., Prodr. 2:527 pro parte quoad P. macrophylla tantum (1825); Benth. in Hook., Niger Fl.: 334 (1849); C. Muell. in Walp., Ann. Bot. Syst. 4:645 (1857). Parinarium subg. Neocarya Blume, Mélange Bot. (1855); Hasskl. in Flora 16:254 (1858); Parinari subg. Neocarya Hauman in Bull. Jard. Bot. Brux. 21:189 (1951).

Ab Parinari tubo calycis brevi, basi altero latere valde inflato sacciformi, laciniis calycis obtusis, staminibus fertilibus 12-17 in altero latere, bracteis parvis differt.

Shrubs or small trees with hermaphrodite flowers 9-12 mm. long Leaf-undersurface with stomatal cavities filled with woolly hairs. Petioles eglandular. Bracts and bracteoles eglandular, not enclosing the young flowers in small groups. Inflorescence terminal, racemoid, usually pyramidal in shape. Receptacle gibbous, of a characteristic shape with the base laterally saccate, hollow, glabrous inside at the base, tomentose outside; calyx-lobes 5, rounded. Stamens 12-17, exceeding the calyx-lobes grouped to one side of the receptacle and with a few staminodes diametrically opposite to them. Ovary inserted laterally, at the mouth of the receptacle, pilose; carpel bilocular. Fruit a fleshy drupe, epicarp sparsely verrucose; endocarp hard, thick and with a rough fibrous surface, with two basal plugs which break away during germination and allow the seedlings to escape. Germination hypogeal, first leaves alternate. (Plate L).

<u>Distribution</u>: A unispecific genus confined to West Africa.

<u>Notes</u> - (1) De Candolle's original diagnosis is not entirely accurate, for this reason a short Latin one is given above. He says that the stamens form a complete circle. This is not true of either of the species which he includes in <u>Neocarya</u>. One species, <u>P</u>. <u>excelsa</u>, is incorrectly included in this section. This is probably due to Sabine's inadequate description of <u>P</u>. <u>excelsa</u>. However, all later authors, cited above, who have adopted De Candolle's section <u>Neocarya</u> have excluded <u>P</u>. <u>excelsa</u> from it and have defined it more accurately. De Candolle had a separate section <u>Petrocarya</u>, (equivalent to <u>Parinari</u> as defined in this work), into which <u>P</u>. <u>excelsa</u> should really have been placed.

(2) The vernacular name for this species in Senegal is 'Neou', and Adanson used this name although he did not propose it as a genus. The name <u>Neou</u> (cited as <u>Neon</u> in the Index Kewensis) is also given as a synonym of <u>Parinari</u> ["<u>Parinarium</u>"] in Juss., Gen.: 342 (1789).

(3) This species has always been rather isolated from the rest of <u>Parinari</u> in the section or subgenus <u>Neocarya</u>. It differs from <u>Parinari</u> sens. strict. in (1) the shape of its receptacle which is glabrous at the base inside, (2) in having more numerous stamens, (3) the bracts not enclosing the flowers in bud and (4) the 'racemoid' inflorescence. Important resemblances to <u>Parinari</u> are found in the stomatal

cavities and fruit structure. *Neocarya* is unique in the family in its saccate receptacle.

Neocarya macrophylla (Sabine) Prance, comb. nov.

Type: *Don* s.n., Sierra Leone, fl. (K).

Parinarium macrophyllum Sabine in Trans. Hort. Soc. 5:452 (1824).

Parinarium senegalense Perr. ex DC., Prodr. 2:527 (1825).

Petrocarya senegalensis (Perr. ex DC.) Steud. Nom. ed. 2, 2:309 (1841).

Petrocarya macrophylla (Sabine) Steud., loc. cit.

Distribution: Senegal, Gambia, Portuguese and French Guinea, Sierra Leone, Liberia, Nigeria.

Plate L.- NEOCARYA MACROPHYLLA (Sabine)Prance flower,ovary,and ovary and style (all x10).

14. <u>DUCKEA</u> Prance, genus novum

<u>Parinarium</u> sensu Hook. f. in Mart., Fl. Bras. 14(2):49-53 (1867) pro parte quoad <u>P</u>. <u>cordatum</u>, <u>P</u>. <u>coriaceum</u>, <u>P</u>. <u>gardneri</u> tantum. <u>Parinari</u> subgenus <u>Pellegriniella</u> pro parte, <u>P</u>. <u>tessmannii</u> exclusum.

<u>Arbores</u> vel <u>frutices</u>. <u>Folia</u> integra, subtus glabra vel lanato-tomentosa; petiolo eglanduloso. <u>Bracteoles</u> eglandulosae parvae, alabastris floralibus haud includentae. <u>Flores</u> in paniculas terminales dispositi. <u>Calycis tubus</u> subcampanulato-turbinatus lateraliter paullo inflatus, excavatus, intus ubique pilosus extus tomentosus, lobi 5 acutis imbricati. <u>Petala</u> 5, sessilia, decidua. <u>Stamina</u> 7 inclusa ad marginem adaxialem calycis tubi disposita, staminodiis 4-7 stamina diametricale opposita orta. <u>Ovarium</u> ad orem calycis tubi lateraliter insertum biloculare, loculis uni-ovulatis. <u>Stylus</u> basilaris filiformis. <u>Fructus</u> drupaceus parvus carnosus extus laevis niger haud verrucosus, endocarpio valde duro tenue extus laeve demum unilateraliter dehiscente.

Ab <u>Parinari</u> fructo laeve haud verrucoso, endocarpio laeve sine obturamentis basalibus, foliis sine cavis stomatalis, bracteolis glomerulos florales haud includentibus differt.

Trees or shrubs with hermaphrodite flowers 6-7 mm. long. <u>Leaf-undersurface</u> glabrous or with a dense woolly tomentum which is easily rubbed off. <u>Petiole</u> eglandular. <u>Bracts</u> and <u>bracteoles</u> eglandular, small, not enclosing the young flowers in small groups. <u>Inflorescence</u> of terminal panicles.

Receptacle subcampanulate-turbinate, slightly swollen to one side, hollow, hairy inside throughout, tomentose outside; calyx-lobes acute. Stamens 7, included, grouped on one side of the receptacle; staminodes opposite the stamens. Ovary inserted laterally at the mouth of the receptacle, carpel bilocular. Fruit a fleshy drupe, epicarp smooth. unwarted; endocarp smooth and very hard, with an appressed beak to one side of the base, with a single longitudinal line of dehiscence allowing the seedling to escape. (Plate LI).

Distribution: Brazil, Guianas.

Type species: *Duckea coriacea* (Benth.) Prance

Note - (1) This genus commemorates Dr. A. Ducke, pioneer of Amazonian botany.

(2) The four species of *Duckea* have been placed in *Parinari* by previous authors, but are clearly distinct in all features other than floral structure and type of inflorescence. The smooth hard endocarp with an appressed beak on one side is quite unlike that of any species of *Parinari* (except *Parinari benna* which is now placed in the new genus *Bafodeya* and which differs in many other characters). Hill (1937), in his investigation of the fruits of various species of *Parinari*, mentioned that the fruits of *P. coriacea* are different from those of all other species of that genus. He suggested that it should be placed in a separate genus stating that Dr. Ducke of Rio de Janeiro agreed with him on this point but neither worker did anything about it. All

the other representatives of Parinari sens. lat. from South America belong to Parinari sens. strict.

1. Duckea coriacea (Benth.) Prance, comb. nov.

Type: Schomburgk 65, British Gúiana, fl. (K; OXF).

Parinarium coriaceum Benth. in Hook. Journ. of Bot. 2:213 (1840).

Distribution: British Guiana, Brazil-Amazonas.

2. Duckea gardneri (Hook. f.) Prance, comb. nov.

Type: Gardner 3139, Brazil, fl. (K; OXF).

Parinarium gardner Hook. f. in Mart. Fl. Bras. 14(2):50 (1867).

Distribution: Brazil Goyaz, Minas Gerais.

3. Duckea cordata (Hook. f.) Prance, comb. nov.

Type: Gardner 2560, Brazil, fl. (K; BM).

Parinarium cordatum Hook. f. in Mart. Fl. Bras. 14(2):50 (1867)

Distribution: Brazil-Piauhy.

This is an imperfectly known species, known only from the type which has no flowers and only young fruit. The fruit in their very immature condition agree with other species of this genus and are certainly bilocular. The leaves have the silvery grey general aspect of this genus.

4. Duckea barbata (Ducke) Prance, comb. nov.

Type: Ducke H.A.M.P. 16835, Brazil, fl. (RB not seen; NY).

Parinarium barbatum Ducke in Arch. Jard. Bot. Rio de Janeiro 3:45 (1922).

Distribution: Brazil-Amazonas, Pará; British Guiana.

Plate LI.- DUCKEA BARBATA (Ducke)Prance
flower,ovary,style and petal (all x20).

15. CYCLANDROPHORA

Hasskl. in Flora, Beibl. 2:47 (1842).

Moquilea Endl., Gen. Pl. Suppl. 3:103 (1843) pro parte quoad sect. *Cyclandrophora* tantum.

Parinarium sensu Hasskl. in Tijdschr. Nat. Geschied Phys. 10:147 (1843).

Parinarium Miq., Fl. Ned. Ind.: 354 (1855) pro parte quoad subgenus *Macrocarya* tantum; C. Muell. in Walp., Ann. Bot. Syst. 4:644 (1857) pro parte quoad section *Cyclandrophora* tantum; Blume, Mélange Bot. (1855), Hasskl. Flora 16:254 (1858) pro parte quoad subgenus *Cyclandrophora* tantum.

Entosiphon R.H. Beddome in Madr. Journ. Sci., Ser. 3, 1: 44 (1864).

Petrocarya auct. non Schreb. pro parte sensu Miers in Journ. Linn. Soc. 17:336 (1879) quoad *P. glaberrima* et *P. scabra* tantum.

Small to large trees with hermaphrodite flowers, 12-20 mm. long. *Leaf-undersurface* always glabrous, and often with minute papillae on veins and reticulations, giving a beaded appearance. *Petioles* eglandular. *Bracts* and *bracteoles* eglandular, not enclosing the young flowers in groups. *Inflorescence* of racemes or little branched panicles. *Receptacle* narrowly campanulate, elongated, hollow, hairy inside throughout, tomentose outside; calyx-lobes acute. *Petals* 4-5. *Stamens* 10-25, exserted beyond petals, grouped towards one side of the receptacle usually with a few staminodes opposite the stamens. *Ovary* inserted laterally at the mouth of the receptacle. Carpel bilocular. *Fruit* a large or medium-sized hard drupe, epicarp glabrous, densely verrucose; pericarp hard, thick, glabrous or only slightly hairy inside, breaking open irregularly at germination. Cotyledons large and strongly ruminate. Germination hypogeal. (Plate LII).

Distribution: Malaysia, Polynesia.

Type species: C. glaberrima Hasskl.

Notes - (1) This genus was described by Hasskarl (1842) but a year later (in Tijdschr. Nat. Geshied Phys. 10:147 (1843)) he reduced it synonomy under Parinarium, where all the species since then have usually been placed. Although the number of species is small, it is a very widespread genus in Malaysia. It is distinguished from related genera by the large, hard drupe with a densely verrucose exterior, by the ruminate cotyledons, the elongate receptacle and the usually racemose inflorescence. Hasskarl originally compared with with Couepia and Thelyra (= Hirtella) and Endlicher actually transferred it to Moquilea. The only character it shares with Parinari is the bilocular ovary.

(2) Dr. A.J.G.H. Kostermans has recently revised Parinari, which he interprets in the old wide sense for the Malaysian region. His forthcoming paper in Reinwardtia will contain the following new species: P. impressa Kostermans, P. jacobsii Kostermans and P. elliptica Kostermans which all belong to Cyclandrophora.

1. Cyclandrophora glaberrima Hasskl. in Flora Biebl. 2:47 (1842).

Type: Hasskarl, Java (not seen).

Parinarium glaberrimum (Hasskl.) Hasskl. in Tijdschr. Nat. Geschied. Phys. 10:147 (1843); in Flora 27:583 (1844).

Parinarium scabrum Hasskl. in Flora 27:585 (1844).

Parinarium laurinum A. Gray, Bot. U.S. Expl. Exped. 1:490 (1854).

Parinarium margarata A. Gray, tom. cit.: 489.

Parinarium lanceolatum Teijsm. & Binn., Cat. Hort. Bot.: 253 (1866).

Parinarium macrophyllum Teijsm. & Binn. In Tijdschr. Nederl. Ind. 29:256 (1867), non Sabine (1824).

Petrocarya glaberrima (Hasskl.) Miers in Journ. Linn. Soc. 17:336 (1879).

Petrocarya scabra (Hasskl.) Miers, loc. cit.

Parinarium racemosum Merr. in Phil. Gov. Lab. Bur. Bull. 17:19 (1904).

Parinarium mindanaense Perkins, Frag. Fl. Philip. 1:119 (1904).

Parinarium curranii Merr. in Phil. Journ. Sct. 4:264 (1909).

Distribution: Indonesia, Philippines, New Guinea, Solomon Is., Palau, Polynesia.

2. Cyclandrophora asperula (Miq.) Prance, comb. nov.

Type: Teysman s.n., Sumatra, st. (K, iso).

Parinarium asperulum Miq., Fl. Ind. Bat. Suppl.: 307 (1860).

Parinarium maingayi King in Journ. As. Soc. Beng. 66:280 (1897).

Parinarium spicatum King, tom. cit.: 279 (1897).

Distribution: Malay Peninsula, Indonesia.

3. Cyclandrophora elata (King) Prance, comb. nov.

Type specimens: King's Collector 3436, Malay, fl. (K); 3711, fr. (K).

Parinarium elatum King in Journ. As. Soc. Bengal 66:280 (1897).

Distribution: Malay Peninsula, Indonesia.

4. Cyclandrophora indica (Bedd.) Prance, comb. nov.

Type: Beddome s.n., S. Madras, India, fl. (K).

Entosiphon indicus Bedd. in Madr. Journ. Sci. Ser. 3(1):44 (1864).

Parinarium indicum (Bedd.) Bedd., Ic. Pl. Ind. Or. 1:22, t. 109 (1874).

Distribution: India (South Madras).

5. Cyclandrophora latifolia (M.R. Henderson) Prance, comb. nov.

Type: Haniff S.F. 21119, Malay Penins., fl. (K).

Parinari latifolia M.R. Henderson in Gard. Bull. Straits Sett. 7:102 (1933).

Distribution: Malay Peninsula.

6. Cyclandrophora travancorica (Bedd.) Prance, comb. nov.

Type: Beddome 292, India, fl. (K).

Parinarium travancoricum Bedd., Ic. Pl. Ind. Or. 1:43 (1874).

Distribution: India (South Madras).

The next species is imperfectly known. The Holotype and the only other herbarium sheet known to exist (Aguilar, Philipp. For. Bureau 24544) were presumably lost when in the last war the Philippine Forestry Bureau, Manila was completely destroyed. I have not yet been able to trace duplicates of either of these sheets. If these are found it will be possible to say whether this is a good species or whether it belongs to the closely related C. glabberrima.

7. Cyclandrophora villamilii (Merr.) Prance, comb. nov.

Type: Villamil, Philipp. For. Bur. 21863 (not seen).

Parinari villamili Merr. in Philipp. Journ. Sci. Bot. 10:308 (1915).

Distribution: confined to the Philippines - Mindanao.

Plate LII.- CYCLANDROPHORA GLABERRIMA Hasskl.
flower,ovary and style (all x10).

16. MARANTHES

Blume, Bijdr. Fl. Nederl. Ind.: 89 (1825); Reichb, Consp.: 204 (1828) ["Maranthus"].

Exitelia Blume, Fl. Jav. Praef.: 7 (1828).

Parinarium Blume, Mus. Bot. Lugd. Bat. 2:99 (1852) pro parte quoad P. griffithianum and P. corymbosum tantum; Benth. in Hook., Niger Fl.: 333 (1849) pro parte quoad sectio Sarcostegia tantum; Blume, Mélanges Bot. (1855); C. Muell. in Walp., Ann. Bot. Syst. 4:645 (1857); Hasskl. in Flora 16:254 (1858) pro parte quoad subgenus Sarcostegia tantum.

Grymania Presl., Epim. Bot.: 193 (1849) pro parte quoad G. salicifolia tantum.

Parinari Hauman in Bull. Jard. Bot. Brux. 21:185-9 (1951) pro parte quoad subgenus Sarcostegia tantum.

Small to large trees with hermaphrodite flowers 9-40 mm. long. Leaf-undersurface glabrous or with a dense woolly tomentum which is easily rubbed off. Petioles usually with 2 glands, rarely eglandular. Bracts and bracteoles eglandular, not enclosing the young flowers in groups. Receptacle of varied shape but narrowed to the base, solid or nearly solid (or rarely hollow, elongate and curved), glabrous inside at base; calyx-lobes rounded. Stamens 23-60, exserted far beyond calyx-lobes, often forming a complete circle, or a small part of the circle and the rest of the circle staminodial. Ovary of 1 (2-3) carpels, inserted laterally at the mouth of the receptacle; carpels bilocular. Fruit a fleshy drupe, epicarp smooth, usually without warts or rarely with a few; endocarp very hard, fibrous with a roughish exterior, with two lateral plates which break away during germination and allow the seedling to escape. Germination epigeal, first leaves opposite. (Plate LIII).

Distribution: mainly African but with one species widely distributed in the East (Malaysia, New Guinea and Australia).

Type species: *Maranthes corymbosa* Blume.

Notes - (1) The earliest description of a species belonging to this genus is that of Blume's *Maranthes corymbosa* which he placed in the Linnean order *Monadelphia Polyandia*. Three years later Blume transferred *M. corymbosa* to his new genus *Exitelia* and in 1852 placed it in *Parinarium* subgenus *Exitelia* and renamed it *P. maranthes*. The African species of *Maranthes* have usually been assigned to the section (or subgenus) *Sarcostegia* of *Parinari* since it was created by Bentham in 1849. Unfortunately the well-known name *Sarcostegia* cannot be used for this genus as it has never been used in generic rank.

(2) The type-species, *Maranthes corymbosa*, was kept apart from *Parinari* for the first 25 years of its existence. Since 1852 all species of *Maranthes* have been placed in *Parinari* and all except *M. corymbosa* have been placed in the distinct section or subgenus *Sarcostegia*. In fact the only important character shared by *Maranthes* and *Parinari* sens. strict. is the bilocular ovary. In all other characters they are different and it is scarcely an exaggeration to say that these two genera are more distinct from each other than

any two genera in the Chrysobalanaceae. As far as is known Maranthes is unique in the family in having epigeal germination and strictly opposite first leaves.

(3) Maranthes replaces the American genus Couepia in Africa and Asia and seems to be most closely related to it. Some species of Couepia are strikingly similar in appearance to species of Maranthes.

Maranthes differs from Couepia in the following characters: (1) bilocular ovary, (2) inflorescence a corymbose panicle, (3) solid receptacle (except in M. gabunensis), (4) dehiscence of endocarp by lateral plates, (5) epigeal germination.

1. Maranthes corymbosa Blume, Bijdr. Fl. Nederl. Ind.: 189 (1825).

Type: Blume s.n., Java (not seen).

Exitelia corymbosa (Blume) Blume, Fl. Jav., Praef.: 7 (1828).

Maranthes multiflora Korth. in Verh. Nat. Gesch. Bot.: 259, t. 70 (1844).

Exitelia multiflora (Korth.) Walp., Rep. Bot. Syst. 5:115 (1845).

Parinarium griffithianum Benth. in Hook., Niger Fl.: 334 (1849).

Grymania salicifolia Presl, Epim. Bot.: 193 (1849).

Parinarium maranthes Blume, Mus. Bot. Lugd. Bat. 2:99 (1852), nom illegit.

Parinarium salicifolium (Presl) Miq., Fl. Ind. Bat. 1(1):357 (1855) non P. salicifolium Engl. (1895).

Parinarium corymbosum (Blume) Miq., Fl. Ind. Bat.

1(1):356 (1855).

Parinarium multiflorum (Korth.) Miq., Fl. Ind. Bat. 1(1):356 (1855).

Petrocarya griffithiana (Benth.) Miers in Journ. Linn. Soc. 17:336 (1879).

Petrocarya maranthes (Blume) Miers, loc. cit.

Parinarium racemosum Vid. Cat. Pl. Prov. Manila: 29 (1880).

Polyalthia pulchrinervia Boerl. Cat. Hort. Bog.: 20 (1899); Ic. Bog.: 106 (1899).

Parinarium palauensis Kanehira in Bot. Mag. Tokyo 45:282 (1931).

Parinarium petiolatum Malm. in Notizbl. Bot. Gart. Berlin: 630 (1932).

Distribution: Andamans, Malaya, Indo-China, Borneo, Indonesia, Philippines, Caroline Islands, New Guinea, Australia, Solomons.

The entire Asiatic material of this genus appears to belong to a single species which is rather variable. Further work is needed to see if any subdivisions should be made.

2. Maranthes aubrevillei (Pellegr.) Prance, comb. nov.

Type: Aubréville 185, Ivory Coast, fl. (P).

Parinari aubrevillei Pellegr. in Bull. Soc. Bot. France 78:440 (1931).

Distribution: Sierra Leone, Ivory Coast.

3. Maranthes chrysophylla (Oliv.) Prance, comb. nov.

Type: Mann 978, Gabon, fl. (K).

Parinarium chrysophyllum Oliv., Fl. Trop. Afr. 2:369 (1871).

Distribution: Liberia, Ivory Coast, Ghana, Nigeria, Guinea, Cameroun, Gabon.

4. Maranthes gabunensis (Engl.) Prance, comb. nov.

Type: Soyaux 45, Gabon, fl. (K).

Parinarium gabunense Engl., Bot. Jahrb. 17:87 (1893).

Distribution: Cameroons, Mayumbe, Cameroun, Gabon and Congo.

This is the only species of Maranthes with a truly hollow receptacle.

5. Maranthes glabra (Oliv.) Prance, comb. nov.

Type: Mann 1832, Rio Muni, fl. (K).

Parinarium glabrum Oliv., Fl. Trop. Afr. 2:370 (1871).

Parinarium montanum Engl. in Wiss. Ergebn. Deutsch. Zentr.-Afr.-Exped. (1907-8), 2:228 (1911), non Aublet (1775).

Parinarium tibatense Engl., Bot. Jahrb. 46:141 (1911).

Parinarium vassonii A. Chev., Expl. Bot. Afr. Occ. Franç. 1:252 (1920) nom nud.

Parinarium gilletii De Wild. in Ann. Mus. Congo Sér. 5(1):245 (1906).

Distribution: Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria, Mayumbe, Cameroun, Rio Muni, Ubangui-Shari, Congo.

6. Maranthes goetzeniana (Engl.) Prance, comb. nov.

Type: Engler 496a, Tanganyika, fl. (B † not seen).

Parinarium goetzenianum Engl., Bot. Jahrb. 34:153 (1905).

Distribution: Confined to Tanganyika.

7. Maranthes kerstingii (Engl.) Prance, comb. nov.

Type specimens: Kersting 320, Togo, fl. (K); 393, fr. (P); 547, fr. (K); 707 (B†); Doering 297, Togo (B†).

Parinari kerstingii Engl., Bot. Jahrb. 46:140 (1911).

Parinari baoulensis A. Chev., Expl. Bot. Afr. Occ. Franç. 1:250 (1920) nom. nud.

Distribution: Togo, Nigeria, Cameroun, Ubangui-Shari, Congo.

8. Maranthes polyandra (Benth.) Prance, comb. nov.

Type: Vogel 3, Nigeria, fl. (K).

Parinarium polyandrum Benth. in Hook., Niger. Fl.: 333 (1849).

Parinarium polyandrum Benth. var. cinerea Engl., Bot. Jahrb. 17:87 (1893).

*Parinarium floribundum Bak. f. in Kew Bull. 1897: 265 (1897).

*Parinarium bequaerti De Wild. in Fedde Repert. 13:108 (1914).

Distribution: Dahomey, Ghana, Togo to Tanganyika, Northern and Southern Rhodesia and the Congo.

If the subspecies, floribunda, is kept up the names preceded by an asterisk are synonyms of it.

9. Maranthes robusta (Oliv.) Prance, comb. nov.

Type: Mann 481, Cameroun, fl. fr. (K).

Parinarium robustum Oliv., Fl. Trop. Afr. 2:370 (1871).

Parinarium klainei Aubrév., Fl. For. Souda-Guin.: 203 (1950), gallice tantum descripta.

Distribution: Ivory Coast, Ghana, Nigeria, Cameroun, Gabon.

Imperfectly known species:

I have not seen the types of the next two species. Further work is necessary to decide whether they are distinct.

10. *Maranthes iodocalyx* (Mildbr.) Prance, comb. nov.

Type: *Mildbraed* 8670, Cameroons (B †).

Parinarium iodocalyx Mildbr. in Notizbl. Bot. Gart. Berlin 8:57 (1921).

11. *Maranthes poggei* (Engl.) Prance, comb. nov.

Type: *Pogge* 914, (B†), Congo.

Parinarium poggei Engl., in Bot. Jahrb. 26:378 (1899).

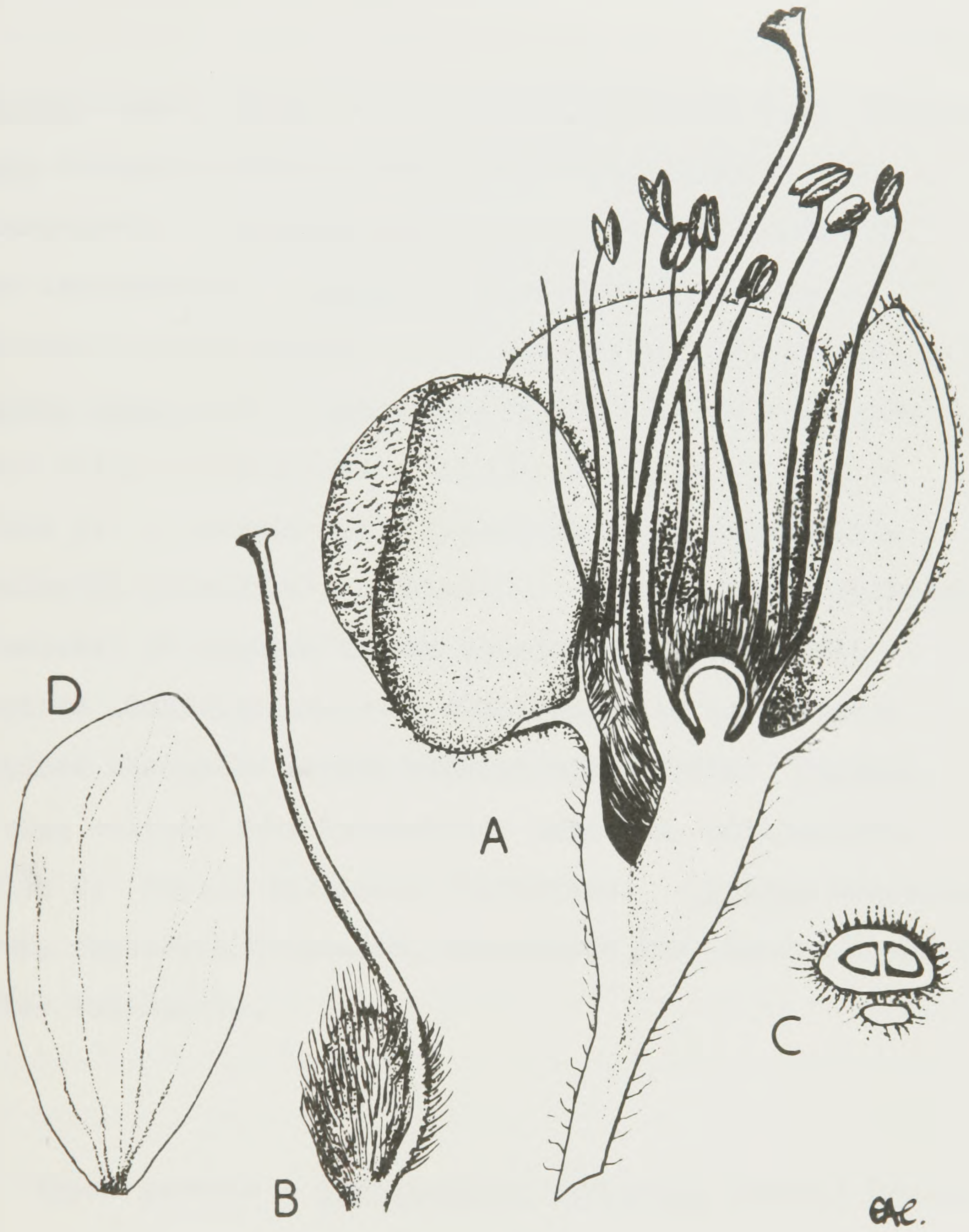

Plate LIII.- MARANTHES CORYMBOSA Blume
A,flower (x12); B,ovary and style (x12); C,ovary (x10); D,petal (x10).

17. KOSTERMANSIA Prance, genus novum

Parinarium auct. non Aubl. quoad P. heteropetalum Scortech. ex King et P. myriandrum Merr. tantum.

Arbores magnae, floribus hermaphroditibus 8-12 mm. longis. Folia integra, subtus glabra, petiolo glanduloso vel eglanduloso. Bracteae eglandulosae glomerulos florum haud includentes. Flores in paniculas axillares et terminales pauci-ramosas brunneo-tomentosas dispositi. Calycis tubus late campanulatus vix elongatus excavatus intus ubique pilosus extus tomentosus, lobis 5 acutis. Petala 5: 2 ceteris multo grandiora valde unguiculata stamine in juventute includentis. Stamina 30-75 exserta, filamentis in ligulam unicam connatis ad receptaculi marginem adaxialem insertis staminodiis ad receptaculi marginem abaxialem contra stamina dispositis. Ovarium ad orem calycis tubi lateraliter insertum, uniloculare, ovulis 2; stylus basilaris filiformis. Fructus drupaceus durus, exocarpio crustaceo, endocarpio duro crasso irregulariter dehiscente.

Typus generis - Kostermansia myriandra (Merr.) Prance

A large tree with hermaphrodite flowers 8-12 mm. long. Leaf-undersurface glabrous and usually with minute papillae on veins and reticulations, giving a beaded appearance. Petioles eglandular. Bracts and bracteoles eglandular not enclosing the young flowers in groups. Inflorescence of little branched terminal or axillary panicles. Receptacle broadly campanulate, not elongated, hollow inside, hairy throughout, exterior tomentose; calyx-lobes acute. Petals 5, two much larger than the others, markedly unguiculate and enclosing the young stamens in the bud. Stamens 25-75, exserted, filaments joined in a single ligule for three quarters of their length, attached to one side of the receptacle; anthers slightly or very hairy; staminodes 5-8, diametrically opposite the stamens. Ovary of 1 (2-3) carpels inserted laterally at the mouth of the receptacle; carpels unilocular, ovules 2. Fruit a hard drupe, epicarp glabrous, verrucose, pericarp hard, thick, glabrous inside, without a special mechanism of seedling escape. Cotyledons filling the seed and only slightly ruminate. (Plate LIV).

Distribution: Malay Peninsula, Borneo, Sarawak, Indonesia.

Type species: K. myriandra (Merr.) Prance

Notes - (1) This genus is named in honour of Dr. A.J.G.H. Kostermans curator of the herbarium of the Forest Research Institute Bogor and Associate of the Herbarium Bogoriense. Dr. Kostermans has made a special study of the Chrysobalanaceae of Malaysia.

(2) Hitherto the plants placed here in Kostermansia have been included in Parinari, despite the fact that they share no important characters with Parinari sens. strict. - not even a bilocular ovary! They are, however, quite closely related to the subgenus Cyclandrophora of Parinari sens. lat., which is elevated to generic rank in this work.

(3) Kostermansia differs from Cyclandrophora in having a staminal ligule, hairy anthers, a unilocular ovary, unguiculate petals and a broadly campanulate, not elongate receptacle.

(4) The only other genus which possesses a staminal ligule is Acioa, which is well represented in Africa and sparsely represented in America. There is little doubt that Kostermansia is related to Acioa but it appears to be sufficiently distinct to merit generic recognition. Kostermansia differs from Acioa in its hairy anthers, broadly campanulate, not elongate receptacle and in having two unguiculate petals enclosing the staminal ligule. There are a number of small fruit differences. In Kostermansia the fruit is not tapered, has a verrucose glabrous epicarp, and a thick hard pericarp, which is glabrous inside.

1. Kostermansia myriandra (Merr.) Prance, comb. nov.

Type: Elmer 21344, Borneo, fl. (K).

Parinarium myriandrum Merr., in Univ. Calif. Publ. Bot. 15:93 (1929).

Distribution: Borneo, Sumatra, Sarawak.

2. Kostermansia heteropetala (Scortech. ex King) Prance, comb. nov.

Type specimens: Scortechini 240 (not seen), 2040, Malay Peninsula, fl. (CGE); King's Collector 664 (not seen), 6899, Malay Peninsula, fl. (BM; K).

Parinarium heteropetalum Scortech. ex King in Journ. As. Soc. Beng. 66:283 (1897).

Distribution: Malay Peninsula.

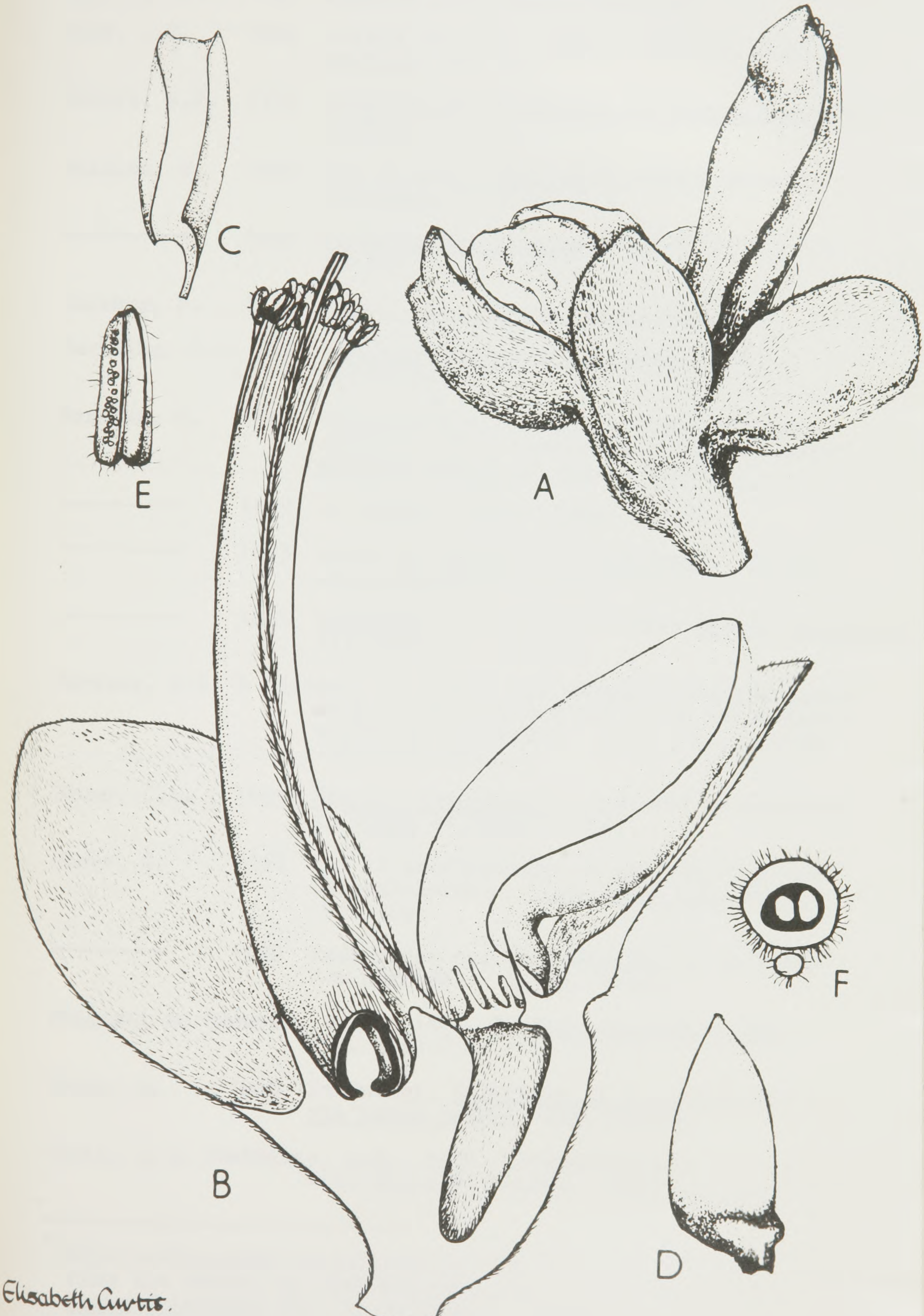

Plate LIV.- KOSTERMANSIA MYRIANDRA (Merr.)Prance
A,flower-bud (x5); B,flower (x10); C,unguiculate petal (x4);
D,petal (x4); E,anther (x30); F,ovary (x20).

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* This publication is untraceable and its contents are taken from the Review by Hasskarl loc. cit. For full details see Flora Malesiana Ser. 1, 4:CLXXIII (1944).

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APPENDIX 1

A LIST OF MATERIALS USED

A. Wood Slides consulted

Species	Reference number	Country, Collector's name & number; Herbarium of Correlated material
Acioa barteri	C.F.I. 4095	Liberia (Cooper 120; FHO)
Afrolicania elaeosperma	C.F.I. 3135	Sierra Leone (Small 617; K)
A. elaeosperma	C.F.I. 12844	Sierra Leone (T.E. Edwardson 111; FHO)
Chrysobalanus atacorensis	C.F.I. 5906	Ghana (C. Vigne 1966; FHO)
Couepia glandulosa	C.F.I. S 353	Surinam (Stahel 353; U)
C. versicolor	C.F.I. S 54	Surinam (Stahel 54; U)
Cyclandrophora asperula	C.F.I. 10277	F.M.S. Malay Pen. (For. Dept. 2018)
C. glaberrima Hassk.	Yale 27193	New Guinea (Waterhouse; Y)
C. glaberrima "	Yale 32059	New Guinea (Waterhouse; Y)
C. glaberrima "	Yale 21134	New Guinea (Waterhouse; Y)
Duckea barbata	C.F.I. 14854	Br. Guiana (For. Dept. 3766; K)
Grangeria borbonica	C.F.I. 4200	Mauritius (uncorrelated)
G. porosa	C.F.I. 21072	Madagascar (C.T.F.T. Paris 8825)
Hirtella hirsuta	C.F.I. s.n.	(uncorrelated)
H. triandra	C.F.I. 3530	Panama (Cooper & Salter 279)
Licania biglandulosa	C.F.I. 6223	Trinidad (Tri. Herb. 12484; FHO)
L. heteromorpha	F.P.R.L. 7178	(uncorrelated)
L. hypoleuca	C.F.I. 8551	Honduras (N.S.Stevenson)
L. splendens	C.F.I. 12002	Java (For. Res. Inst. Buitenzorg 13463; BO)
L. tomentosa	C.F.I. 20926	Brazil (Rio de Janeiro Bot. Gdn.)

Magnistipula bangweolensis	C.F.I. 20920	N. Rhodesia (Mostyn 160; FHO)
Maranthes aubrevillei	C.F.I. 15040	Sierra Leone (H.C. King 283)
M. corymbosa	C.F.I. 7722	F.M.S. (For. Dept. 552; FHO)
M. corymbosa	C.F.I. 10092	F.M.S. (For. Dept. 1793; K)
M. corymbosa	Yale 22853	N. Guinea (Waterhouse; Y)
M. polyandra	C.F.I. 20803	Nigeria (FHI 43900; FHO)
Neocarya macrophylla	C.F.I. 20801	Nigeria (FHI 5305; FHO)
Parastemon urophyllum	C.F.I. 12003	Java (Anderson 5423; SAR)
Parinari excelsa	C.F.I. 874	Tanganyika
P. excelsa	C.F.I. 6323	Ivory Coast (French Exped.)
P. curatellifolia	K. 990	Rhodesia (Milne Redhead; K)
P. curatellifolia	F.P.R.L. 2014	Nyasaland (uncorrelated)
P. oblongifolia	C.F.I. 10112	F.M.S. (For. Dept. 1848 8104; K)
P. oblongifolia	C.F.I. 10155	F.M.S. (For. Dept. 1892 3223; K)

In addition to these slides, the entire wood collection at the Commonwealth Forestry Institute, Oxford, and many samples from the Chicago Field Museum of Natural History, were examined by hand lens to confirm the findings from the sectioned material.

B. Floral Vascular Anatomy

Neocarya macrophylla - Crighton 148 (FHO)

Magnistipula bangweolensis - Angus 286 (FHO)

Chrysobalanus ellipticus - Onochie FHI 23306 (FHO)

Licania (Geobalanus) sp. - Curtiss 727 (F)

Afrolicania elaeosperma - Ainslie 8 (FHO)

Hunga gerontogea - Balansa 2337 (P)

C. Material used for Pollen Slides

1. Acioa barteri	Daramola FHI 45684(FHO)	Nigeria
2. A. dinklagei	Andoh 5677 (FHO)	Ghana
3. A. somnolens	Melinon 230 (P)	French Guiana
4. Afrolicania elaeosperma (1)	Thomas 131 (FHO)	Sierra Leone
5. Agelaea heterophylla (Connaraceae)	Chapman 251 bis (FHO)	Nyasaland
6. Angelesia splendens	Elmer 20916 (BM)	Borneo
7. Bafodeya benna	Pobeguin 900 (P)	French Guinea
8. Byrsocarpus orientalis (Connaraceae)	Fanshawe 1567 (FHO)	Northern Rhodesia
9. Chorystylis spirensii (Saxifragaceae)	Semsei 2515 (FHO)	Tanganyika
10. Chrysobalanus icaco	E.W. Broadway 8626(FHO)	Trinidad
11. Cliffortia nitidula (Rosaceae)	G. Jackson 1904 (FHO)	Nyasaland
12. Couepia chrysocalyx	Huber 9359 (BM)	Brazil
13. C. multiflora	A.C. Smith 2502 (F)	British Guiana
14. Cunonia capensis (Cunoniaceae)	Burtt Davy 20095 (FHO)	South Africa
15. Cyclandrophora glaberrima	BNBFD 6224 (K)	British N. Borneo
16. Dichapetalum flexuosum (Dichapetalaceae)	Cansdale 3976 (FHO)	Ghana
17. Dichotomanthes tristanaecarpa (Rosaceae)	Cultivated Kew (FHO 18057)	
18. Dryas octopetala (Rosaceae)	C.F.I. Pollen Col.	Great Britain
19. Duckea barbata	Krukoff 1137 (F)	Brazil
20. Escallonia pendula (Saxifragaceae)	Sandeman 11097 (OXF)	Peru
21. Filipendula hexapetala (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain

22.	Fragaria vesca (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
23.	Grangeria borbonica	S.A. (OXF)	Western Australia
24.	Grielum sp. (Rosaceae)	White 5433 (FHO)	South Africa
25.	Hagenia abyssinica (Rosaceae)	White 1062 (FHO)	Kenya
26.	Hirtella glandulosa	M. Barreto 6785 (F)	Brazil
27.	H. racemosa	E.W.Broadway 6619 (FHO)	Trinidad
28.	H. zanzibarica	Greenway 5375 (FHO)	Tanganyika
29.	Hunga gerontogea	Bernier 1245 (P)	New Caledonia
30.	Kostermansia myriandra	Kostermans 13630(K)	Borneo
31.	Leucosidea sericea (Rosaceae)	C.M. McGregor 15/45 (FHO)	Southern Rhodesia
32.	Licania cuprea	Fanshawe 133 (FHO)	British Guiana
33.	L. octandra	Fanshawe (F.D.B.G.) 7053 (K)	British Guiana
34.	L. retusa	Curtiss 727 (F)	Florida
35.	L. sclerophylla	Huber 2617 (BM)	Brazil
36.	L. tomentosa	Huber 9360 (BM)	Brazil
37.	Magnistipula bangweolensis	Hoyle 1274 (FHO)	Rhodesia
38.	M. eglandulosa	Angus 535 (FHO)	N. Rhodesia
39.	M. fleuryana	Le Testu 9611 (P)	Gabon
40.	M. tessmannii	Le Testu 9086 (P)	Gabon
41.	Malus sylvestris (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
42.	Maranthes polyandra	Hoyle 1056 (FHO)	Sudan
43.	Neocarya macrophylla	Gledhill 21 (FHO)	Sierra Leone
44.	Parastemon urophyllus	Ashton BRUN 948 (K)	Borneo
45.	Parinari albida	Collins 874 (K)	Siam
46.	P. curatellifolia	Hallard 55 (FHO)	Nigeria
47.	Pelargonium zonale (Geraniaceae)	fresh material	
48.	Philadelphus coronarius (Saxifragaceae)	Béguinot 1857 (OXF)	Italy
49.	Phytolacca dodecandra (Phytolaccaceae)	A. Angus 1384 (FHO)	N. Rhodesia

50. Potentilla argentea (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
51. Prinsepia utilis (Rosaceae)	K. Nand 75 (OXF)	India
52. Prunus padus (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
53. P. spinosa (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
54. Pygeum africanum (Rosaceae)	Chapman 563 (FHO)	Nyasaland
55. Pyrus communis (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
56. Rhabdodendron macrophyllum	Ule 8986 (K)	Brazil
57. R. sylvestris	Fanshawe & Maguire 32141 (K)	British Guiana
58. Rosa pimpinellifolia (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
59. Rubus caesius (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
60. Serjania caracasana (Sapindaceae)	Sandeman 2043 (OXF)	Brazil
61. Sorbus terminalis (Rosaceae)	C.F.I. Pollen Col.	Gt. Britain
62. Stylobasium lineare	Royce 6633 (FHO)	Western Australia
63. S. spathulatum	Perry 2480 (K)	Western Australia
64. Trichocladus ellipticus (Hamamelidaceae)	Semsei 2471 (FHO)	Tanganyika
65. Tropaeolum peltophorum (Tropaeolaceae)	Sandeman 4268 (OXF; FHO)	Peru

D. Material used for Seedling Studies

H.P.Y. = Herbarium Plantularum Yangambiense

1. Acioa dewevrei var. gilleti - H.P.Y. 4511; H.P.Y. 1337; H.P.Y. 1542; H.P.Y. 1453; H.P.Y. 1569; H.P.Y. 1366; H.P.Y. 1630; H.P.Y. 2032; H.P.Y. 1843.
2. Afrolicania elaeosperma - Deighton 1971 (K)
3. Chrysobalanus atacorensis - H.P.Y. 3167; H.P.Y. 3647
4. C. icaco - Fanshawe 3457 (F.D.B.G. 7035; K)
5. Couepia comosa - Fanshawe 3391 (F.D.B.G. 6955; K)

6. C. exflexa - <u>Fanshawe</u> 1367 (F.D.B.G. 4103; K)

7. C. versicolor - <u>Fanshawe</u> 2232 (F.D.B.G.4968; K)

8. Cyclandrophora glaberrima - <u>Prance</u> 1205 (FHO)

9. Hirtella paniculata - <u>Fanshawe</u> 2320 (F.D.B.G.5056; K)

10. H. racemosa - <u>Fanshawe</u> 2306 (F.D.B.G.5042; K)

11. Licania buxifolia - <u>Fanshawe</u> 1623 (F.D.B.G.4359; K)

12. L. divaricata - <u>Fanshawe</u> 2253 (F.D.B.G.4989; K, F.D.B.G.2251; K, F.D.B.G. 4987; K)

13. L. heteromorpha - <u>Fanshawe</u> 2253 (F.D.B.G.5243; K, F.D.B.G.3687; K, F.D.B.G. 4959; K)

14. L. kunthiana - <u>Fanshawe</u> (F.D.B.G.5019; K, F.D.B.G.5026; K, F.D.B.G. 4351; K)

15. L. venosa - <u>Fanshawe</u> 922 (F.D.B.G.3658; K)

16. Magnistipula bangweolensis - <u>Fanshawe</u> 2642 (K); 3376 (K)

17. M. butayei - <u>Louis</u> 16126 (BR); H.P.Y.3781; H.P.Y.3787; H.P.Y.5048; H.P.Y.3731; H.P.Y.3926

18. M. montana - <u>Michelson</u> 756 (BR)

19. M. sp. II - <u>Pierlot</u> 1741 (BR)

20. Maranthes corymbosa - <u>Prance</u> 1203 (FHO)

21. M. glabra - H.P.Y.1476; H.P.Y.1530; H.P.Y.103; H.P.Y. 2229; H.P.Y.1692; H.P.Y. 1759; H.P.Y.2118; H.P.Y.1652; H.P.Y.1760; H.P.Y.4321; etc.

22. Neocarya macrophylla - <u>Hill</u> (1939) e descr.

23. Parinari campestris - <u>Fanshawe</u> 2438 (F.D.B.G.5174; K)

24. P. excelsa - <u>Fanshawe</u> 738 (K); H.P.Y.1697; H.P.Y.1925; H.P.Y.3674; H.P.Y.3069; H.P.Y.2571

25. P. parvifolia - <u>Fanshawe</u> 1607 (F.D.B.G.4343; K)

26. Stylobasium spathulatum - <u>Prance</u> 1201 (FHO); 1202 (FHO)

E. Herbarium Material Consulted

* = used for compilation of data for statistical analysis
Plate = used for flower plate.

1. CHRYSOBALANUS

1. C. icaco - Linn. Herb. 641 Type fl. (LINN); Rehder 822 fl. (K)*;; Curtiss 5845 fl. (K)*; Broadway s.n. fl. (FHO)*; Tonduz 7022 fr. (K)*; Pringle 6629 fl. (K)*; Schipp 932 fr. (K)*; Nash 62 fr. (K)*; Ekman 5805 fl., fr. (K)*; 12477 fl., fr. (K)*; Wilson-Browne 595 (F.D.B.G.5967) fl. (K)*; Froes 21590 fl., (K)*; Gardner 1150 fl., fr. (K; OXF)*; Eaton 333 fl. (F)*, Plate.

C. icaco var. pellocarpa - Broadway 6680 fr. (K; FHO)*; 5286 fl. (F)*; Patter 16 fl., fr. (K)*; R.O. Williams 12493 fr. (K)*; Baker 9 fl. (K)*; Curtiss 280 fl., fr. (K); Jenman 4976 fl. (K)*; 2258 fr. (K)*; Britton & Brace 528 fr. (F)*; Fanshawe F.D.B.G.2568 fl. (FHO)*; Rhoads 8427 fl. (FHO)*.

2. C. orbicularis -.Sieber 31 Type, fl. (K)*; Mann 498 Type, fl. (K)*; Vogel 34 Type, fl. (K)*; Brunner 73 Type, fl. fr. (K)*; Leeuwenberg 2669 fl. (FHO)*; Taylor 5249 fl. (FHO)*; Kennedy 2498 fr. (FHO)*; Grey 166 fl. (K)*; Dawe 77 fl. (K)*; Baldwin 9053 fr. (K)*; Warnecke 382 fl., fr. (K)*; Gossweiler 29 fr., fl. (K)*; Welwitsch 1291 fl., fr. (BM)*.

3. C. ellipticus - Don 897 Type, fl. (K; BM)*; Heudelot 897 fl. (OXF)*; Jones FHI 18849 fl. (FHO)*; Espirito Santo 1947 fl. (K); Adames 159 fl., fr. (K)*; Kennedy 2388 fl. (FHO)*; Baldwin 10500 fl. (K)*; Louis 9473 fl. (FHO)*; Hodges 12 fl., fr. (K)*; Fendler 107 fl., fr. (K)*; Schomburgk 92 fl. (K)*; 39 fl. (K)*; Smeathman s.n. Type fl. (galled) (BM)*; Brenan 8935 fl. (FHO)*.

4. C. atacorensis - Chevalier 24175 Type fl. (K)*; Keay FHI 28071 fl. (K)*; White 3327 fr. (FHO)*; Leonard 234 fl. (K)*; Brenan 8935 fl. (K; FHO)*; Kennedy 1802 fr. Gossweiler 14154 fl. (K)*.

5. C. cuspidatus - Imray s.n. Type, fl., fr. (K)*.

2. LICANIA

1. L. affinis - Schomburgk 823 Type, fl. (K); 1361 fl. (K); Jenman 6624 fl. (K); Melinon 287 fl. (K).

2. L. albiflora - Fanshawe 1678 (F.D.B.G. 4414) Type, fl. (K).

3. L. apetala - Schomburgk 897 fl. (K; OXF)* (type of L. floribunda); 906 fl. (K; OXF)* (type of L. pendula); Hostmann 363 fl. (K)*; B.W. 4811 fl. (K)*; Kuntze 1014, Fragment from K, (type of L. kuntzeana); Broadway 6761 fl. (K)*.

4. L. arborea - Cuming 1109 Type, fl. (K)*; Palmer 342 fl., fr. (K)*; Hinton 5957 fr. (K)*; 3832 fr. (K)*; Tonduz 13808 fl. (K)*; Kellerman 7063 fl. (F)*; Tucker 915 fl. (F).

5. L. benthami - Spruce 3278 Type, fl. (K; OXF); Rusby 2420 fl. (K).

6. L. biglandulosa - Crueger 105 Type, fl. (K)*; Eggers 1458 fl. (K)*; Prestoe s.n. fl. (K)*; Mackay s.n. fl. (FHO)*; Brooks 12484 fl., fr. (FHO)*; Alexander 5695 fr. (K)*; Marshall 12688 fr. (K)*; Broadway 6636 fr. (FHO; MO)*.

7. L. bothynophylla - Martius 449 Type, fl. (K); Mexia 5409 fr. (K; BM; F).

8. L. boyanii - Tutin 293 Type, fl. (K); 230 fl. (K).

9. L. buxifolia - Sandwith 327 Type, fl. (K)*; F.D.B.G. 2309 fl. (K; FHO)*; Anderson 139 fr. (K)*; Jenman 4110 fl. (K)*.

10. L. canescens - Melinon 13 Type, st. (K)*; Atkinson 88 (F.D.B.G. 5837) fl. (K)*; Krukoff 8764 fl. (K)*; H.J.B.R. 19794 fr. (K)*.

11. L. compacta - Schomburgk 519 Type, fl. (K; OXF).

12. L. coriacea - Beccari s.n. fl. (K)*; Schomburgk 50 fl. (K; BM; OXF)*; Pinkus F.D.B.G. 2834 fl. (K; FHO)*; A.C. Smith 2226 fl. (F)*; Hohenkerk 679 fl. (K)*; Jenman 4041 fl. (K)*; F.D.B.G. 2255 fl. (K)*.

13. L. crassifolia - Schomburgk 388 Type, fl. (K; BM; OXF); Waby 8442 fl. (K); Hohenkerk 676 fr. (K); De Vriese s.n. fr. (K).

14. L. crassivenia - Spruce 2678 Type, fl. (K; BM; OXF).

15. L. cruegeriana - Crueger 205 Type, st. (K).

16. L. cuprea - Jenman 6300 Type, fl. (K)*; F.D.B.G. 2421 fr. (K; FHO)*; 456 fr. (K)*; Fanshawe 133 (F.D.B.G. 2742) fl. (K; FHO)*; Cowan 39277 fr. (K)*.

17. L. cuspidata - H.H. Smith 1773 Type, fr. (K; BM).

18. L. cyathodes - Martin s.n. Type, fl. (K); Wachenheim 141 fl. (K; BM); Persaud 97 fl. (F).

19. L. cymosa - Blanchet 3200 Type, fl. (OXF).

20. L. davillifolia - Melinon s.n. Type, fl. (K)*; Ducke H.J.B.R. 19774 fl., fr. (K)*; 19793 fr. (K); Wachenheim st. (K)*.

21. L. dealbata - Gardner 2836 Type, fl., fr. (K; BM).

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22. L. densiflora - Jenman 3604 fl. (K)*; Sandwith 341 fl. (K)*; 336 fl., fr. (K)*; F.D.B.G. 3467 fl. (K)*; Anderson s.n. fr. (BM)*.

23. L. discolor - Ule 8393 Type, fl. (K); A.C. Smith 2923 fr. (K); 2270 fl. (F); Wilson-Browne 484 fl. (K); 480 fl. (K).

24. L. divaricata - Schomburgk 463 Type, fl. (K; BM; OXF); Hohenkerk 705 fl. (K); F.D.B.G. 2628 fl. (K; FHO); Fanshawe F.D.B.G. 4051 fr. (K); Tutin 294 fl. (BM); 232 fl. (BM).

25. L. egensis - Krukoff 6227 fr. (K; BM).

26. L. elliptica - Krukoff 5014 Type, fl. (K; BM); Maguire 24066 fl. (K); 24068 fl. (K).

27. L. emarginata - Spruce 2699 Type, fl. (K; BM; OXF); Krukoff 6860 fl. (K; BM); 8761 fl. (K; BM); 8907 fl. (K; BM) 7058 fl. (BM); 8869 fl. (K; BM; F).

28. L. gardneri - Gardner 2564 Type, fr., fl. (K; BM; OXF); 4539 fl. (K; BM); Martius 911 fl. (K); Burchell 7185 fl. (K); Sandeman 2119 fl. (K; OXF).

29. L. glabra - Spruce 2197 Type, fr. (K; OXF); 3023 fl. (K); 3503 Type, fr. (K); Ducke 25033 fr. (K); 4766 fr. (BM); Krukoff 5252 fl. (K).

30. L. glazioviana - Glaziou 2561 Type, fl. (K).

31. L. grisea - B.W. 6865 Type, fl. (K)*; 3060 Type, fr. (K)*; F.D.B.G. 2365 fr. (FHO)*.

32. L. guianensis - Aublet s.n. Type, st. (BM)*; Schomburgk 1719 fl. (K)*; 1006 fl. (K)*; De la Cruz 3031 fl. (K)*; Jenman 3842 fl. (K)*; 4282 fl. (K)*; Lanjouw & Lindeman 3461 fl. (K)*; Hohenkerk 39A fr. (K)*;

Fanshawe 168 (F.D.B.G.2904) fl. (K)*; Ducke 1552 fl. (BM)*.

33. L. heteromorpha - Numerous esp. Schomburgk 873 Type, fl. (K; OXF)*; Spruce 1472 fr. (K)*; 1649 fl. (K)*; De la Cruz 2542 fl. (F)*; Fanshawe 82 (F.D.B.G.2681) fl. (FHO)*; Ducke 19789 fl. (F)*; 9087 fl., fr. (K)*; Anderson 39 fl. (K)*.

34. L. hoehnei - Hoehne s.n. fl. (FHO); Handro s.n. fl. (FHO).

35. L. hookeri - (L. pallida Kuntze) Spruce 3302 Type, fl. (K); Ducke 8371 fl. (BM).

36. L. humilis - Glaziou 21116 fl. (K; P)*; 21113 fl., fr. (K; P)*.

37. L. hypoleuca - Hinds s.n. Type, fr. (K); Matuda 3110 fr. (K); Thieme 5464 fl. (K); Schipp 103 fl. (K); 392 fr. (K); Gentle 1249 fl. (K).

38. L. incana - Aublet s.n. Type, st. (BM)*; Maguire 24254 fl. (NY; K)*; Davis 296 (F.D.B.G.2287) fl. (FHO)*; Lanjouw & Lindeman 1838 fl. (K)*; Jenman 3742 fr. (K)*.

39. L. intrapetiolaris - Spruce 3539 Type, fl. (K; BM; OXF).

40. L. kunthiana - Schomburgk 728 Type, fl., fr. (K; OXF)* Plate: Gardner 5448 fl. (K; BM)*; Miers 3814 fl. (K; BM)*; Pinkus 191 fl., fr. (F)*; Froes 2004 fl. (K)*; Krukoff 6897 fr. (K)*; Ducke 18821 fl., fr. (K)*.

41. L. latifolia - Spruce 457 Type, fr. (K; OXF)*; Krukoff 7084 fr. (K; BM)*; 6618 fr. (K)*; Burchell 9625 fl. (K)*; Ducke 16341 fl. (K)*; 15799 fr. (BM)*; 15475 fl. (BM)*; 8761 fl. (BM)*.

42. L. laurifolia - Ducke 7958 Type, fl. (BM); 15019 fl. (BM).

43. L. laxa - Fanshawe 1665 (F.D.B.G.4401) Type, fl. (K).

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44. L. laxiflora - Schomburgk 976 fl. (K)*; Sandwith 586 fl. (K)*; Fanshawe (F.D.B.G.3755) fl. (K)*; Fanshawe & Maguire 23511 fr. (K)*.

45. L. leptostachya - Schomburgk 111 Type, fl. (K); Wilson-Browne F.D.B.G.6491 fl. (K); Froes 1735 fl. (K); Ducke 8929 fl. (BM); Sigueira 4043 fl. (BM); De la Cruz 1775 fl., fr. (F).

46. L. leucosepala - Duchassaing s.n. Type, fl. (K); Eggers 1060 fl. (K); Jones s.n. fl. (K); Ramage s.n. fl. (K; BM); H.H. Smith 478 fl. (K); 1838 fr. (K).

47. L. licaniaeflora - Martin s.n. Type, fragm. fl. (K)*; Melinon s.n. fl. (K)*; Persaud 141 fr. (F)*; Wilson-Browne 482 (F.D.B.G.5888) fl. (K)*; Capucho 347 fl. (F)*.

48. L. longipedicellata - Ducke H.J.B.R.23603 Type, fl. (K); 1041 fl. (K).

49. L. longistyla - Spruce 3232 Type, fl. (K; OXF); Jenman 4301 fl. (K); Froes 21495 fl. (K).

50. L. lucida - Krukoff 7267 fl. (BM).

51. L. macrophylla - Spruce 139 fl. (K; OXF); Ducke 7821 fr. (K); 1147 fl. (BM); 21325 fl. (K); 15529 fl. (BM); 7824 fl. (K); Sagot 1109 fl. (K); Amshoff 326 fl. (K).

52. L. majuscula - Melinon s.n. fl. (K)*; F.D.B.G. 2141 fl. (K)*; Davis F.D.B.G.2438 fl., fr. (K; FHO)*; Maguire & Cowan 40493 fr. (K)*; A.C. Smith 3095 fr. (K)*.

53. L. membranacea - Sagot 1081 Type, fl. (K; BM); Le Cointe H.J.B.R. 15498 fl. (K); Siguiera H.J.B.R. 19768 fl. (K).

54. L. micrantha - Hostmann 1257 fl. (K)*; B.W. 3410 fl. (K)*; Spruce 2690 fl. (K; OXF)*; Persuad 79 fr. (K)*; 161 fr. (F)*; 95, fl. (F)*; F.D.B.G. 3060 fl. (K)*.

55. L. microcarpa - Spruce 3696 Type, fr. (K; OXF)*; F.D.B.G. 2365 fl. (K)*; 2629 fl. (K)*; Hohenkerk 816 fr. (K)*; Klug 3740 fl. (K; F)*; Matuda 3565 fr. (F)*; 3110 fl. (F)*.

56. L. microphylla - Fanshawe 1078 Type, fr. (K).

57. L. minutiflora - Melinon s.n. Type, fl. (K); F.D.B.G. 4740 fl. (K); 3334 fl. (K).

58. L. mollis - Schomburgk 910 Type, fl. (K; OXF)*; Krukoff 7267 fl. (K); Spruce 3314 fr. (K)*; F.D.B.G. fl. (K)*; 3768 fr. (K)*; Schultes & Lopez 9481 fl. (F)*.

59. L. oblongifolia - Krukoff 6812 Type, st. (K); 7216 fr. (K); Ducke 23601 fl. (K).

60. L. octandra - Krukoff 11041 fr. (K)*; Jenman 7316 fl. (K)*; Drake s.n. fl. (K)*; F.D.B.G. 7053 fl. (K)*; Spencer Moore 586 fl. (BM)* (type of L. aperta); Schomburgk 593 fl. (K)*; 136 fl. (OXF)* (type of L. pubiflora); 230 fl. (OXF)*; Spruce 329 fr., fl. (K)*; Ule 7886 fl. (K)*; Klug 729 fl. (F)*.

61. L. oligantha - Beard 492 Type, st. (K).

62. L. orinocensis - Rusby & Squires 426 Type, fr. (K).

63. L. ovalifolia - B.W. 6457 Type, fl. (K).

64. L. pallida - Britten (L. brittoniana) - Rusby 2442 Type, fl. (K)*; Krukoff 6139 fl. (K; BM: MO); 6306 fr. (K; BM; MO)*; 5165 fl. (K; BM)*; 8507 fl. (F)*.

65. L. parinarioides - Ducke 25394 fl. (K)*; 18809 fl. (K)*; 16415 fl. (BM)*; 16299 fl. (BM)*; 10912 fl. (BM)*; 2583 fr. (BM)*; Krukoff 4880 fl. (BM)*; Schunke 151 fl. (F)*.

66. L. parviflora - Schomburgk 977 Type, fl. (K; OXF)*; Martius s.n. fl. (K)*; Kuhlmann H.J.B.R. 17973 fl. (K)*; Spruce 1576 fr. (K)*; 2885 fl. (OXF)*; 3302 fl. (OXF)* (type of

L. pallida Hook. f.); Ducke 19780 fr. (K)*.

67. L. parvifolia - Ducke 8979 fl. (BM).

68. L. persaudii - Persaud 95 Type, fl. (K)*; 161 fr. (K)*; Fanshawe 1700 (F.D.B.G. 4436) Type, fl. (K)*; F.D.B.G. 3127 fl. (K)*; 3822 fl. (K)*.

69. L. platypus - Levy 222 Type, fl. (K)*; Cuming 1272 Type, fl. (K)*; Allen 930 fl. (K)*; 941 fl. (K)*; Palmer 428 fr. (K)*; Campbell s.n. fl. (K)*; Matuda 16450 fl. (F)* Plate.

70. L. poeppigii - Krukoff 8138 fl. (K); 6668 fl. (BM; F); Kuhlmann H.J.B.R. 17970 fl. (K).

71. L. polita - Spruce 2676 Type, fl. (K; BM; OXF); 2762 fl. (OXF); Ducke 18816 fl. (K).

72. L. pyrifolia - Purdie s.n. Type, fl. (K); Crueger s.n. fl. (K); Williams 12052 fl. (K); Broadway 2884 fl. (K).

73. L. retifolia - Langlassé 992 Type, fl. (K).

74. L. retusa - Ule 9568 Type, fl. (K).

75. L. rigida - Gardner 1592 Type, fl. (K; BM; OXF)*; Vice-Consul Ceara s.n. fr. (K)*; Virgilis s.n. fl. (K; F)*; Ducke 1603 fl. (BM)*; Martius 902 fr. (K)*.

76. L. riparia - Froes 1961 Type, fl. (K)*; 1935 fl. (K); F.D.B.G. 2250 fl. (K); Krukoff 8640 fl. (BM); Moses 38 fl. (BM).

77. L. robusta - Ducke H.J.B.R. 18815 fl. (K); Melinon s.n. fl. (K); B.W. 2906 fr. (K); 6816 fl. (K).

78. L. rondonii - Krukoff 8886 st. (K); 8751 st. (K; BM).

79. L. roraimensis - Pinkus 61 (F.D.B.G. 2825) Type, fl. (K); Peverdy 53 (F.D.B.G. 2823) fl. (FHO).

80. L. rufescens - Schomburgk 601 Type, fl. (K); 935 fl. (K; BM); Wilson-Browne 380 (F.D.B.G. 5794) fl. (K); F.D.B.G. 2822 fl. (K; FHO); Maguire 24795 fl. (K).

81. L. salzmannii - Salzmann s.n. Type, fl. (K); da Silva 27743 fl. (F).

82. L. sclerophylla - Burchell 7638 fr. (K)*; Spruce 840 fl. (K)*; 987 fr. (K)*; Macedo 1128 fl. (BM)*; Huber 2617 fl. (BM)*; Ducke 16418 fl. (BM)*; 15967 fl. (BM)*; 11397 fl. (BM)*; 10123 fl., fr. (BM)*; 2458 fl. (BM)*.

83. L. sparsipila - Peck 858 Type, fl. (K)*; Schipp 102 fl. (K; MO)*; 598 fr. (BM; MO)*.

84. L. spicata - Miers 4095 Type, fl., fr. (K; BM); Glaziou 11943 fl. (K); 8399 fl. (K); 19137 fl. (K).

85. L. sprucei - Spruce 1801 Type, fl. (K)*; s.n. fr. (K)*; Glaziou 9738 fl. (K)*; Ducke 23597 fl. (K)*.

86. L. stenocarpa - Krukoff 8553 fr. (BM).

87. L. subcordata - Krukoff 7088 st. (BM) (Det. Standley).

88. L. takutuensis - A.C. Smith 3302 fl. (K).

89. L. ternatensis - Crueger s.n. Type, fl. (K); Imray 166 Type, fl. (K); Marshall 11912 fl. (K); Hart 6420 fl. (K); Richardson 12668 fl. (FHO); Eggers 1073 fl. (K); Hodge 578 fr. (BM).

90. L. tomentosa - Gardner 992 Type, fr. (K; BM; OXF)*; 2559 Type, fl. (K; BM; OXF)*; Whitford 3 fl. (K)*; C.F. Baker 64 fl. (K)*, fr. (MO)*; Huber 3025 fl. (K)*; 9360 fl. (BM)*.

91. L. triandra - Spruce 2490 Type, fl. (K; BM; OXF); Ducke 19777 fl., fr. (K).

92. L. turbinata - Gardner 1149 fl. (K; OXF).

93. L. urceolaris - Spruce 2422 Type, fl. (K; OXF); 261 fr. (K).

94. L. utilis - Spruce 877 Type, fl. (K); Glaziou 14678 fl. (K); Burchell 9316 fl. (K); Ducke 15192 fl. (K); 19798 fl., fr. (K); Krukoff 6361 fr. (K).

95. L. venosa - numerous esp. Rusby & Squires 423 Type, fl. (K)*; Persaud 13 fr. (F)*; Jenman 3839 fl. (K)*; de la Cruz 4384 fl. (K)*; Davis 280 (F.D.B.G. 2271) fl. (K; FHO)*.

L. (Angelesia) splendens - numerous esp. Merrill 1224 fl. (BM)* Plate; Galau S 15726 fr. (K; SAR)*; Rosli S 14958 fl. (K; SAR)*; Mujin SAN 27402 fr. (SAR)*; Kostermans 6881 fr. (K)*; 6390 fl. (L)*; 7084 fr. (L)*; 6353 fr. (K; L)*; Elmer 20916 fl. (BM)*; Hassan Pukol BRUN 5401 fr. (K)*.

L. (Geobalanus) - numerous esp.
(G. oblongifolius) Nash 734 fl., fr. (K; MO); Curtiss 727 fl. fr. (K; F; MO); 5779 fr. (MO); Rothrock s.n. fl. (F); Harper 883 fl. (MO); 1433 fr. (MO); Janish 642 fl. (MO); Killip 32791 fl. (MO); Pollard 1120 fr. (MO); Hitchcock s.n. fl., fr. (MO); Moldenke 333 fl. (MO; K); Blanton 6433 fl. (MO); Cronquist 5332 fl. (MO); J.P. Standley 495 fl. (MO); Fredholm 5438 fl. (MO); Reynolds 10066 fl., fr. (MO); Skehan 6/14 fl., fr. (MO); Woodson & Schery 80 fl. (MO); 110 fl. (MO).

(G. pallidus) J.K. Small, G.K. Small & Mosier s.n. fl., fr. (K); Murrill s.n. fl. (MO); Palmer 27327 fl. (MO); 27280 fl. (MO); Rolfe 388 fr. (MO); Fergusen s.n. fr. (MO);

P.C. Standley 57625 fl. (F); Sands s.n. fl. (K); Chapman s.n. fl. (K).

3. AFROLICANIA

A. elaeosperma - Zenker 1629 Type, fl. ♂ (K)*; Mildbraed 7730 Type, fl. ⚥ (K)*; Deighton 2465 fr. (K)*; 1971 fr. (K)*; 13555 fr. (FHO)*; 1508 fl. ♂ (K)*; Klaine 2634 fl. ♂ (K)*; Pomeroy 217 fl. ♂ (K)*; Chipp 299 fr. (K)*; Talbot 3098 fl. ⚥ (K)*, Plate: Thornewill 201 fr. (K)*; 195 bud (K)*; Kennedy 2496 fl. ♂ (FHO)*; Ainslie 8 fl. ♂ (FHO)*, Plate; Thomas 131 fl. ♂ (FHO)*.

4. PARASTEMON

P. urophyllus - Ashton BRUN 948 fl. (K; FHO; L)*; Suip Tabib 8497 fl. (K; SAR)*; Pickles SAR 2994 fr. (FHO; SAR)*; Kostermans 6072 fr. (K)*; Melegrito 3040 fr. (FHO; K)*; Purseglove 5622 fr. (K; SAR)*; Brunig SAR 2471 fl. (SAR)*; Jacobs 5676 fr. (L; K)*; Rahmat SAR 1511 fr. (SAR)*; Anderson SAR 4179 fr. (SAR)*; SAR 2833 fl. (SAR)*; Meijer SAN 19197 fl. (SAR)*, Plate; Sinclair & Kadim 10325 fl. (SAR)*. Haviland & Hose 3240 st. (SAR)* (type of P. spicatus); Haviland 723 fl. (SAR; K)* (type of P. spicatus); Abg. Daud SAR 428 fl. (SAR)*; Ilias Paie SAR 8337 fr. (SAR)*; Jacobs 5415 fr. (L; SAR)*.

P. versteeghii - Versteegh & Kalkman BW 4694 fl. (L)*, Plate; BW 4801 fr. (K; L)*; Lam 3529 fl. (K)*; Koster BW 1114 fr. (L)*: Pleyte 744 fl. (K)*.

5. GRANGERIA

G. borbonica - Bouton s.n. fl. (K)*; Ayres s.n. fl. (K)*; Grey s.n. fl. (K)*; Vaughan 86 fl. (K)*; Richard s.n. fl. (K)*; Barclay s.n. fl. (K)*; Bozer s.n. fl. (K)*.

G. porosa - Hildebrant 3317 Type, fl. (K)*; Pervillé 476 fl. (K)* Plate; 507 fr. (K)*; Decary 8182 fl. (P)*; Serv. For. Madag. 12756 fl. (P)*; 8053 fl. (P)*; 7645 fr. (P)*; 58 fl., fr. (K)*; Richard s.n. fl. (K)*; Boivin 2210 fl. (K)*; Perrier de la Bâthie 350 fr. (P)*; Baron 5755 fl. (K)*.

6. HUNGA

1. H. gerontogea - Le Rat 460 Type, fl. (P)*; Hennecart 196 fl., fr. (P)*; Deplanche 519 fl., fr. (P)*; Bernier 1245 fl. (P)*; Guillaumin & Baumann 12085 st. (Z)*; Guillaumin 13371 st. (Z)*; Däniker 2968 fl. (Z)*; Compton 2320 fl. (BM)* (type of Parinari neocaledonica); Prony 1873 fl. (Z)*; Balansa 2336 fl. (Z; P)* (type of Licania balansae); Däniker 576 fl. (Z)*; Compton 2245 fl. (BM)* (type of Parinarium minutiflorum); Franc 2029 fl. (Z)*; Rohrdorf 123 st. (Z)*; Guillaumin & Baumann 6506 st. (Z)*; 6685 st. (Z)*; Hürlimann 667 st. (Z)*.

2. H. lifouana - Däniker 2470 Type, fl. (Z)*; 2470a fl. (Z)*; 2470b fl. (Z)*.

3. H. longifolia - Brass 27462 Type, fl. (L; K)*.

4. H. papuana - Forbes 257 fl. (BM)*; 893 fr. (K)*; 504 st. (L)*.

5. H. rhamnoides Balansa 2335 Type, fr. (P)*; 3549 Type, fl. (P; Z)*; Guillaumin et al. 1441 st. (Z)*; 6847 fl. (Z)*; Baumann 5810 fl. (Z)*; Franc 2411 fl. (Z)*; 2015 fr. (Z)*; Fetscherin s.n. fl. (P)*; Pancher s.n. fr. (P; Z)*; Deplanche 519 fr. (P; Z)*.

7. COUEPIA

1. C. guianensis - Aublet s.n. Type, fr. (BM); F.D.B.G. 2978 fl. (K)*; B.W. 3080 fl. (K)*; 3027 fl. (K)*; 54 fl. (K)*.

2. C. bracteosa - Schomburgk 485 Type, fl. (K; OXF)*; 2424 fl. (FHO)*; Ducke 184 fl. (F)*; 15348 fr., fl. (BM)*; Spruce 1496*; 2003 fl. (OXF)*; Chagas 1956 fr. (NY)*; I.N.P.A. 6045 fr. (NY)*; Tutin 289 fr. (K)*.

3. C. canescens - Tate 870 Type, fl. (K).

4. C. canomensis - Martius s.n. Type, fl. (BR; K; M)*; King 142 fl. (F)*; Krukoff 6896 fr. (BR)*; Murca Pires 135 fr. (NY)*; Ducke 464 fl. (K).

5. C. caryophylloides - Wachenheim 274 Type, st. (K); 11 Type, fl. (P); B.W. 6350 fl. (K); Maguire 24060 fl. (K; F).

6. C. cataractae - Ducke 15136 Type fl. (K).

7. C. chrysocalyx - Spruce 4614 Type, fl. (OXF)*; 844 fl. (K); Huber 9359 fl. (F)*; Klug 2656 fl. (F)* Plate; Cazalet & Pennington 7690 fl. (FHO); 7760 fr. (FHO)*.

8. C. cognata - Hostmann 795 Type, fl. (K; OXF)*; de la Cruz 2107 fl. (K)*; Jenman 6301 fl. (K)*; F.D.B.G. 2383 fl., fr. (K).

9. C. comosa - Schomburgk 28 Type, fl. (K)*; Tutin 20 fl., fr. (K)*; Jenman 761 fl. (K)*; 976 fl. (K); Appun 623 fl., fr. (K)*; Sandwith 687 yg. fr. (K); F.D.B.G. 4916 fl. (K).

10. C. divaricata - Ducke 779 fl. (K)*; Guedes 2141 fr. (BM)*.

11. C. dodecandra - Campbell s.n. fl., fr. (K)*; Rovirosa 179 fl. (K)*; 3798 fr. (F; K)*; 3102 fl. (F)*; Lundell 4186 fl. (BM)*.

12. C. duckei - Krukoff 1249 fl. (G;(K)*.

13. C. elata - Ducke 25001 Type, fl. (K); 921 fl. (K).

14. C. eriantha - Spruce 313 Type, fl. (K; OXF)*; 1138 Type, fl. (K; OXF)*; s.n. fl. (F)*; Ducke 908 fl. (F)*; 7919 fl. (BM)*; Batten Poole 31 fl. (K)*.

15. C. excelsa - Ducke 19758 Type, fl. (P; K).

16. C. exflexa - Fanshawe 722 (F.D.B.G. 3458) Type, fl. (K); 722a Type, fr. (K).

17. C. glandulosa - Hostmann 859 Type, fl. (BM; K)*; 1119 fl. (K); Melinon 18 fr. (P)*; Kleinhoonte 988 fl. (K)*.

18. C. glaucescens - Spruce 1752 Type, fl. (OXF)*; Dahlgren s.n. fl. (F)*; Ducke 35562 fl., fr. (K)*; Rusby 2678 fl., fr. (F)*; Krukoff 4576 fl. (K).

19. C. glazioviana - Glaziou 18217 Type, fl. (K).

20. C. grandiflora - Martius s.n. Type, fl. (M); M. barreto 6783 fr. (K)*; 6784 fl. (F)*; Gardner 2563 fl. (OXF)*; Burchell 4985 fl., fr. (K)*; Riedel 702 fl. (K); Glaziou 21117 fl. (K).

21. C. habrantha - Krukoff 7252 Type, fl. (K); Fanshawe & Maguire 23363 fl. (F)* Plate.

22. C. insignis-Blanchet 3209 Type, fl. (P).

23. C. krukovii - Krukoff 6007 Type, st. (BM; K); 6208 Type, fl. (K; BM).

24. C. latifolia - Krukoff 6005 Type, fr. (K; BM).

25. C. leptostachya - Spruce 1536 Type, fl. (OXF; K; M)*.

26. C. longipendula - Ule 8854 Type, fl. (K)*; Ducke 43 fl., fr. (F)*; 23592 fl. (K)*; 19 fl. (K)*.

27. C. macrophylla - Spruce 4049 Type, fl. (OXF)*; G. Klug 2089 fl. (F)*.

28. C. magnoliifolia - Spruce 1414 Type, fl. (K; OXF)*; Ducke 24988 fr. (K)*; 35559 fl. (K)*; 156 fl. (K)*.

29. C. martiana - Martius s.n. Type, fr. (M); Gardner 1284 Type, fr. (K)*; 1056 fl. (K)*.

30. C. multiflora - Schomburgk 112 Type, fl. (K; OXF)*; A.C. Smith 2502 fl. (F)*; Ducke 15138 fr., fl. (K)*; 2950 fl. (K)*; Jenman 1088 fl. (K).

31. C. myrtifolia - Spruce 2262 Type, fl. (K; OXF);; 3072 Type, fl. (BR); 174 Type, fl. (K); Sagot 262 Type, fl., fr. (K)*; Krukoff 1930 fl. (BM)*; Cuatrecasas 6913 fl. (F)*; F.D.B.G. 334 fl., fr. (K)*; 3320 fl., fr. (K)*; Froes 1930 fl. (K).

32. C. obovata - Ducke 24495 Type, fr. (K)*; 35561 fl. (K)*; 406 fl. (K).

33. C. ovalifolia - Schott s.n. Type, fl. (K)*; Alston & Lutz 136 fl., fr. (BM)*; Williams 13305 fr. (F)*; Glaziou 6167 fl. (K); 7876 fl. (K); Blanchet 3387 fl. (OXF).

34. C. paraënsis - Sieber s.n. Type, fl. (M); Spruce s.n. fl. (OXF)*; 719 fr. (K)*; 1014 fl. (K); Ducke 8409 fl. (BM)*; 8928 fl. (BM)*; Krukoff 4576 fl. (F)*.

35. C. paraguariensis - Fiebrig 1379 Type, fl. (K).

36. C. parillo - Talbot s.n. fl. (K); Martin s.n. fl. (K; BM).

37. C. pauciflora - F.D.B.G. 3638 fl., fr. (K)*; 4242 fr. (K)*; 3966 fl. (K); Gleason 539 fl. (K)*; Persaud 142 fl. (K)*; Jenman 4184 fl. (K).

38. C. polyandra - Tonduz 13858 fl. (BM; K)*; 13890 fr. (BM)*; Linden 1603 fl. (K)*; Purpus 12074 fl. (K); Ortega 85 fl. (K); Hinton 14008 fl. (K).

39. C. racemosa - Spruce 2322 Type, fl., fr. (OXF)*; 1776 Type, fl. (K; OXF)*; Ducke 407 fl. (F)*; 15684 fr. (BM)*; 15133 fl. (K); Krukoff 4913 fl. (F)*.

40. C. reflexa - Ducke 19757 Type, fl. (K).

41. C. robusta - Rodrigues H.A.M.G. 9651 Type, fl. (K; P); Huber 15116 fl. (K).

42. C. rufa - Lutz 3575 Type, fl. (P; BM).

43. C. Schottii - Schott s.n. Type, fl. (W).

44. C. spicata - Ducke 25002 Type, fl. (K; P); 661 fl. (K).

45. C. stipularis - Ducke 35583 Type, fl. (K); 1755 fl. (K).

46. C. subcordata - Spruce 1423 Type, fl. (K; OXF)*; Ll. Williams 3173 fl. (F)*; Ducke 198 fl. (K)*; 17966 fl. (K); Poeppig s.n. fl. (K).

47. C. suberosa - Riedel 504 fl. (OXF).

48. C. thyrsiflora - Spruce 3681 Type, fl. (K; BM).

49. C. uiti - Martius s.n. fl. (M); Gardner 2561 fl. (OXF)*; Burchell 7665 fl. (K; OXF)*; Lutzelburg 1917; 3001 fl. (M)*; Blanchet 2775 fl. (OXF; BM)*.

50. C. ulei - Ule 5547 Type, fl. (K)*; Ll. Williams 8157 fl., fr. (F)*; Krukoff 6037 fl. (K)*.

51. C. villosa - Maguire 24782 Type, fl. (K; BR).

8. HIRTELLA

1. H. americana - numerous (OXF; FHO; K) esp. Clifford Herb. s.n. Type, fl. (BM); Castillo 24A fl. (FHO)*; Lundell 2425 fl. (BM)*; 4878 fr. (F)*; Matuda 3270 fr. (K); Curtiss 260 fl. (K).

2. H. angustifolia - Pohl 4370 fl. (OXF).

3. H. angustissima - Sandwith 1246 Type, fl. (K); Tutin 60 fl. (K); Jenman 970 fl. (K); 884 fl. (K); Whitton 81 fl. (K).

4. H. bicornis - Spruce s.n. fl. (K); 322 fl. (K); Traill 214 fl. (K); Melinon s.n. bud (K).

5. H. brachystachya - Spruce 2268 Type, fl. (K; OXF); Ducke 35576 fl. (K).

6. H. bracteata - Martius s.n. Type, fl. bud. (K).

7. H. bullata - Schomburgk 132 Type, fl. (K); Spruce 3084 fl. (K; BM; OXF)*; Steyermark 57094 fl. (F)*; Krukoff 4916 fl. (F)*; Butt & Boyan 53 (F.D.B.G. 7877) fl. (K).

8. H. burchelli - Burchell 6571 Type, fr. (K); 6416 Type, fl. (K); 6331 fl. (K).

9. H. caduca - Fanshawe & Maguire 23005a Type, fl. (K); 23498 Type, fl. (K; BR).

10. H. carbonaria - Little 6275 Type, fl., fr. (K; NY)*; Cuatrecasas fl., fr. (F)*.

11. H. caudata - B.W. 4376 Type, fl., fr. (K)*; F.D.B.G. 7854 fl. (K)*.

12. H. ciliata - Macedo 4012 fl., fr. (K)*; Gardner 1591 fl., fr. (K; OXF)*; 2562 fl. (OXF)*; F.D.B.G. 2586 fl., fr. (F)*; Froes 20456 fr. (NY)*; Black 55-18736 fr., fl. (NY)*; Glaziou 10699 fl. (K); Ducke 8088 fl. (BM).

13. H. collina - Spencer Moore 141 Type, fl. (BM); Krukoff 1244

fl. (K); Glaziou 21109 fl. (K); Robert 490 fl. (BM).

14. H. coriacea - Gardner 1591 fl. (OXF)*; 993 fr. (OXF)*.

15. H. corymbosa - Sellow s.n. Type, fl. (K).

16. H. cotticaënsis - Maguire & Stahel 24103 fl. (K).

17. H. davisii - Davis 352 (F.D.B.G. 2345) Type, fl. (K)*; F.D.B.G. 4540 fr. (K)*; Fanshawe (F.D.B.G. 4493) fl. (K)*; Fanshawe & Maguire 22912 fr. (K).

18. H. duckei - Ducke 6756 Type, fl., fr. (BM)*; Krukoff 6834 fl., fr. (F; K)*.

19. H. elongata - Martius s.n. Type, fl. (K); Haught 2604 fl. (F)*; Ducke 7365 fl., fr. (BM)*; 6785 fl. (BM)*; Spruce 2520 fl., fr. (K; OXF)*; 3196 fl. (OXF)*; Froes 20892 fr. (NY)*; Reitz & Klein 1690 fr. (NY)*.

20. H. eriandra - Schomburgk 886 Type, fl. (K); Spruce 117 fl. (K); Traill 213 fl. (K); Ducke 7980 fl. (BM).

21. H. excelsa - Krukoff 5491 fr. (K; BM); 4786 fr. (K; BM).

22. H. floribunda - Chamisso s.n. Type, fl. (K); Sellow s.n. fl. (K); Claussen s.n. fl. (K); Gardner 4541 fl. (K; BM; OXF); Glaziou 19138 fl. (K).

23. H. glabrata - Ule 8984 Type, fr. (K)*; Ducke 23586 fl. (K)*; 35580 fl. (K)*; 465 fl. (K)*.

24. H. glandistipula - Ducke H.J.B.R. 15057 Type, fl. (K).

25. H. glandulosa - Barreto 8873 fl. (K)*, Plate; Dahlgren 951 fl. (F)*; Gardner 1947 fr., fl. (OXF)*; Burchell 5969 fl. (OXF)*; 3861 fl., fr. (K); 9780 fr. (K); Ule 7306 fl. (K); Macedo 3887 fl. (K).

26. H. glaziovii - Glaziou 4946 Type, fl. (K).

27. H. guianiae - Spruce 3523 Type, fl. (K; BM); Trail 215a st. (K).

28. H. guyanensis - Schomburgk 168 Type, fl. (K)*; Fanshawe F.D.B.G. 4184 fl. (K)*; 3042 Type, young-fr. (K)*; Jenman 4734 fl. (K)*.

29. H. hebeclada - Hoehne 23823 fl. (F)*; Miers 4049 fl., fr. (BM); 4637 fl. (K)*; Gardner 370 fl., fr. (K; OXF)*; Pohl s.n. fl. (OXF)*; Rambo 37841 fr. (NY)*; Glaziou 11942 fl. (K).

30. H. hookeri - Gardner 947 Type, fl., fr. (K)*.

31. H. jamaicensis - Harris 5604 Type, fr. (BM)*; s.n. fl., fr. (BM)*; Prior s.n. fl. (K); Imray 319 fl. (K).

32. H. lightioides - Bang 2418 Type, fl. (K); R.S. Williams 1568 fl. (K; BM).

33. H. longifolia - Spruce 2904 Type, fl. (K; OXF).

34. H. macrophylla - Spruce 3095 Type, fl., fr. (K; OXF)*; Steyermark 60561 fl. (F)*; King 1948 fl. (K)*; Bernard 769 fl. (K)*.

35. H. macrosepala - Davis 590 (F.D.B.G. 2631 Type, fl. (FHO; K)*; F.D.B.G. 5344 fl. (K).

36. H. manigera - Jenman 6663 fr., fl. (K)*; 3980 fl. (K; BM)*; Maguire & Cowan 39298 fr. (K)*; Sandwith 92 fl. (K)*; Cowan & Lindeman 39023 fl. (F)*.

37. H. martiana - Gardner 4540 Type, fl. (OXF)*; 3138 fl., fr. (K); Glaziou 12657 fl., fr. (K)*; Ule 7274 fl. (K)*; Burchell 749A fl. (K); Martius s.n. fl. (BM).

38. H. media - Ll. Williams 9480 fl. (F)*.

39. H. megacarpa - Drummond & Hemsley 2614 Type, fr. (K); Ede 68 st. (K).

40. H. melinonii - Melinon s.n. Type, fl. (K).

41. H. mollicoma - Ekman 16363 fl. (F)*; BLain 25 fr. (F)*.

42. H. multiflora - Purdie s.n. Type, fl. (K); Marsh 644 fl. (K); Harris & Britton 10753 st. (K); Harris 3180 fl. (BM); 660 fl. (BM); Ramage s.n. fl. (BM).

43. H. myrmecophila - Ducke 385 fl. (F)*; 25008 fl. (K); 17977 fl. (K); 8557 fl. (BM).

44. H. obidensis - Ducke 19764 Type, fl. (K)*; Davis 175 (F.D.B.G. 2166) fl. (FHO)*; Krukoff 5979 fl. (F; K)*; 8100 fl. (K)*; B.W. 6167 fl. (K).

45. H. paniculata - numerous (K; FHO) esp. F.D.B.G. 2857 fl. (FHO)*; F.D.B.G. 2507 fl. (K; FHO) Plate; Broadway 2951 fl. (F)*; 5583 fl. (K)*; Schomburgk 7 fl. (OXF)*; Fendler 1019 fl. (K)*; Simmonds 15018 fl. (K)*.

46. H. pendula - Beard 166 fl., fr. (K)*; Anderson s.n. fl., fr. (K)*; Ramage s.n. fl. (BM: K)*; Box 1747 fl. (BM).

47. H. physophora - Spruce s.n. fl. (K); Ducke 23587 fl. (K); 25009 fl. (K); 25004 fl. (K); Krukoff 6874 fl. (K).

48. H. pilosissima - Ll. Williams 1183 fl. (F)*; Martius s.n. fl. (K)*.

49. H. pohlii - Pohl s.n. frag. (K), fl. (M), Type.

50. H. praealta - Sagot 792 Type, fr. (K; BM; P).

51. H. punctillata - Ducke 15044 Type, fl. (K).

52. H. purusana - Krukoff 6983 fr. (K); Ducke 3913 fl. (BM).

53. H. racemosa - numerous (OXF; F; K etc.) esp. Maguire & Cowan 39357 fr. (K)*; Maguire & Fanshawe 23364 fl. (K)*; Sandeman 2014 fl. (OXF)*; 2148 fl. (K); Hinton 10773 fl. (K); Mexia 9236 fl. (K); Jenman 7552 fl. (K); 2466 fr. (K).

54. H. racemosa var. hexandra - Spruce s.n. fl. (OXF)*; A.C. Smith 2189 fl., fr. (F)*; Schomburgk 80 fl. (OXF)*; Wilson-Browne 307 (F.D.B.G. 5736) fl. (K).

55. H. rasa - King 4249 fl., fr. (K; BM)*; Krukoff 5525 fl. (K; BM)*; Swartz s.n. fl. (BM).

56. H. rotundata - Ule 9043 Type, fl. (K).

57. H. rugosa - Sintenis 232 fl. (BM; K); 1509 fl. (K); 5256 fl. (K); 6067 fl. (BM); Garber 82 fl., fr. (K).

58. H. scabra - Schomburgk 1051 Type, fl. (K)*; Steyermark 59395 fl., fr. (F)*; Spruce 3548 fl. (K; F)*; Ule 8616 fl. (K); Lasser 1704 fl. (K).

59. H. scaberula - Spruce 2418 Type, fl. (K; OXF).

60. H. selloana - Sellow s.n. Type, frag. (K); Mexia 5473 fl. (K; BM).

61. H. silicea - Crueger s.n. Type, fl. (K); Broadway 4025 fl. (K)*; 6616 fl. (FHO)*; Sandwith 1721 fr., bud (K)*; Eggers 5818 (K)*; Britton et al. 1329 fl. (K)*.

62. H. sprucei - Blanchet 3568 (K; BM); Krukoff 4684 st. (K); 10558 fl. (K); Glaziou 12658 fl. (K); Hassler 10700 fl. (K); Ducke 8374 fl. (BM).

63. H. standleyi - Klug 3022 Type, fl., fr. (K; NY)*; 2869 fl. (K)*.

64. H. strigulosa - Hostmann 175 Type, fl. (K); Lanjouw & Lindeman 3377 fl. (K); 2949 fl. (K); Sagot 1382 fl. (K; BM); Poiteau s.n. fl. (K).

65. H. subglanduligera - Ule 9414 Type, fl. (K).

66. H. subscandens - Spruce 3533 Type, fl. (K; BM; OXF).

67. H. subsetosa - Fanshawe & Maguire 23437 Type, fl. (K).

68. H. tentacula - H.A.M.P. 9792 fl., fr. (BM)*; Huber 417 fl. (BM)*; Ducke 1251 fl., fr. (K)*.

69. H. thouarsiana - Serv. For. Madag. 13568 fr. (P)*; Drake 702 fl. (P)*; Bâthie 6240 fl. (P)*; Baron 6249 fl., fr. (K); 6980 fl. (K).

70. H. tocantina - Ducke 15046 fl. (K); 18236 fl. (K).

71. H. triandra - Stevenson 86 fl. (F; FHO)*; Skutch 2088 fl., fr. (F)*; Valour 1019 fl., fr. (F)*; Haught 4024 fl. (F)*; Allen 1689 fl. (F)*; Silva 178 fr. (NY)*; Bartlett 12741 fl. (K); Wright 155 fl., fr. (K).

72. H. ulei - Ducke 1745 fl., fr. (K)*; 15079 fl. (K)*; Ule 8853 fl. (K)*.

73. H. zanzibarica - numerous FHO esp. Dale K3579 fl. (FHO)*; Greenway 5376 (FHO); Roundspery 2280 fr. (K); Haerdi 333/0 fl., fr. (K).

9. MAGNISTIPULA

1. M. albida - Le Testu 5472 Type, fl. (P; FHO)*.

2. M. bangweolensis - numerous K; BM; FHO esp. Fries 732 Type, fl. (K; BR); Brenan & Greenway 8060 fl., fr. (FHO)*; Greenway & Hoyle 8355 fl. (FHO)*; Holmes FH. T.T. 2779 fl. (FHO)*; R.G. Miller 224 fr. (FHO)*; De Saegher 87 fl. (BR)*; Lewis 24 fr. (FHO)*; Chapman 40 fl. (FHO); Angus 286 fl. (FHO)*; Semsei 120 fl. (FHO)*; Fanshawe 2930 fr. (K); Stolz 2276 fr. (P).

3. M. butayei - Butaye 1440 Type, fl. (BR); Herman 2039 fl. (K)*, Plate: Gilbert 1295 fr. (BR)*; Goosens 6012 fl. (BR)*; Louis 16819 fr. (BR)*; Leonard 270 fl. (BR)*; Robyns 3602 fl. (BR)*; Corbisier-baland 1357 fl. (BR)*.

4. M. conrauana - Conrau 65, Type, fl. (B)*.

5. M. cuneatifolia - Le Testu 9376 Type, fl. (BM)*.

6. M. cupheiflora - Mildbraed 8307 st. (K); D.G. Thomas 118 fl. (FHO)*.

7. M. eglandulosa - numerous F; FHO esp. Borle 254 Type, fl. (FHO; F)*; Lynes 327A fr. (BR)*; Rhea 12 fl. (FHO)*; Angus 535 fl. (FHO)*; Martin 889/38 fl. (FHO)*; Holmes 1347 fl. (FHO)*.

8. M. fleuryana - Baldwin 12522 fl. (K)*; 7017 fl. (K); Le Testu 9611 fl.,fr. (P)*; 9551 fl. (P; BM)*.

9. M. glaberrima - Zenker 4509 Type, fl. (K; B)*; Le Testu 6026 fl. (P)*.

10. M. katangensis - Duvigneaud 1399 Type, fl. (BR; FHO).

11. M. montana - Michelson 741 Type, fl. (BR)*; 762 fr., fl. (BR)*; 756 st. (BR)*; Pierlot 2769 fl. (BR)*; 3204 fr. (BR)*; 1741 fl. (BR)*; 2465 fl. (BR)*.

12. M. pallidiflora - Zenker 4525 fl. (M; B; P).

13. M. sapinii - Sapin s.n. Type, fl. (BR); Soleman 6133 fl. (FHO)*; de Witte 628 fl. (BR)*; 580 fl. (BR)*; Overlaert 941 fl. (BR)*; Risopoulos 665 fl. (BR); 624 fl. (BR); Greenway 6161 fl. (FHO).

14. M. tessmannii - Tessman 81 Type, fl. (K; P); Le Testu 9086 fl; (P)*; 9419 fl. (P)*; 8036 fl. (P)*; 8790 fl. (P)*; 1333 fl. (P)*; Gossweiler 6968 fl., fr. (BM)* Plate; Talbot s.n. fl. (BM)*.

15. M. youngii - Young 410 Type, fl. (K; BM).

16. M. zenkeri - Zenker 2469 Type, fl. (K; B)*.

10. ACIOA

1. A. guianensis - Aublet s.n. Type, fl. bud (BM); Poiteau s.n. fl. (K); Perrotet s.n. fl. (P).

2. A. somnolens - Melinon 230 Type, fl. (P).

3. A. schultesii - Schultes & Lopez 9958 Type, fl. (K).

4. A. barteri - Thomson 66 Type, fl. (K)*; Barter 2183 Type, fl. (K)*; Bates 1740 fl. (FHO)*; J. Smith 7 fl. (FHO)*; Chesters O.B.S. 216 fl. (FHO)*; O.B.S. 160 fl. (FHO)*; Kennedy 3148 fr. (FHO)*; Daramola 45684 fl. (FHO)*; Macgregor 373 fl., fr. (FHO)*; Baldwin 9108 fl. (K)*; Dinklage 2101 fl. (K)*.

5. A. bellayana - Griffon du Bellay s.n. Type, fl. (P); Zenker 3726 fl. (FHO) Plate; Klaine 101 fl. (K); Soyaux 123 fl. (K).

6. A. brazzai - Thollon 565 Type, fl. (P); 4209 Type, fl. (P).

7. A. buchneri - Gossweiler 14039 fl. (K).

8. A. campestris - Soyaux 362 Type, fl. (K).

9. A. chevalieri - Dybowski 118 Type, fl. (P; BR).

10. A. cinerea - Zenker 2903 Type, fl. (K; BM).

11. A. dawei - Dawe 224 Type, fl. (K; FHO).

12. A. dewevrei - Louis 11162 fl. (K)*; 5903 fl. (K)*; 8503 fl. (BM)*; Léonard 943 fr. (K)*; Germain 4813 fl. (K)*; Gossweiler 13913 fr. (BM)*; 13820 fr. (BM)*; Young 524 fl. (BM)*.

13. A. dichotoma - Talbot 3048 Type, fl. (BM).

14. A. dinklagei - Dinklage 2023 Type, fl. (K; BM)*; 1648 Type, fl. (BM)*; Andoh 5677 fl. (FHO; K)*; Vigne 973 fl. (FHO; K)*; 204 fl. (FHO)*; 156 fl. (FHO)*; Darko 1038 fr. (K)*.

15. A. floribunda - Welwitsch 1289 Type, fl. (K)*; 12896 Type, fr. (K)*; Flamigni 10451 fl. (FHO; K)*; Gossweiler 4405 fl. (K)*; Monteiro, Santos & Murta 258 fl. (BM)*.

16. A. hirsuta - Chevalier 19818 fl. (K).

17. A. johnstonei - Johnstone 74/31 Type, fl. (FHO; K)*; Maitland 1401 fr. (FHO)*.

18. A. klaineana - Ujor FHI. 3793 fr. (K)*; Talbot 1529 fl. (K)*; 3153 fl. (K)*; Preuss 263 fl. (K)*; Onochie FHI. 33153 fr. (K)*; Soyaux 111 fl. (K)*; Zenker 4507 fl. (K)*.

19. A. lujai - Luja 38, fl. (BR); Germain 1447 fl. (K)*; Matagne 250 fr. (K)*; Carlier 307 fr. (K)*; Liben 3385 fr. (K)*; Gossweiler 14039 fl. (BM)*.

20. A. mannii - Mann 1427 Type, fl. (K); Staudt 513 fl. (K); Maitland s.n. fl. (K); 467 fl. (K); Winkler 1104 fl. (BM).

21. A. pallescens - Griffon du Bellay 261 Type, fl. (P); Lecompte s.n. fl., fr. (P)*; J. Smith 75 fl. (FHO)*; Motuba FHI. 32654 fl. (K)*; Talbot 1716 fr. (K)*; 1599 fl. (K)*; Johnstone s.n. fl. (K)*; Zenker 855 fl. (K)*; 3641 fr. (BM)*.

22. A. parvifolia - Thomas 5621 fl. (K); 5502 fl. (K); Klein 55 fl. (FHO); Unwin & Smyth 36 fl. (K).

23. A. pierrei - Klaine 196 Type, fl. (K; P; E); 510 fl. (BM); Le Testu 2114 fl. (K; BM); 1779 fl. (BM).

24. A. rudatisi - Rudatis 30 Type, fl. (K; BM)*; Diestel 654 Type, fl. (K); Jones & Onochie FHI. 18992 fr. (FHO)*; Maitland s.n. fl. (K)*; 545 fl. (K)*; Olorunfemi FHI. 30628 fl. (K)*.

25. A. sapinii - Sapin s.n. Type, fl. (BR).

26. A. scabrifolia - Miquel 24 Type, fl. (P); Chevalier 14889 fl. (K)*; Farmer 265 fl. (K)*; Langdale-Brown 2627 fr. (K)*; Deighton 5405 fr. (K)*; Baldwin 10665 fl. (K)*.

27. A. staudtii - Staudt 263 Type, fl. (K).

28. A. talbotii - Talbot 1533 Type, fl. (K; BM).

29. A. tholloni - Thollon 794 Type, fl., fr. (P)*.

30. A. unwinii - Unwin & Smyth 36 Type, fl. (K).

31. A. whytei - Whyte s.n. Type, fl. (K)*; Garrett s.n. fl. (K)*; Deighton 5801 fl. (K)*; 5116 fl. (K)*; Thomas 2684 fr. (K)*; 2522 fr. (K)*; Small 191 fl. (K)*; Smyth 241 fr. (K)*.

11. PARINARI

1. P. campestris - Aublet s.n. Type, fr. (BM); Ducke 1256 fl. (K)*; Crueger s.n. fr. (K)*; Persaud 58 fr. (F)*; Brooks 12257 fl. (K); Sagot 204 fl. (K).

2. P. montana - Aublet s.n. Type, fr. (BM); A.C. Smith 3320 fr. (K)*; Krukoff 5862a fl. (K; F)*; Plate; Windack & Monachino 39675 fl. (K)*; Ducke 15025 fl. (K); Huber 7045 (type of P. pajura) fl. (BM; K).

3. P. anamensis - Pierre 339 Type, fr. (K; BM); Kerr 604 fl. (K)*; 2309 fr. (K)*; 2559 fr. (F; K)*; Collins 874 fl., fr. (K)*; 970 fr. (K)*; Harmand 109 fr. (BM).

4. P. bicolor - Luzon F.B. 28022 Type, fl. (K); Ramos 35041 fl. (BM; K); Ceballos F.B. 26600 fl. (K); Pascasio F.B. 34721 st. (K).

5. P. borneensis - Elmer 27396 Type, fl. (K; BR; BM); Kostermans 6615 fr. (K); 10396 fr. (K); 6544 fr. (K); [illegible] (K).

6. P. brasiliensis - Pohl s.n. Type, fl. (BR); Schott s.n. fl. (K); Glaziou 9391 fl. (BM).

7. P. brachystachya - Schomburgk 785 Type, fl. (K; OXF)*; Krukoff 1501 fr. (K)*; Spruce 1597 fl. (OXF)*; F.D.B.G. 3406 fl. (K)*.

8. P. canarioides - Kostermans 7152 Type, fl. (K)*; 8646 fl. (L; K)*; 10759 fr. (K)*; 4376 fl. (K)*; 10017 fl. (K)*.

9. P. capensis - numerous FHO esp. Burke 518 Type, fl. (K); Corby s.n. fr. (FHO)*; Angus 4 fl. (FHO)*; 1691 fl. (FHO)*; White 1887 fr. (FHO)*; Hoyle 1267 fl. (FHO); 1278 fl. (FHO)*; Edmonds 11/47 fr. (FHO)*.

10. P. cardiophylla - Ducke 24183 Type, fl. (K); 24182 Type, fl. (K).

11. P. chapelieri - Baron 6578 Type, fr. (K).

12. P. congensis - numerous (K; BR; FHO) esp. Leonard 520 fl. (FHO)*; Heciberg s.n. fr. (FHO)*; Vermoesen s.n. fl. (FHO)*.

13. P. congolana - Camp 691 Type, fl. (BR)*; Sapin s.n. fr. (BR)*; Laurent 429 fl. (BR)*; Dubois 915 fr. (BR)*; Flamigny 711 fl., fr. (BR)*.

14. P. costata - Koorders 30270 fr. (L); Maingay 621/2 fl., fr. (K); Curtis 259 fl. (K); Henderson SF 21431 fl. (K); Ngadiman SF 36915 fr. (K).

15. P. curatellifolia - numerous FHO, esp. Heudelot 362 Type, fl. (OXF)*; Holmes 940 fl. (FHO)*; Hoyle 579 fl. (FHO)*; 511 fl. (FHO)*; Eggeling 1486 fl. (FHO)*; Angus 1622 fr. (FHO)*; Jackson 2040 fl., fr. (FHO)*.

16. P. excelsa - numerous FHO, esp. Don s.n. Type, fl., fr. (K); White 3503 fl. (FHO)*; Kennedy 1726 fr. (FHO)*; 1643 fl. (FHO)*; 387 fl. (FHO)*; Enti FH 7184 fr. (FHO)*; Heudelot s.n. fl. (OXF)*; Chapman 137 fr. (FHO)*.

17. P. glazioviana - Glaziou 2560 Type, fl. (K); 2128 Type, fl. (K); 7602 fl. (K); 13796 fl. (K); Martius 2600 fl. (BR).

18. P. helferi - Helfer s.n. Type, st. (K); Lace 2983 fl. (K); Parkinson S 249 fl. (K); Manny Ba Pe 9414 fl. (K).

19. P. insulara - Herb. U.S. Expl. Exped. s.n. Type, fr. (K); Mead 1992 fr. (FHO)*; Sykes 70 fl. (FHO)*; Whitmee s.n. fl. (OXF)*; Vaupel 484 fl. (M)*; Greenwood 520B fr. (K).

20. P. laxiflora - Ducke 11051 Type, fl. (K); 35555 fl. (K); 2418 fl. (K); Froes 1982 fl. (K).

21. P. nonda - Mueller s.n. Type, fl. (K)*; M'Gillivray s.n. Type, fl. (BM); Hill 138 fr., fl. (K)*; Brass 27725 fl. (K)*; 27920 fl. (K)*; Brandenhorst 15 fl. (K)*.

22. P. oblongifolia - Maingay 623 Type, fl. (K)*; Sow Mal FD 23797 fr. (FHO)*; Henderson SF 29619 fl. (K)*; SF 29670 fl. (FHO)*; Ngadiman SF 36910 fr. (K)*; King's Col. 10422 fl. (K).

23. P. obtusifolia - Gardner 3137 Type, fl. (K; OXF); Pereira & Pabst 7376 fl. (F); Burchell 6087 fl., fr. (K); Uster 357 fl. (K); Glaziou 21112 fl. (K); Macedo 4261 fl. (K).

24. P. pachyphylla - H.H. Smith 1775 Type, fl., fr. (K)*; Bernardi 1215 fl. (K)*; W. Williams 9972 fl., fr. (F)*.

25. P. papuana - L.S. Smith NGF 1004 Type, st. (L).

26. P. parilis - King 3870 fl., fr. (F; K; BM)*.

27. P. parvifolia - Sandwith 139 Type, fl. (K); Jenman 3992 fl. (K).

28. P. polyneura - Teysman s.n. Type, st. (K); Maingay 2593 fl. (K); King's Col. 6087 fr. (L; K); 4624 fl. (L; BM).

29. P. rodolphi - Rodrigues H.A.M.G. 9648 Type, fl. (K).

30. P. rubiginosa - Ridley 16016 Type, fl. (K); S.F. 11301 fl. (K).

31. P. salomonensis - Walker & White BSIP 149 Type, fr. (K); L.S. Smith NGF 1193 st. (K).

32. P. sprucei - Spruce 3539 Type, fl. (OXF; K).

33. P. Sumatrana - Koorders 8562 Type, fr. (K); 30270 fr. (K); 30331 fl., fr. (K).

34. P. verdickii - Verdick 568 Type, fl. (BR); Goetze 1473 Type, fl. (BR; E); Schmitz 738 fl. (BR); 2301 fr. (BR); Ritschard 1676 fl. (BR); 1682 fl. (K); Quarré 5438A fl. (BR; K).

35. P. parva - Boden-Kloss 14676 Type, fl. (K).

36. P. sericeo-argentea - Mail FDBNB 2875 Type, fl. (K).

37. P. sp. I - Singh SAN 21399 Type, fl. (L; K).

12. BAFODEYA

B. benna: Scott Elliot 5480 Type, fl. (K)*, Plate; 5052 Type, fl. (K)*; Pobéguin 900 fl. (P)*; Chevalier 13068 fl.-fr. (P)*; 13164 fl., fr. (P)*; Deighton 5445 fl., fr. (K)*; Dalziel 8386 fr. (K)*; Schnell 6807 fr. (BR)*; Farmar 181 fl., fr. (K)*; 228 fl. (K)*; Small 330 fr. (K)*.

13. NEOCARYA

N. macrophylla - numerous K, FHO, esp. - Don s.n. Type, fl. (K)*; A.P.D. Jones 606 fl. (FHO)*, Plate; Crighton 148 fl. (FHO)*, Plate; Irvine 3231 fl. (FHO); Wallace 113 fr. (FHO); Trochain 3070 fr. (P).

14. DUCKEA

D. coriacea - Schomburgk 65 Type, fl. (OXF)*; Riedel s.n. fl., fr. (OXF)*; Froes 23215 fl. (NY)*: 22630 fl. (NY)*; Ducke 1364 fl. (F)*; 1700 fr. (NY)*; Pires & Silva 4401 fr. (NY)*; Spruce 1811 fl. (OXF)*.

D. gardneri - Gardner 3138 Type, fl. (OXF)*; Glaziou 15943 fl. (P)*; 14677 fl. (P; NY; F; BR)*.

D. barbata - Ducke H.A.M.P. 16835 Type, fl. (NY)*; 364 fl. (NY)*; Krukoff 1137 fl. (NY)*, Plate; A.C. Smith 2609 fl. (NY)*; 3559 fr. (K; F)*; Capucho 384 fl. (F)*.

D. cordata - Gardner 2560 Type, fr. (K; BM).

15. CYCLANDROPHORA

C. asperula numerous esp. - Teysman s.n. Type, st. (K); Symington 23343 fl. (FHO)*; Schut K2 fl. (K)*; Kostermans 13931 fr. (K)*; 7015 fr. (K)*; Griffith 2049 fr. (K)*; Soekaria b.b. 35169 fl. (K)*; Sinclair 39511 fl. (K)* etc., etc.

C. elata - King's Col. 3711 Type, fr. (K)*; Hose 475 fl. (K)*; Flaminch SF 32570 fl., fr. (K)*; Ashton BRUN 3184 fl. (K)*; Brand SAN 25260 fr. (K).

C. glaberrima numerous esp. - Mckee 2928 fr. (K)*; F.D.N. Born 6224 fl., fr. (K)*, Plate; J. Mead 1994 fr. (FHO)*; Vaupel 237 fl. (M)*; Elmer 20714 fl. (F)*; Kuswata & Solpadmo 45 fr. (K)*; Parham 284 fr. (K)*.

C. indica - Beddome s.n. Type, fl. (K).

C. latifolia - Haniff S.F. 21119 Type, fl. (K).

C. maingayi - Maingay 618 Type, fr. (K)*; Griffith 2049 Type, fl. (K)*; Hamid FD 11594 fl. (FHO)*.

C. travancorica - Beddome 292 Type, fl. (K)*; Bourdillon 584 fr. (K)*; Lawson 34 fl. (K)*.

C. impressa - Beccari 2510 Type, fl. (K); 2955 fr. (K); Rosli S. 14922 fl. (SAR); Jugah s.n. fr. (SAR); Galau S 14829 fl. (SAR).

C. jacobsii - Jacobs 5543 Type, fl. (K); 9378 fl. (K).

C. elliptica - Horne 242 Type, fl. (K).

16. MARANTHES

1. M. corymbosa - numerous K, FHO, esp, Mail F.D.B.N.B. 1839 fl. (K)*; Edano P.N.H. 18047 fl. (K)*; Plate; Buwalda 5398 fl. (K)*; Kostermans 13856 fl. (K)*; 1200 fr. (K)*; White NGF 10473 fl. (K)*; Kuswata & Solpadmo 67 fr. (K)*; Mas FD 12371 fr. (FHO)*; Symington FD 20872 fl. (FHO)*; Pawanchee FD 13751 fr. (FHO).

2. M. aubrevillei - Aubréville 185 Type, fl. (P)*; 847 fl. (BR), fr. (K)*; 2051 fl. (P)*; King 283 fl. (K)*; Burbridge 609 fl. (K).

3. M. chrysophylla - Mann 978 Type, fl. (K)*; G.P. Cooper 297 bud (FHO)*; 446 fl. (K)*; Wagemans 2209 fl., fr. (BR)*; Talbot s.n. fl. (K)*.

4. M. gabunensis - Nannan 286 fl. (BR)*; Madoux 248 fl. (BR)*; Zenker s.n. fr. (F)*; 3661 fr. (E)*; Brenan 9470 fl. (FHO)*; Vermoesen 1442 fr. (BR)*; Gossweiler 6889 fl. (K)*; Soyaux 45 Type, fl. (K).

5. M. glabra - Mann 1832 Type, fl. (K)*; Vigne 138 fl. (FHO)*; 229 fl. (FHO)*; Corbisier 1050 fl. (BR)*; Kennedy 1540 fr. (FHO)*; 1123 fr. (FHO)*; 229 fl. (FHO)*; Liben 2323 fr. (FHO).

6. M. goetzeniana - Greenway 1728 fl. (K); 4044 fl. (K); 1588 fl. (K); Bryce 127 fl. (K).

7. M. kerstingii- Kersting 320 Type, fr. (K; BM)*; 547 Type, fl. (K)*; Cons. For. N. Nig. s.n. fl. (FHO)*; Lely 737 fl. (K); Batten Poole 106 fl. (K).

8. M. polyandra - Vogel 3 Type, fl. (K); Kennedy 3146 fl. (FHO)*; Vigne 1130 fr. (FHO)*; Latilo FHI 34424 fl. (FHO)*; Peal 113 fl. (FHO)*; Hoyle 683 fl. (FHO)*; 1056 fl. (FHO)*; 1034 fr. (FHO); Greenway & Hoyle 1056 fl. (FHO)*; White 3484 fr. (FHO)*; Schmitz 3666 fr. (BR)*; Bequaert s.n. (Type of Parinari bequaertii), fl. (BR)*; de Witte 6605 fl. (BR)*; Schweinfurth 3989 fl. (M)*; Duff 249/42 fl. (FHO)*; Brenan 7998 fr. (K).

9. M. robusta - Mann 481 Type, fl. (K)*; Vigne 4043 fl. (FHO)*; Irvine 2625 fr. (FHO)*; Taylor L 2 fl. (FHO)*; Jones FHI 18850 fl. (FHO)*.

16. KOSTERMANSIA

1. K. myriandra - Elmer 21344 Type, fl. (K; BM); 21848 fr. (K); Puasa & Enggoh 10621 fl. (K); 10187 fl. (K); Boschbomopraefst bb.13841 fl. (K; P); Kostermans 13630 fl. (K); Singh SAN 22524 fr. (SAR); Woods 3 fl. (K); Lowe s.n. fl. (K).

2. K. heteropetala - King's Col. 6899 Type, fl. (K); Scortechini 2040 Type, fl. (CGE).

3. K. sp. I - Haviland & Hose 3156 Type, fl. (K); Rosli S 14959 fl. (SAR); Galau S 15729 fr. (SAR); S. 15160 fr. (SAR).

APPENDIX 2

A SUMMARY OF KÜSTER'S ANATOMICAL WORK

The summary is given on the diagram in the pocket of this work, where the different features are numbered. The numbers refer to the following anatomical characters:-

1. Cells of the outer epidermis palisade-like elongated.
2. ..... with the outer wall thickened.
3. ..... with the outer wall thickened with a wedge-shaped decurrent mass of secondary thickening.
4. ..... with outer and lateral walls thickened.
5. ..... with lateral walls only, thickened.
6. ..... thickened on the inner wall.
7. ..... inner and lateral walls thickened.
8. ..... with collenchymatous thickening.
9. ..... mucilaginous.
10. ..... developing hypoderm without mucilagination.
11. ..... developing a mucilaginous hypoderm.
12. ..... with a siliceous hypoderm above the nerves.
13. Cells with silica-bodies.
14. Cells of the lower epidermis thickened on the lateral walls.
15. ..... thickened on the lateral and inner walls.
16. ..... with collenchymatous thickening.
17. ..... with papillose differentiation.
18. ..... showing dimorphy.
19. ..... mucilaginous.
20. ..... developing a mucilaginous hypoderm.
21. ..... exhibiting a striated pattern.
22. ..... covered with lenticels.
23. Stomata without accessory cells.
24. Mesophyll in the centre.
25. ..... with discontinuous lacunae parallel to veins.
26. ..... having fatty bodies.
27. ..... having silica-bodies.

28. Nerves with sclerenchymatous ring and plates.

29. ..... with sclerenchymatous ring only.

30. ..... without sclerenchymatous ring or plates.

31. ..... of leaf-undersurface ridge-like.

32. Palisade glands on the leaf upper surface.

33. ..... on the leaf lower surface.

34. ..... absent.

35. Secretory cavities present.

36. Paired glands present.

37. Crystals in the palisade-like hypoderm cells.

38. Leaf lower surface with an arachnoid indumentum.

39. Peltate hairs present.

40. Stellate hairs present.

41. Glandular hairs present.

42. Spicular cells in the mesophyll.

43. Silica bodies in the nerves globular.

44. ..... cone-shaped.

45. ..... globular and cone-shaped.

46. Tannin sacs in secondary cortex.

47. Symmetrical stomata evenly distributed on both sides of the leaf.

48. Simple pits in the wood prosenchyma.

49. Silica-membrane absent.

APPENDIX 3

METHOD FOR PREPARATION OF POLLEN SLIDES

About 15-20 anthers were collected from a herbarium sheet and placed in a pointed centrifuge tube. The whole process of preparation is done in these tubes.

(1) Add approximately 10 ml. 10% NaOH and simmer gently for 40 minutes in an oil bath.

(2) Centrifuge and decant, wash in distilled water, centrifuge again and decant.

(3) Add a few ml. glacial acetic acid. Centrifuge and decant.

(4) Add about 5 ml. freshly made up acetolysis mixture (9 parts acetic anhydride, 1 part conc. H_2SO_4). The H_2SO_4 must be added drop by drop while vigorously agitating the mixture all the time.

(5) Heat in a water bath for about 20 minutes, to bring to boiling point and until the mixture turns a dark colour.

(6) Cool, centrifuge and decant.

(7) Add a few ml. of glacial acetic acid. Centrifuge and decant.

(8) Wash in distilled water, centrifuge and decant.

(9) Add about 10 ml. 10% NaOH and simmer for about 20 minutes.

(10) Centrifuge, decant.

(11) Wash twice in distilled water, decant.

The residue is now ready for mounting and staining. A few drops of the residue are placed in a welled slide. Add two drops of Safranin, and when this has mixed in, add a small quantity of glycerine jelly. Warm gently until the jelly has melted and is evenly distributed, and then allow to cool and set. A small quantity of this jelly may now be taken and melted onto a slide. This is then covered and surrounded by wax to make a permanent preparation.

This technique is an adaptation of that used by Dr. G.W. Dimbleby for soil pollen analysis in the Commonwealth Forestry Institute, Oxford.

APPENDIX 4

DATA USED FOR THE STATISTICAL ANALYSIS AND THE CONTENTS OF THE GROUPS OBTAINED BY ASSOCIATION-ANALYSIS

A. Data used for the analyses of

Ma = Magnistipula; P = Parinari; H = Hi

G = Grangeria; A = Acioa.

Note - The original generic names are used i
created in the present work.

	Species	Char										
		1	2	3	4	5	6	7	8	9	10	11
1	M.butayei	1	0	0	0	0	0	1	0	0	0	0
2	M.fleuryana	1	1	0	0	0	1	1	0	0	0	0
3	M.eglandulosa	1	0	0	0	0	0	1	0	0	0	0
4	M.sapinii	1	1	0	0	0	0	1	0	0	0	0
5	M.bangweolensis	1	0	0	0	0	0	1	0	0	0	0
6	M.montana	1	0	0	0	0	1	1	0	0	0	0
7	M.sp II	1	0	0	0	0	1	1	0	0	0	0
8	P.capensis	1	1	1	1	0	0	1	0	1	0	0
9	P.excelsa	1	1	1	1	0	0	1	0	1	1	0
10	P.curatellifolia	1	1	1	1	0	0	1	0	1	0	0
11	P.congolana	1	1	1	1	0	1	1	0	1	1	0
12	P.oblongifolia	1	1	1	1	0	0	1	0	1	1	0
13	P. nonda	1	1	1	1	0	0	1	0	0	1	0
14	P.montana	1	1	1	1	0	0	1	1	1	0	0
15	P. parilis	1	1	1	1	0	0	1	0	1	1	0
16	P.brachystachya	1	1	1	1	0	0	1	0	1	1	0
17	P.bequaertii	0	0	1	0	1	0	1	0	1	0	0
18	P.polyandra	0	0	1	0	1	0	1	0	1	1	0
19	P.corymbosa	0	0	1	0	1	0	1	0	1	0	0
20	P.glabra	0	0	1	0	1	0	1	0	1	1	0
21	P.floribunda	0	0	1	0	1	1	1	0	1	0	0
22	P.glaberrima	1	1	1	0	1	0	1	0	0	0	0
23	P.asperula	1	1	1	0	1	0	1	0	0	0	0
24	P.~~maingayi~~	1	1	1	0	1	0	1	0	0	0	0
25	P.travancorica	1	1	1	0	1	0	1	0	0	0	0
26	P.elata	1	1	1	0	1	0	1	0	0	0	0
27	P.coriacea	1	1	1	0	0	0	1	0	0	0	0
28	P.gardneri	1	1	1	0	0	0	1	0	0	0	0
29	P.barbata	1	1	1	0	0	0	1	0	0	0	0
30	P.macrophylla	1	0	1	0	1	0	1	0	0	0	0
31	P.benna	1	1	1	0	0	0	1	0	0	1	0
32	P.tessmanii	1	0	1	0	0	0	1	0	0	1	0
33	P.canarioides	1	0	1	0	0	0	1	0	0	0	0
34	H.racemosa	1	0	0	0	1	0	1	0	0	0	0
35	H.triandra	0	0	0	0	1	0	1	0	0	0	0
36	H.coriacea	1	0	0	0	1	0	1	0	0	1	0
37	H.scabra	1	0	0	0	1	0	1	0	0	1	0
38.	H.hexandra	1	0	0	0	1	0	1	0	0	0	0
39	H.paniculata	1	0	0	0	1	0	0	0	0	0	0
40	H.elongata	1	0	0	0	1	0	1	0	0	0	0
41	H.americana	1	0	0	0	1	0	1	0	0	0	0
42	H.glandulosa	1	0	0	0	1	0	1	0	0	0	0
43	H.mollicoma	1	0	0	0	1	0	1	0	0	0	0
44	H.silicea	1	0	0	0	1	0	1	0	0	0	0
45	H.macrophylla	0	1	0	0	1	0	1	0	0	0	0
46	H.zanzibarica	1	0	0	0	1	0	1	0	0	0	0
47	H.thouarsiana	1	0	0	0	1	0	1	0	0	0	0
48	H.myrmecophila	1	0	0	0	1	0	0	0	0	0	0
49	H.duckei	1	0	0	0	1	0	1	0	0	0	0
50	H.ciliata	1	0	0	0	1	0	1	0	0	0	0
51	H.media	0	0	0	0	1	0	1	0	0	0	0
52	H.obidensis	1	0	0	0	1	0	1	0	0	0	0
53	H.hebeclada	1	0	0	0	1	0	1	0	0	0	0
54	C.chrysocalyx	0	0	0	0	1	0	1	0	1	0	0

	Species	1	2	3	4	5	6	7	8	9	10
55	C. magnoliaefolia	1	0	0	0	1	0	1	0	0	0
56	C. canomensis	1	0	0	0	1	0	1	0	0	0
57	C. longipendula	1	0	0	0	1	0	1	0	0	0
58	C. bracteosa	1	0	0	1	1	0	1	0	0	0
59	C. macrophylla	0	0	0	0	1	0	1	0	0	0
60	C. subcordata	1	0	0	1	1	0	1	0	0	0
61	C. uiti	1	0	0	0	1	0	1	0	0	0
62	C. multiflora	0	0	0	0	1	0	1	0	0	0
63	C. ovalifolia	1	0	0	0	1	0	1	0	1	0
64	C. grandiflora	0	0	0	0	1	0	1	0	0	0
65	C. ulei	1	0	0	0	1	0	1	0	1	0
66	C. steudeliana	1	0	0	0	1	0	1	0	0	0
67	C. robusta	0	0	0	0	1	0	1	0	0	0
68	C. divaricata	0	0	0	0	1	0	1	0	0	0
69	C. myrtifolia	0	0	0	0	1	0	1	0	0	0
70	C. paraensis	0	0	0	0	1	0	1	0	0	0
71	C. glaucescens	0	0	0	0	1	0	1	0	0	0
72	C. racemosa	1	0	0	0	1	0	1	0	1	0
73	C. dodecandra	1	0	0	0	1	0	1	0	0	0
74	P. pachyphylla	1	1	1	1	0	0	1	0	1	1
75	P. insulara	1	1	1	1	0	0	1	0	1	0
76	P. congensis	1	1	1	1	0	0	1	0	1	1
77	P. albida	1	1	1	1	0	0	1	0	1	1
78	P. gabunensis	0	0	1	0	1	0	1	0	0	0
79	H. martiana	1	0	0	0	1	0	1	0	0	0
80	P. robusta	0	0	1	0	1	0	1	0	0	1
81	C. martiana	0	0	0	0	1	0	1	0	0	0
82	C. versicolor	0	0	0	0	1	0	1	0	0	0
83	C. caryophylloides	0	1	0	0	1	0	1	0	0	0
84	C. pauciflora	1	0	0	0	1	0	1	0	0	0
85	C. obovata	0	0	0	0	1	0	1	0	0	0
86	C. glandulosa	0	0	0	0	1	0	1	0	0	0
87	C. comosa	0	0	0	0	1	0	1	0	0	0
88	C. polyandra	0	0	0	0	1	0	1	0	0	0
89	C. floccosa	0	0	0	0	1	0	1	0	0	0
90	H. tentaculata	1	0	0	0	1	0	1	0	0	0
91	H. jamaicensis	0	0	0	0	1	0	1	0	0	0
92	H. rasa	0	0	0	0	1	0	1	0	0	0
93	H. davisii	1	0	0	0	1	0	1	0	0	0
94	H. caudata	1	0	0	0	1	0	0	0	0	0
95	H. guyanensis	1	0	0	0	1	0	1	0	0	1
96	H. glabrata	1	0	0	0	1	0	1	0	0	0
97	H. manigera	1	0	0	0	1	0	0	0	0	0
98	H. ulei	1	0	0	0	1	0	1	0	0	0
99	H. pendula	0	0	0	0	1	0	1	0	0	0
100	P. campestris	1	1	1	1	0	0	1	0	1	1
101	G. borbonica	0	0	0	0	0	0	0	0	0	0
102	G. porosa	0	0	0	0	0	0	0	0	0	0
103	G. madagascariensis	0	0	0	0	0	0	0	0	0	0
104	P. myriandra	1	1	0	0	1	0	1	0	0	0
105	P. chrysophylla	0	1	1	0	1	0	1	0	1	1
106	P. aubrevillei	0	0	1	0	1	1	1	0	1	0
107	P. kerstingii	0	0	1	0	1	1	1	0	1	0
108	H. carbonaria	0	0	1	0	1	0	1	0	0	0
109	M. conrauana	1	1	0	0	0	1	1	1	0	0
110	M. zenkeri	1	1	0	0	0	1	1	1	0	0
111	M. glaberrima	1	0	0	0	0	0	1	1	0	0
112	M. cuneatifolia	1	1	0	0	0	1	1	0	0	0
113	M. cupheifolia	1	0	0	0	0	0	1	0	0	0
114	M. albida	1	0	0	0	0	0	1	0	0	0
115	H. guaineae	1	0	0	0	1	0	1	0	0	0
116	H. bullata	1	0	0	0	1	0	1	0	0	0
117	H. macrosepala	0	0	0	0	1	0	1	0	0	0
118	H. pilosissima	1	0	0	0	1	0	0	0	0	0
119	C. eriantha	0	0	0	0	1	0	1	0	0	0
120	C. duckei	0	0	0	0	1	0	1	0	1	0

	Species	1	2	3	4	5	6	7	8	9	1(
121	C. habrantha	0	0	0	0	1	0	1	0	0	[illegible]
122	C. leptostachya	0	0	0	0	1	0	1	0	0	[illegible]
123	C. calophlebia	1	0	0	0	1	0	1	0	1	[illegible]
124	P. sericeo-argentea	1	1	1	1	0	0	1	0	0	[illegible]
125	P. borneense	1	0	1	1	0	0	1	0	1	[illegible]
126	P. impressa	1	1	1	0	1	0	1	0	0	[illegible]
127	A. pallescens	1	0	0	0	1	0	1	0	0	[illegible]
128	A. johnstonei	1	0	0	0	1	0	1	0	1	[illegible]
129	A. floribunda	1	0	0	0	1	0	1	0	0	[illegible]
130	A. tholloni	1	0	0	0	1	0	1	0	1	[illegible]
131	A. barteri	1	0	0	0	1	0	1	0	1	[illegible]
132	P. sp. I	1	1	1	0	0	0	1	0	0	[illegible]
133	A. scabrifolia	1	0	0	0	1	0	1	0	1	[illegible]
134	A. whytei	1	0	0	0	1	0	1	0	1	[illegible]
135	A. rudatis	1	0	0	0	1	0	1	0	0	[illegible]
136	A. klaineana	1	0	0	0	1	0	1	0	1	[illegible]
137	A. dinklagei	1	0	0	0	1	0	1	0	1	[illegible]
138	A. lujai	1	0	0	0	1	0	1	0	0	[illegible]
139	A. dewevrei	1	0	0	0	1	0	1	0	0	[illegible]
140	A. gilletii	1	0	0	0	1	0	1	0	1	[illegible]

B. Data used for the analysis

P = Parastemon; A = Angelesia; G = Ge

L = Licania; H = Hunga; C = Ch

	Species	1	2	3	4
1	P. versteeghii	5	1	1	0
2	P. urophyllus	2	1	1	0
3	A. elaeosperma	20	1	1	1
4	G. pallidus	16	1	1	0
5	G. oblongifolius	15	1	1	0
6	Gr. borbonica	15	1	0	0
7	Gr. madagascariensis	8	1	0	0
8	Gr. porosa	7	1	0	0
9	L. rhamnoides	8	0	0	0
10	L. balansae	6	0	0	0
11	P. neocaledonica	7	0	0	0
12	P. minutifolia	7	0	0	0
13	H. longifolia	8	0	0	0
14	L. gerontogea	8	0	0	0
15	L. lifouana	7	0	0	0
16	L. gerontogea var. frankii	5	0	0	0
17	C. icaco	22	1	1	1
18	L. arborea	12	1	1	1
19	L. coriacea	11	1	1	1
20	L. incana	5	1	1	1
21	L. cuprea	3	1	1	1
22	L. apetala	8	1	1	1
23	L. guianensis	35	1	1	1
24	L. heteromorpha	9	1	1	1
25	L. kunthiana	6	1	1	1
26	L. micrantha	3	1	1	1
27	L. microcarpa	5	1	1	1
28	L. mollis	10	1	1	1
29	L. latifolia	10	1	1	1
30	L. octandra	8	1	1	1
31	L. parinarioides	20	1	1	1
32	L. parviflora Benth.	5	1	1	1
33	L. apetala II	10	1	1	1
34	L. platypus	19	1	1	1
35	L. rigida	14	1	1	1
36	L. sclerophylla	8	1	1	1
37	L. tomentosa	30	1	1	1
38	L. grisea	3	1	1	1
39	L. persaudii	11	1	1	1
40	L. laxiflora	7	1	1	1
41	L. canescens	5	1	1	1
42	L. venosa	6	1	1	1
43	L. majuscula	12	1	1	1
44	L. licanaeflora	24	1	1	1
45	A. splendens	10	1	1	1
46	H. longifolia	9	1	1	1
47	C. pellocarpus	17	1	1	1
48	C. savanarum	17	1	1	1
49	C. atacoriensis	14	1	1	1
50	C. ellipticus	22	1	1	1
51	C. orbicularis	26	1	1	1
52	P. spicatum	2	1	1	1
53	L. buxifolia	5	1	1	1
54	L. davillaefolia	7	1	1	1
55	L. densiflora	4	1	1	1
56	L. humilis	5	1	1	1
57	L. pallida Britt.	14	1	1	1
58	L. sparsipilis	8	1	1	1

Species	1	2	3	4
59. L. biglandulosa	12	1	1	1
60 L. latifolia	7	1	1	1
61 A. papuana	7	0	0	1
62 L. sprucei	10	1	1	1

C. Contents of the Groups suggested by Association Analysis

[15] PARINARI capensis 8, P. excelsa 9, P. curatellifolia 10, P. congolana 11, P. oblongifolia 12, P. nonda 13, P. montana 14, P. parilis 15, P. brachystachya 16, P. pachyphylla 74, P. insulara 75, P. congensis 76, P. albida 77, P. campestris 100, P. sericeo-argentea 124.

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[2] COUEPIA bracteosa 58, C. subcordata 60.

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[6] PARINARI glaberrima 22, P. asperula 23, P. maingayi 24, P. travancorica 25, P. elata 26, P. macrophylla 30

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[11] PARINARI corymbosa 19, P. polyandra 18, P. glabra 20, P. floribunda 21, P. bequaertii 17, P. robusta 80, P. gabunensis 78, P. chrysophylla 105, P. aubrevillei 106, P. kerstingii 107,

HIRTELLA carbonaria 108.

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[68] HIRTELLA bullata 116, H. pilosissima 118, H. guainae 119, H. tentaculata 90, H. jamaicensis 91, H. macrosepala 117, H. rasa 92, H. davisii 93, H. cordata 94, H. guianensis 95, H. glabrata 96, H. manigera 97, H. ulei 98, H. pendula 99, H. racemosa 34, H. triandra 35, H. coriacea 36, H. scabra 37, H. hexandra 38, H. paniculata 39, H. elongata 40, H. americana 41, H. glandulosa 42, H. mollicoma 43, H. silicea 44, H. macrophylla 45, H. zanzibarica 46, H. thouarsiana 47, H. myrmecophila 48, H. duckei 49, H. ciliata 50, H. media 51, H. obidensis 52, H. hebeclada 53, H. martiana 79.

COUEPIA chrysocalyx 54, C. magnoliaefolia 55, C. canomensis 56, C. longipendula 57, C. macrophylla 59, C. uiti 61, C. multiflora 62, C. ovalifolia 63, C. grandifolia 64, C. ulei 65, C. steudeliana 66, C. robusta 67, C. divaricata 68,

C. myrtifolia 69, C. paraënsis 70, C. glaucescens 71, C. racemosa 72, C. dodecandra 73, C. martiana 81, C. versicolor 82, C. carophylloides 83, C. pauciflora 84, C. obovata 85, C. glandulosa 86, C. comosa 87, C. polyandra 88, C. floccosa 89, C. eriantha 118, C. duckei 120, C. habrantha 121, C. leptostachya 122, C. calophlebia 123.

PARINARI myriandra 104

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[19] PARINARI coriacea 27, P. gardneri 28, P. barbata 29, P. benna 31, P. tessmannii 32, P. canarioides 33.

MAGNISTIPULA butayei 1, M. fleuryana 2, M. eglandulosa 3, M. sapinii 4, M. bangweolensis 5, M. montana 6, M. sp. II 7, M. conrauana 109, M. zenkeri 110, M. glaberrima 111, M. cuneatifolia 112, M. cupheiflora 113, M. albida 114.

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[3] GRANGERIA borbonica 101, G. porosa 102, G. madagascariensis 103.

Note - The species are followed by their number in the original data.

A. Data used for the analyses of the Hirtelleae

Ma = Magnistipula; P = Parinari; H = Hirtella; C = Couepia;

G = Grangeria; A = Acioa.

Note - The original generic names are used in this table and not the new ones created in the present work.

	Species	Characters 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	M.butayei	1	0	0	0	0	0	1	0	0	0	0	3	3	3	2	3	4	4	1	7	5
2	M.fleuryana	1	1	0	0	0	1	1	0	0	0	0	3	3	3	2	2	4	4	1	7	22
3	M.eglandulosa	1	0	0	0	0	0	1	0	0	0	0	3	3	4	2	3	4	4	1	7	9
4	M.sapinii	1	1	0	0	0	0	1	0	0	0	0	3	3	4	2	3	4	4	1	7	10
5	M.bangweolensis	1	0	0	0	0	0	1	0	0	0	0	3	3	4	2	3	4	4	1	7	10
6	M.montana	1	0	0	0	0	1	1	0	0	0	0	3	3	3	2	3	4	4	1	9	7
7	M.sp II	1	0	0	0	0	1	1	0	0	0	0	3	3	3	1	3	4	4	1	7	8
8	P.capensis	1	1	1	1	0	0	1	0	1	0	0	1	3	1	3	1	2	1	1	7	5
9	P.excelsa	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	7	4
10	P.curatellifolia	1	1	1	1	0	0	1	0	1	0	0	1	3	1	3	1	2	1	1	7	5
11	P.congolana	1	1	1	1	0	1	1	0	1	1	0	1	3	1	3	1	2	1	1	7	11
12	P.oblongifolia	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	7	6
13	P. nonda	1	1	1	1	0	0	1	0	0	1	0	1	3	1	3	1	2	1	1	7	5
14	P.montana	1	1	1	1	0	0	1	1	1	0	0	1	3	1	3	1	2	1	1	7	5
15	P. parilis	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	7	6
16	P.brachystachya	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	7	4
17	P.bequaertii	0	0	1	0	1	0	1	0	1	0	0	2	2	2	3	2	3	1	2	55	17
18	P.polyandra	0	0	1	0	1	0	1	0	1	1	0	2	2	3	3	2	3	1	2	52	12
19	P.corymbosa	0	0	1	0	1	0	1	0	1	0	0	2	2	3	3	2	3	1	2	26	9
20	P.glabra	0	0	1	0	1	0	1	0	1	1	0	2	2	3	3	2	3	1	2	25	12
21	P.floribunda	0	0	1	0	1	1	1	0	1	0	0	2	2	3	3	2	3	1	2	62	20
22	P.glaberrima	1	1	1	0	1	0	1	0	0	0	0	1	2	3	3	4	3	2	3	17	15
23	P.asperula	1	1	1	0	1	0	1	0	0	0	0	1	3	3	3	4	3	2	3	10	18
24	P.maingayi	1	1	1	0	1	0	1	0	0	0	0	1	3	3	3	4	3	2	3	13	12
25	P.travancorica	1	1	1	0	1	0	1	0	0	0	0	1	3	3	3	4	3	2	3	12	12
26	P.elata	1	1	1	0	1	0	1	0	0	0	0	1	2	3	3	4	3	2	3	19	20
27	P.coriacea	1	1	1	0	0	0	1	0	0	0	0	1	3	2	3	2	1	3	1	7	6
28	P.gardneri	1	1	1	0	0	0	1	0	0	0	0	1	3	3	3	2	1	3	1	7	6
29	P.barbata	1	1	1	0	0	0	1	0	0	0	0	1	3	3	3	2	1	3	1	7	7
30	P.macrophylla	1	0	1	0	1	0	1	0	0	0	0	4	3	1	3	1	2	1	4	16	10
31	P.benna	1	1	1	0	0	0	1	0	0	1	0	3	3	1	3	1	1	2	1	7	6
32	P.tessmanii	1	0	1	0	0	0	1	0	0	1	0	3	3	3	3	4	1	4	1	10	5
33	P.canarioides	1	0	1	0	0	0	1	0	0	0	0	1	3	3	3	1	3	1	1	7	5
34	H.racemosa	1	0	0	0	1	0	1	0	0	0	0	1	2	3	1	2	1	3	3	6	4
35	H.triandra	0	0	0	0	1	0	1	0	0	0	0	1	2	4	3	2	1	3	3	3	5
36	H.coriacea	1	0	0	0	1	0	1	0	0	1	0	1	2	4	2	2	1	3	3	6	4
37	H.scabra	1	0	0	0	1	0	1	0	0	1	0	1	2	4	2	2	1	3	1	5	5
38.	H.hexandra	1	0	0	0	1	0	1	0	0	0	0	1	2	4	1	2	1	3	3	6	5
39	H.paniculata	1	0	0	0	1	0	0	0	0	0	0	1	3	4	1	2	4	3	3	3	4
40	H.elongata	1	0	0	0	1	0	1	0	0	0	0	1	2	4	3	2	1	3	3	7	7
41	H.americana	1	0	0	0	1	0	1	0	0	0	0	1	3	4	1	3	1	3	1	3	7
42	H.glandulosa	1	0	0	0	1	0	1	0	0	0	0	1	2	4	1	2	1	3	1	6	8
43	H.mollicoma	1	0	0	0	1	0	1	0	0	0	0	1	3	4	1	2	1	3	1	3	7
44	H.silicea	1	0	0	0	1	0	1	0	0	0	0	1	2	4	1	2	1	3	1	6	5
45	H.macrophylla	0	1	0	0	1	0	1	0	0	0	0	1	3	4	1	2	1	3	1	3	4
46	H.zanzibarica	1	0	0	0	1	0	1	0	0	0	0	1	3	3	1	2	1	3	1	7	8
47	H.thouarsiana	1	0	0	0	1	0	1	0	0	0	0	1	2	3	1	2	1	3	1	6	6
48	H.myrmecophila	1	0	0	0	1	0	0	0	0	0	0	1	3	4	1	2	1	3	3	3	5
49	H.duckei	1	0	0	0	1	0	1	0	0	0	0	1	3	4	1	2	1	3	3	5	6
50	H.ciliata	1	0	0	0	1	0	1	0	0	0	0	2	3	4	1	2	1	3	1	7	5
51	H.media	0	0	0	0	1	0	1	0	0	0	0	1	3	3	3	2	1	3	1	3	4
52	H.obidensis	1	0	0	0	1	0	1	0	0	0	0	1	2	4	1	3	1	3	1	7	6
53	H.hebeclada	1	0	0	0	1	0	1	0	0	0	0	1	2	4	3	3	1	3	3	6	6
54	C.chrysocalyx	0	0	0	0	1	0	1	0	1	0	0	1	1	2	3	1	3	4	3	90	23

	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
55	C. magnoliaefolia	1	0	0	0	1	0	1	0	0	0	0	1	1	2	3	2	3	4	3	25	10
56	C. canomensis	1	0	0	0	1	0	1	0	0	0	0	1	2	3	3	1	3	4	3	43	11
57	C. longipendula	1	0	0	0	1	0	1	0	0	0	0	1	2	3	3	1	3	4	3	32	26
58	C. bracteosa	1	0	0	1	1	0	1	0	0	0	0	1	2	2	3	1	3	4	1	25	10
59	C. macrophylla	0	0	0	0	1	0	1	0	0	0	0	1	1	2	3	1	3	4	3	285	40
60	C. subcordata	1	0	0	1	1	0	1	0	0	0	0	1	1	2	3	1	3	4	1	40	10
61	C. uiti	1	0	0	0	1	0	1	0	0	0	0	1	1	2	3	1	3	4	1	38	10
62	C. multiflora	0	0	0	0	1	0	1	0	0	0	0	1	2	2	3	2	3	4	1	28	11
63	C. ovalifolia	1	0	0	0	1	0	1	0	1	0	0	1	2	2	3	2	3	4	1	19	8
64	C. grandiflora	0	0	0	0	1	0	1	0	0	0	0	1	1	3	3	2	3	4	1	63	17
65	C. ulei	1	0	0	0	1	0	1	0	1	0	0	1	1	2	3	1	3	4	3	19	9
66	C. steudeliana	1	0	0	0	1	0	1	0	0	0	0	1	3	2	3	1	3	4	3	16	14
67	C. robusta	0	0	0	0	1	0	1	0	0	0	0	2	2	2	3	2	3	4	3	43	11
68	C. divaricata	0	0	0	0	1	0	1	0	0	0	0	1	3	2	3	2	3	4	1	17	10
69	C. myrtifolia	0	0	0	0	1	0	1	0	0	0	0	1	3	3	3	2	3	4	3	24	11
70	C. paraensis	0	0	0	0	1	0	1	0	0	0	0	1	3	3	3	2	3	4	1	17	12
71	C. glaucescens	0	0	0	0	1	0	1	0	0	0	0	1	2	2	3	2	3	4	1	35	13
72	C. racemosa	1	0	0	0	1	0	1	0	1	0	0	1	3	2	3	1	3	4	3	28	9
73	C. dodecandra	1	0	0	0	1	0	1	0	0	0	0	1	3	2	3	1	3	4	1	10	7
74	P. pachyphylla	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	7	4
75	P. insularis	1	1	1	1	0	0	1	0	1	0	0	1	3	1	3	1	2	1	1	7	4
76	P. congensis	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	7	6
77	P. albida	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	7	4
78	P. gabunensis	0	0	1	0	1	0	1	0	0	0	0	1	2	3	3	2	3	1	2	45	40
79	H. martiana	1	0	0	0	1	0	1	0	0	0	0	1	2	3	1	3	1	3	3	7	8
80	P. robusta	0	0	1	0	1	0	1	0	0	1	0	2	2	2	3	2	3	1	2	24	9
81	C. martiana	0	0	0	0	1	0	1	0	0	0	0	1	1	2	3	1	3	4	1	55	12
82	C. versicolor	0	0	0	0	1	0	1	0	0	0	0	1	3	2	3	2	3	4	1	18	10
83	C. caryophylloides	0	1	0	0	1	0	1	0	0	0	0	1	3	2	3	2	3	4	1	22	8
84	C. pauciflora	1	0	0	0	1	0	1	0	0	0	0	1	2	2	3	3	3	4	3	75	19
85	C. obovata	0	0	0	0	1	0	1	0	0	0	0	1	1	3	3	2	3	4	1	20	13
86	C. glandulosa	0	0	0	0	1	0	1	0	0	0	0	1	3	3	3	2	3	4	1	17	9
87	C. comosa	0	0	0	0	1	0	1	0	0	0	0	1	1	2	3	1	3	4	1	70	21
88	C. polyandra	0	0	0	0	1	0	1	0	0	0	0	1	2	2	3	2	3	4	1	12	8
89	C. floccosa	0	0	0	0	1	0	1	0	0	0	0	1	1	2	3	2	1	4	1	16	7
90	H. tentaculata	1	0	0	0	1	0	1	0	0	0	0	1	3	4	1	2	1	3	1	3	5
91	H. jamaicensis	0	0	0	0	1	0	1	0	0	0	0	1	3	4	3	3	1	3	3	3	4
92	H. rasa	0	0	0	0	1	0	1	0	0	0	0	1	3	4	3	3	1	3	1	5	7
93	H. davisii	1	0	0	0	1	0	1	0	0	0	0	1	3	4	1	[illegible]	1	3	3	3	5
94	H. caudata	1	0	0	0	1	0	0	0	0	0	0	1	3	3	1	2	1	3	3	6	6
95	H. guyanensis	1	0	0	0	1	0	1	0	0	1	0	1	3	4	3	2	1	3	3	6	9
96	H. glabrata	1	0	0	0	1	0	1	0	0	0	0	1	3	3	1	[illegible]	1	3	1	6	7
97	H. manigera	1	0	0	0	1	0	0	0	0	0	0	1	3	3	1	2	1	3	3	6	5
98	H. ulei	1	0	0	0	1	0	1	0	0	0	0	1	3	4	1	2	1	3	1	7	5
99	H. pendula	0	0	0	0	1	0	1	0	0	0	0	1	3	4	3	2	1	3	3	3	7
100	P. campestris	1	1	1	1	0	0	1	0	1	1	0	1	3	1	3	1	2	1	1	8	5
101	G. borbonica	0	0	0	0	0	0	0	0	0	0	0	1	1	3	1	1	1	1	3	15	2
102	G. porosa	0	0	0	0	0	0	0	0	0	0	0	1	3	3	1	[illegible]	1	1	3	7	2
103	G. madagascariensis	0	0	0	0	0	0	0	0	0	0	0	1	3	3	1	2	1	1	3	7	2
104	P. myriandra	1	1	0	0	1	0	1	0	0	0	1	1	3	3	3	1	3	2	3	73	8
105	P. chrysophylla	0	1	1	0	1	0	1	0	1	1	0	2	2	2	3	2	3	1	2	28	15
106	P. aubrevillei	0	0	1	0	1	1	1	0	1	0	0	2	2	3	3	2	3	1	2	28	10
107	P. kerstingii	0	0	1	0	1	1	1	0	1	0	0	2	2	3	3	2	3	1	2	42	14
108	H. carbonaria	0	0	1	0	1	0	1	0	0	0	0	1	2	3	1	2	1	3	1	3	5
109	M. conrauana	1	1	0	0	0	1	1	1	0	0	0	3	3	3	2				1	7	12
110	M. zenkeri	1	1	0	0	0	1	1	1	0	0	0	3	3	3	2				1	8	20
111	M. glaberrima	1	0	0	0	0	0	1	1	0	0	0	3	3	3	1				1	8	7
112	M. cuneatifolia	1	1	0	0	0	1	1	0	0	0	0	3	3	3	2				1	7	12
113	M. cupheifolia	1	0	0	0	0	0	1	0	0	0	0	3	3	3	2				3	7	7
114	M. albida	1	0	0	0	0	0	1	0	0	0	0	3	3	3	3				3	5	7
115	H. guaineae	1	0	0	0	1	0	1	0	0	0	0	1	2	4	2				3	5	5
116	H. bullata	1	0	0	0	1	0	1	0	0	0	0	1	2	4	1				3	5	7
117	H. macrosepala	0	0	0	0	1	0	1	0	0	0	0	1	3	3	1				3	6	7
118	H. pilosissima	1	0	0	0	1	0	0	0	0	0	0	1	3	4	2				3	4	4
119	C. eriantha	0	0	0	0	1	0	1	0	0	0	0	1	1	3	3				3	40	20
120	C. duckei	0	0	0	0	1	0	1	0	1	0	0	1	2	2	3				3	30	8

	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
121	C. habrantha	0	0	0	0	1	0	1	0	0	0	0	1	2	3	3			3	3	25	9
122	C. leptostachya	0	0	0	0	1	0	1	0	0	0	0	1	2	3	3				3	21	11
123	C. calophlebia	1	0	0	0	1	0	1	0	1	0	0	1	3	3	3				1	25	9
124	P. sericeo-argentea	1	1	1	1	0	0	1	0	0	0	0	1	3	3	3				3	8	5
125	P. borneense	1	0	1	1	0	0	1	0	1	1	0	1	3	1	3	4	3	1	1	5	7
126	P. impressa	1	1	1	0	1	0	1	0	0	0	0	1	3	3	3	4	3	2	3	13	17
127	A. pallescens	1	0	0	0	1	0	1	0	0	0	1	1	3	3	2	3	1	4	3	43	35
128	A. johnstonei	1	0	0	0	1	0	1	0	1	0	1	1	3	4	1	3	1	4	3	21	15
129	A. floribunda	1	0	0	0	1	0	1	0	0	0	1	1	3	4	1	3	1	4	3	28	27
130	A. tholloni	1	0	0	0	1	0	1	0	1	0	1	1	3	3	2	3	1	4	3	37	70
131	A. barteri	1	0	0	0	1	0	1	0	1	0	1	1	3	3	2	2	1	4	3	21	18
132	P. sp. I	1	1	1	0	0	0	1	0	0	0	0	1	3	3	3	1	2	1	1	7	7
133	A. scabrifolia	1	0	0	0	1	0	1	0	1	0	1	1	3	3	2	2	1	4	3	7	22
134	A. whytei	1	0	0	0	1	0	1	0	1	0	1	1	3	4	2	3	1	4	3	35	25
135	A. rudatis	1	0	0	0	1	0	1	0	0	0	1	1	3	3	2	3	1	4	3	19	21
136	A. klaineana	1	0	0	0	1	0	1	0	1	0	1	1	3	4	1	3	1	4	3	28	40
137	A. dinklagei	1	0	0	0	1	0	1	0	1	0	1	1	3	3	3	3	1	4	3		34
138	A. lujai	1	0	0	0	1	0	1	0	0	0	1	1	3	3	3	3	1	4	3	35	30
139	A. dewevrei	1	0	0	0	1	0	1	0	0	0	1	1	3	3	1	3	1	4	3	17	14
140	A. gilletii	1	0	0	0	1	0	1	0	1	0	1	1	3	3	1	3	1	4	3	26	26

B. Data used for the analysis of the *Chrysobalaneae*

P = *Parastemon*; A = *Angelesia*; G = *Geobalanus*; Gr = *Grangeria*;
L = *Licania*; H = *Hunga*; C = *Chrysobalanus*.

	Species	Characters														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	P. versteeghii	5	1	1	0	0	0	0	0	1	0	1	0	1	0	1
2	P. urophyllus	2	1	1	0	0	0	0	0	1	0	1	0	0	0	1
3	A. elaeosperma	20	1	1	1	0	0	0	1	1	1	1	0	1	0	3
4	G. pallidus	16	1	1	0	0	1	0	1	1	0	0	1	1	0	2
5	G. oblongifolius	15	1	1	0	0	1	0	1	1	0	0	1	1	0	2
6	Gr. borbonica	15	1	0	0	0	0	0	0	0	0	0	1	1	0	1
7	Gr. madagascariensis	8	1	0	0	0	0	0	0	0	0	0	1	0	0	1
8	Gr. porosa	7	1	0	0	0	0	0	0	0	0	0	1	0	0	1
9	L. rhamnoides	8	0	0	0	0	0	0	1	1	0	0	1	0	1	3
10	L. balansae	6	0	0	0	0	0	0	1	1	0	0	1	0	1	3
11	P. neocaledonica	7	0	0	0	0	0	0	1	1	0	0	1	0	1	3
12	P. minutifolia	7	0	0	0	0	0	0	1	1	0	0	1	0	1	3
13	H. longifolia	8	0	0	0	0	0	0	1	1	0	0	1	0	1	3
14	L. gerontogea	8	0	0	0	0	0	0	1	1	0	0	1	0	1	3
15	L. lifouana	7	0	0	0	0	0	0	1	1	0	0	1	0	1	3
16	L. gerontogea var. frankii	5	0	0	0	0	0	0	1	1	0	0	1	0	1	3
17	C. icaco	22	1	1	1	1	1	1	1	1	0	0	0	1	0	2
18	L. arborea	12	1	1	1	1	0	0	1	0	0	0	0	1	0	3
19	L. coriacea	11	1	1	1	0	0	0	1	0	0	0	1	1	0	3
20	L. incana	5	1	1	1	0	0	0	1	0	0	0	1	1	0	3
21	L. cuprea	3	1	1	1	0	0	0	1	0	0	0	1	1	0	3
22	L. apetala	8	1	1	1	0	1	0	1	0	0	0	0	1	0	3
23	L. guianensis	35	1	1	1	0	1	0	1	0	0	0	0	1	0	3
24	L. heteromorpha	9	1	1	1	0	0	0	1	0	0	0	0	1	0	3
25	L. kunthiana	6	1	1	1	0	0	0	1	0	0	0	1	1	0	3
26	L. micrantha	3	1	1	1	0	0	0	1	0	0	0	1	0	0	3
27	L. microcarpa	5	1	1	1	0	0	0	1	0	0	0	1	1	0	3
28	L. mollis	10	1	1	1	0	0	1	1	0	0	0	1	0	0	3
29	L. latifolia	10	1	1	1	0	0	0	1	0	0	0	1	1	0	3
30	L. octandra	8	1	1	1	0	1	0	1	0	0	0	1	1	0	3
31	L. parinarioides	20	1	1	1	0	0	0	1	1	0	0	0	1	0	3
32	L. parviflora Benth.	5	1	1	1	0	0	0	1	0	0	0	1	1	0	3
33	L. apetala II	10	1	1	1	0	1	0	1	0	0	0	1	1	0	3
34	L. platypus	19	1	1	1	0	1	0	1	0	0	0	1	1	0	3
35	L. rigida	14	1	1	1	0	0	0	1	0	0	0	0	1	0	3
36	L. sclerophylla	8	1	1	1	0	1	0	1	0	0	0	1	1	0	3
37	L. tomentosa	30	1	1	1	0	1	0	1	1	0	0	0	1	0	3
38	L. grisea	3	1	1	1	0	0	0	1	0	0	0	1	1	0	3
39	L. persaudii	11	1	1	1	0	1	0	1	1	0	0	1	1	0	3
40	L. laxiflora	7	1	1	1	0	0	0	1	0	0	0	0	1	0	3
41	L. canescens	5	1	1	1	0	0	0	1	0	0	0	1	0	0	3
42	L. venosa	6	1	1	1	1	0	0	1	0	0	0	1	0	0	3
43	L. majuscula	12	1	1	1	0	0	0	1	0	0	0	0	1	0	3
44	L. licanaeflora	24	1	1	1	0	0	0	1	1	0	0	0	1	0	3
45	A. splendens	10	1	1	1	0	0	0	1	1	0	0	1	1	0	3
46	H. longifolia	9	1	1	1	0	0	0	1	1	0	0	1	1	0	3
47	C. pellocarpus	17	1	1	1	1	1	1	1	1	0	0	0	1	0	2
48	C. savanarum	17	1	1	1	1	1	1	1	1	0	0	0	1	0	2
49	C. atacoriensis	14	1	1	1	1	1	1	1	1	0	0	0	1	0	2
50	C. ellipticus	22	1	1	1	1	1	1	1	1	0	0	0	1	0	2
51	C. orbicularis	26	1	1	1	1	1	1	1	1	0	0	0	1	0	2
52	P. spicatum	2	1	1	1	0	0	0	0	1	0	1	0	0	0	1
53	L. buxifolia	5	1	1	1	0	0	0	1	0	0	0	1	1	0	3
54	L. davillaefolia	7	1	1	1	0	0	0	1	0	0	0	1	1	0	3
55	L. densiflora	4	1	1	1	0	0	0	1	0	0	0	1	1	0	3
56	L. humilis	5	1	1	1	0	0	0	1	1	0	0	1	1	0	3
57	L. pallida Britt.	14	1	1	1	0	1	0	1	0	0	0	1	1	0	3
58	L. sparsipilis	8	1	1	1	0	1	0	1	1	0	0	0	1	0	3

	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
59.	L. biglandulosa	12	1	1	1	0	1	0	1	1	0	0	0	1	0	3
60	L. latifolia	7	1	1	1	1	0	0	1	0	0	0	1	1	0	3
61	A. papuana	7	0	0	1	0	0	0	1	1	0	0	1	0	0	3
62	L. sprucei	10	1	1	1	0	1	0	1	1	0	0	0	1	0	3